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The behavioural ecology of bachelor male groups in the African striped mouse, *Rhabdomys pumilio*

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1463937

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, in fulfilment of the requirements for the degree of Master of Science

Johannesburg, 2018

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the degree Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



Sthandiwe Nomthandazo Kanyile

10/05/2018

ABSTRACT

Males in several animal species vary in traits which confer competitive ability. Younger and old, small and large males thus regularly make use of different behavioural tactics (i.e. alternative reproductive tactics, ARTs) in order to secure mates and increase their fitness. In the Succulent Karoo, males of the African striped mouse *Rhabdomys pumilio* adopt one of three main ARTs, i.e. philopatric, roaming, or territorial tactics; the tactic chosen is influenced by body mass. Additionally, the occurrence of bachelor groups (two or more males sharing a nest without any female) in striped mice has recently been observed. The present study was concerned with investigating the composition and function of these bachelor groups in striped mice, especially to assess whether they represent a fourth ART. For this, I used data collected from 2009 to 2016 to determine the season (breeding versus non-breeding) during which bachelor groups occurred and how they originated. At the start of the breeding season, I compared bachelor males with the known ARTs with regard to their scrotality, body mass, and age. I also determined the tactics of bachelor males before and after they were bachelors, and whether these tactic changes were associated to changes in body mass. My results indicate that bachelor groups are mainly formed by unrelated philopatric males which have dispersed from their natal groups. These groups most frequently occur in the breeding season, when population density is low to intermediate. Bachelor males occupy the intermediate position in the body mass spectrum in striped mice, being heavier than philopatrics but lighter than breeders, and do not differ in body mass from roamers. After the bachelor tactic, more males employed the roamer than the territorial breeding tactic. I hypothesise that the bachelor tactic is a "transitional tactic" which facilitates the change from a low fitness tactic (philopatric) to a higher fitness tactic (roaming or breeding) by allowing relatively small males to cooperate in social thermoregulation. These findings provide valuable insight on a phenomenon which has not been studied before in striped mice.

Keywords: African striped mouse, alternative reproductive tactics, bachelor, behavioural plasticity, group-living, social flexibility

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CHAPTER ONE
INTRODUCTION

Behavioural responses to changing environments

Changing environments are an inevitable feature of most organisms' lives. These environmental changes can be short-term changes that occur within the lifespan of individuals or longer-term changes that occur over generations (López-Maury *et al.* 2008). The responses of animals to environmental change can thus be considered at scales ranging from immediate responses to short term changes, to longer term changes in the nature and expression of relations and reproductive potential, to ultimately, evolutionary change which spans generations (Lee 1991).

In the long term, organisms can respond to gradual environmental change via genetic selection, leading to genetic adaptation (Hansen *et al.* 2012). This process of evolutionary change is slow. Human-induced (anthropogenic) environmental change, however, occurs at a much faster rate, thus requiring organisms to immediately respond to such changes or face extinction of their population (Sih *et al.* 2011). Organisms can cope with short-term changes in environmental conditions through dispersal and/ or phenotypic plasticity (Sih *et al.* 2011; Hansen *et al.* 2012). Dispersal, however, is not always an option due to possible physical barriers to movement. This is a challenge that is likely to intensify with the persistence of habitat fragmentation and destruction by anthropogenic forces (Chaine and Clobert 2012). Animals may thus swiftly respond to rapid environmental fluctuations by displaying behavioural plasticity (i.e. phenotypic plasticity, the ability of a single genotype to produce different phenotypes over a range of environments; Rymer *et al.* 2016). For example, one of the many effects of global warming is that spring may arrive much earlier than before. Some animals which breed in spring have accordingly adjusted to this timing by arriving at nesting grounds to breed earlier in the spring (Both *et al.* 2004; Pulido 2007). Another example is where increased warming due to climate change can lead to persistently biased sex ratios, especially in species where sex determination is temperature-dependant. Some species such as the Australian water dragon *Physignathus lesueurii* have responded to this change by shifting their preferred nesting site to a shady area in warmer regions (Doody *et al.* 2006).

Phenotypic variation

Broadly, two types of phenotypic plasticity can be distinguished: developmental and activational (West-Eberhard 2003; Snell-Rood 2013). Developmental plasticity (also referred to as "differences in ontogenetic development", Komers 1997) refers to the ability of a

genotype to express different phenotypes in different environments as a consequence of different developmental trajectories activated by those environments (Komers 1997; West-Eberhard 2003; Snell-Rood 2013). Developmental plasticity can encompass for example a) developmental changes in physiology or morphology, such as changes in bones, limbs and muscles that influence locomotion or foraging (Komers 1997); and b) changes in the nervous system or the modification of behaviour as a result of experience within the lifetime of an animal (Stephens 1991). Developmental changes in physiology or morphology as a result of varying environments are taxonomically widespread but are usually not reversible (Komers 1997; Schew and Ricklefs 1998). The irreversible nature of developmental plasticity may sometimes result in maladaptive outcomes, particularly when organisms experience a change in environment from ontogeny to adulthood (Frankenhuis and Giudice 2012). In such instances, physiological and morphological changes induced by an environment experienced during the early life stages of an organism may be incongruous to the environment that the organism experiences as an adult, rendering the changes maladaptive.

In environments where juveniles experience similar environments to adults, developmental plasticity may play a particularly important role. For instance, the presence of predators during the juvenile (early life) stages of some invertebrates (e.g. crustaceans, molluscs, rotifers), causes morphological changes that would confer an advantage to these invertebrate species (Dodson 1989). Specifically, when juvenile daphnia *Daphnia pulex* are exposed to the predator, larval glassworm *Chaoborus americanus*, the daphnia undergo morphological changes characterised by small protuberances (neck teeth) on the dorsal anterior of the head (Spitze 1992; Tollrian 1995; Weber and Declerck 1997). Also, in two closely related species of sticklebacks *Gasterosteus* spp., greater morphological plasticity was shown by the species with a more variable diet (Day *et al.* 1994). This demonstrates how different developmental trajectories can be triggered in different environments, resulting in behavioural plasticity.

Differences in sexual and social behaviour due to early environmental influences have also been demonstrated in several species, mainly in studies comparing adults of the same species in captivity and in nature (Beach and Jaynes 1954). For instance, the mating behaviour of many birds and some fish is characterised by elaborate patterns of display and courtship which form an integral preamble to the mating act itself. The stimuli that elicit display and courtship have been demonstrated to be dependent upon early life experiences (Beach and Jaynes 1954). Adult male cichlids show courtship and mating responses only to females, but males that were initially reared in isolation reportedly attempted to indiscriminately mate

with both females and males (Noble and Curtis 1935). Similarly, early defeats in a fighting situation were reported to affect the aggressiveness of mice later in life (Jenkins 1928).

While developmental plasticity is well studied, phenotypic changes based on a single genotype exhibited by mature organisms throughout their lifespan can also occur (Piersma and Drent 2003). For example, activational behavioural plasticity (elsewhere referred to as "innate behavioural plasticity", Mery and Burns (2010) or as "behavioural flexibility", Piersma and Drent 2003; Schradin 2013) occurs when an individual expresses different behaviours as it encounters different situations or environments (Snell-Rood 2013). It describes the differential activation of an existing underlying network, that is, the triggering of pre-existing neurons and muscles as a response to conditions encountered later in life (Smith-Gill 1983; Scheiner and Lyman 1991; Snell-Rood 2013). It differs from developmental plasticity which requires developmental changes such as neuron or muscle growth early in an organism's life-span. Activational or innate behavioural responses occur when the modification of a behaviour in response to environmental factors is a consequence of population scale evolution over multiple generations. In other words, a predetermined phenotypic trait is expressed as a response to a predetermined environmental stimulus (Mery and Burns 2010). In many cases, animals are born with certain innate predispositions to perform behaviours which may be more or less modified by different experiences in different environments, demonstrating how both innate mechanisms and learning can interact to assist animals in responding optimally to their prevailing circumstances (Mery and Burns 2010; Piersma and Drent 2003).

Environments are usually highly variable, such that no single behavioural phenotype will be consistently optimal ((Via *et al.* 1995; Candolin and Wong 2012). In environments which change predictably over time (for example, seasonal environments), some long-lived individuals can track and anticipate changes and may thus adjust their physiology, morphology and behaviour to perform optimally in predictably varying environments (Piersma and Drent 2003). Such cyclically varying phenotypic adjustments within an individual are termed life-cycle stages (Willmer *et al.* 2009; Piersma and Drent 2003). This is exemplified by the rock ptarmigan *Lagopus mutus*, an Arctic Tundra living species of grouse which changes its plumage consistent with seasonal changes (Montgomerie *et al.* 2001). When the Tundra is covered with snow, both males and females of this species are camouflaged by white plumage. In the spring when the snow melts, females moult their white plumage and grow brown and green feathers while males remain conspicuously white, making them attractive to females but also conspicuous to predators. These males may attempt to make themselves inconspicuous by soiling their white plumage when opportunities for mating disappear and eventually moult their white plumage when the mating season is over (Montgomerie *et al.* 2001). Animals can fine-tune their timing of such phenotypic changes using information from

the environment or natural photoperiodic rhythms (Wingfield and Kenagy 1991; Piersma and Drent 2003). However, in environments which change unpredictably, rapidly and over shorter time scales, individuals which exhibit continuous but reversible transformations in behaviour may have a selective advantage. Indeed, it is in dynamic environmental conditions that behavioural plasticity evolves as a way of tracking environmental change (Mery and Burns 2010).

In environments where change is not cyclical and can thus not be anticipated (as considered in the above Arctic Tundra rock ptarmigan), long-lived and short-lived species can benefit from behavioural plasticity. If environmental conditions change too rapidly, longer-lived species are particularly vulnerable since a lag may develop between environmental change and optimum trait values, possibly leading to extinction (Refsnider and Janzen 2012). Thus, behaviourally plastic mechanisms of dealing with environmental change may then offer a short term solution (Tuomainen and Candolin 2011; McFarland *et al.* 2014). While shorter-lived species with more generations per time-period are expected to evolutionary adapt to change quicker since a lag is less likely to develop between environmental change and optimum trait values, individuals of these species have the disadvantage of being unable to delay reproduction in unfavourable environmental conditions because of their short life span (Refsnider and Janzen 2012). Thus, these species may also benefit from behavioural plasticity in the face of environmental change. Examples of such behavioural responses are changes in movement patterns, habitat choice, foraging, social behaviour and reproductive behaviour. These responses influence, for example, survival, distribution and reproductive success, consequently altering the dynamics of the population, including social organisation (Tuomainen and Candolin 2011).

Intraspecific variation in social organisation

The social organisation of a species describes the relationships and social interactions between individuals, which influence the composition of groups (Schradin *et. al* 2012, Schradin 2013). Animals exhibit great diversity in social organisation (Taborsky 1994), ranging from solitary species such as the whistling rat *Parotomys brantsii* (Jackson 1999) to species which form complex societies such as naked mole rat *Heterocephalus glaber* (Faulkes *et al.* 1990, Lott 1991). Group living offers many benefits to group members, such as decreased thermoregulatory costs through huddling (Scantlebury *et al.* 2006), increased vigilance (Waterman 1997), and the collective defence of valuable and contestable resources (Wirtz 1982, Adams 1994). However, group living can also induce costs, mainly reproductive competition (Emlen 1982b), and also the transmission of parasites/disease (Godfrey *et al.*

2009), and within-group food competition (Majolo *et al.* 2008). Thus, the trade-off between the costs and benefits of group living may result in changes in social organisation, where, for instance, individuals may disperse from their natal groups to breed solitarily. To explain this change in the social system, two hypotheses have been proposed.

1. The reproductive competition model (Emlen 1982b) maintains that reproductive competition is the main driver of dispersal. Here, individuals may leave their social groups and breed solitarily to avoid the costs of reproductive competition, which may manifest as sexual suppression, as occurs in male sifakas *Propithecus verreauxi*, where the sexual activity of subordinate males may be physiologically supressed (Kraus *et al.* 1999), or infanticide within the group as found in wild house mice *Mus musculus* (McCarthy and Vom Saal 1985).
2. The ecological constraints (habitat saturation) model (Emlen 1982a) predicts that philopatry occurs when opportunities for independent breeding are limited and when remaining philopatric offers more benefits than dispersing. For instance, under conditions of high population densities, offspring are likely to remain philopatric because limiting resources such as free territories and mating opportunities will be scarce (Schoepf and Schradin 2012a). Thus, remaining in the natal territory may increase the chances of survival of young adults by providing them with a "safe" place wherein they can learn beneficial skills such as parental care and territory defence. For example, Bergmuller *et al.* (2005), experimentally provided vacant territories (thus removing ecological constraints) to the group-living cichlid *Neolamprologus pulcher* and found that the helpers (philopatrics) left their natal groups to start independent breeding, but remained in their groups in the absence of these vacant territories, demonstrating that ecological factors may constrain cichlid helpers to group-living.

Variation in the social organisation is also prevalent within species (Eggert 1992), largely as a consequence of environmental variability. Here, the composition of social groups within and between populations can change between solitary living, pair living and group living with multiple breeding individuals depending on prevailing environmental conditions (Schradin *et al.* under review). By measuring individual fitness, Davis (1992), showed that intraspecific variation in social organisation within populations occurs as a result of individuals choosing the reproductive tactic with the highest fitness (alternative reproductive tactics, ARTs), depending on ecological conditions. The change in tactics may be due to variations in morphological, physiological and/or behavioural characteristics (Ronald and Sluijter 1990; Taborsky and Brockmann 2010). ARTs occur where investment in reproduction can be exploited by competitors of the same sex, and thus high reproductive competition and intrasexual variation may give rise to ARTs (Taborsky and Brockmann 2010; Hill *et al*. 2015). These conditions can, in principle, exist in both males and females but they are more frequent in males which may explain why ARTs have been better described in males than in females (Taborsky and Brockmann 2010; Hill *et al.* 2015; Engqvist and Taborsky 2016). It is worth

noting that when only one sex exhibits ARTs, the social organisation does not necessarily change. For example, the existence of bourgeois and satellite male ARTs in a population with no female ARTs does not lead to different social organisations when the relative prevalence of each male ART changes. However, when both sexes of a species exhibit ARTs, the entire social organisation can change, resulting in intraspecific variation in social organisation (Schradin *et al.* 2010).

Alternative reproductive tactics (ARTs)

Different kinds of ARTs can be distinguished, depending on when and how tactic-specific phenotypic determination occurs. A tactic may be either fixed or flexible (Engqvist and Taborsky 2016). Fixed tactics occur when the decision of which tactic to use is irreversibly made at one stage of an individual's life (usually during early life). For instance, in many insects, males either develop elaborate weapons that would be crucial for future territorial fights or forego this investment because of small body size. This is exemplified by adult dung beetles *Onthophagus acuminatus* in which males which grow larger than the threshold size develop horns, and males which do not reach this threshold body size either grow no horns at all or grow rudimentary horns (Emlen 1997; Engqvist and Taborsky 2016). Large males with horns guard and defend tunnels containing females while the smaller, hornless males sneak matings with females in unguarded tunnels. These dung beetles cannot switch between tactics (Emlen 1997; Engqvist and Taborsky 2016). This is different to flexible tactics where, for instance, males may use one tactic while they are young and then switch to another tactic when they are older (Engqvist and Taborsky 2016). For example, two types of tactics can be found in the damselfly *Calopteryx maculate* (Forsyth and Montgomerie 1987). When males are younger, they establish and defend territories but adopt a sneaker tactic once they are older. Male-male competition forces older male damselflies to abandon territoriality, and the sneaker tactic allows males with a decreased resource holding potential (RHP) to continue reproducing even after they can no longer hold a territory (Forsyth and Montgomerie 1987).

ARTs are thought to be governed by genetically based strategies which are decision rules that determine which tactic an individual will follow (Dominey 1984; Schradin *et al.* 2012; Hill *et al.* 2015). Gross (1996) distinguishes between three different kinds of strategies, as considered below.

1. Alternative Strategies are characterised by genetic polymorphisms, where different tactics are coded by different genotypes. Selection is frequency-dependent and different tactics yield

the same average fitness. For example, in the marine isopod *Paraceceis sculpta*, females may mate with small sneaker males, intermediate-sized males that mimic females or large fighter males (Shuster 1989). The three male phenotypes are thought to be coded for by three different alleles at a single locus. All three phenotypes have equal fitness.

2. Mixed Strategies have more than one tactic, are genetically monomorphic and result from frequency dependent selection. In this type of selection, the fitness of a given phenotype is dependent on its frequency relative to other existing phenotypes in a population. Different tactics also yield the same average fitness under this strategy (Hartle *et al.* 1997). According to Gross (1996), this is a theoretical possibility since there are no documented cases of such a strategy.

3. In a Conditional Strategy, the individual employs a tactic that fits its status. In other words, a tactic that would maximise its fitness given its condition (e.g. age, body mass) at that time. In this strategy, the tactics have unequal fitness, are genetically facultative and selection is status-dependent. The traits which confer competitive ability to individuals (e.g. age or size) can vary considerably between individuals and thus when a tactic with the highest fitness (called the bourgeois tactic) is also the most costly to employ, only the most competitive individuals will adopt it (Gross 1996; Hill *et al*. 2015). The smaller or younger and less competitive males (also referred to as sneaker or satellite males) may then adopt a less beneficial tactic which may yield lower fitness but is the best that they can do given their status (i.e. making-the-best-of-a-bad-job tactic; Gross 1996; Hill *et al.* 2015; Engqvist and Taborsky 2016). For instance, in the ground nesting bee *Perdita portalis,* small male larvae develop into a distinctly small-headed phenotype with wings, mating outside the nest (Danforth 1991). In contrast, bigger male larvae metamorphose into a fighter phenotype that has mandibles, is flightless and mates within the nest. The tactic employed is thus determined by larval size, and it is thought that the larger-male tactic individuals obtain greater average fitness than the smaller-male tactic individuals (Danforth 1991).

Gross's (1996) definitions and categorisation of strategies have been met with criticism (Schradin *et al.* 2012). A study by Schradin and Lindholm (2011) found that the relative fitness of male reproductive tactics varied between different years in the striped mouse *Rhabdomys pumilio*. In this species, spatially and temporally fluctuating environmental conditions may result in a change in the fitness of different male tactics, such that tactics that could be normally considered suboptimal yield similar fitness to those that are usually dominant. In light of these findings, Schradin and Lindholm (2011) introduced the term "single strategy", to replace the terms conditional and mixed strategies because the differentiation between these two strategies is not always absolute.

Phenotypic flexibility and ARTs

In terms of ARTs, phenotypic flexibility (hereafter flexibility) refers to the ability of individuals to switch between different tactics (phenotypes) in response to changes in environmental conditions. I consider two case studies: (1) Fraser *et al.* (2014) studied the phenotypic and genomic plasticity of ARTs in sailfin mollies *Poecilia latipinna,* in which alternative phenotypes are based on either plasticity or genetic polymorphisms, which coexist in the same populations. There is considerable variation in body size and mating behaviour in male sailfin mollies (Fraser *et al.* 2014). Males can use either courtship or "sneaking" mating behaviour but the plasticity of the behaviour is dependent on genetically determined male body size. An elaborate courtship display tactic is employed by large males, while small males employ a "sneaker" tactic. Intermediate-sized males exhibit plasticity and will either employ a courtship tactic when large males are absent or a sneaker tactic in the presence of large males. The decision of which tactic to follow is thus genetically determined in large and small males but determined by environmental conditions in intermediate-sized males (Fraser *et al.* 2014). In this system, it is possible to expose both "fixed" and "flexible" genotypes under the same environmental conditions, which can be useful to understand the mechanisms driving the flexibility of ARTs (Fraser *et al*. 2014). (2) Following long-term and extensive field studies of the African striped mouse *Rhabdomys pumilio*, Schradin *et al.* (2012) developed the concept of social flexibility to describe how and when the social system of an entire population changes as a function of individuals of both sexes changing their tactics depending on prevailing environmental conditions. Specifically, individuals of the entire population 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 (Schradin *et al.* 2012). Such flexibility is an important adaptation to unpredictably changing environmental conditions, allowing individuals to switch back and forth between group/solitary living and different reproductive tactics depending on prevailing environmental conditions (Randall *et al.* 2002; 2005; Schradin *et al.* 2012). The great gerbil *Rhombomys opimus* also exhibits social flexibility which is considered to be an adaptation to living in its unpredictable desert environments (Randall *et al*. 2005). In this species, females can switch from living in groups to living solitarily depending on food availability and abundance, while the males adjust their reproductive tactics according to the distribution of females (Randall *et al*. 2005).

Switch-Points of ARTS

One of the aims of the study of plastic ARTs is to understand the evolution and regulation of switch-points, i.e. the point at which individuals switch tactics (Schradin and Lindholm 2011). In conditional strategies (see Box 1 below), a particular tactic is expressed when individuals pass a threshold (switch-point) for the indicator trait after which the fitness benefits of that tactic are greater than they would be using an alternative tactic (Hill *et al.* 2015). Individuals might switch from one tactic to another, for instance, when they reach a certain age or body size. For example, in the eastern grey squirrel *Sciurus carolinensis*, males may adopt one of two tactics: active pursuit (used by dominant males which defend access to females); or satellite (used by subordinate males which remain scattered in the female's home range; Thompson 1977; John 1993). The active-pursuit tactic is adopted only by males which are ≤ 2.75 years, with the switch-point between the tactics occurring at about 3 years (John 1993). The relationship between age and the switch point suggests that the tactics employed by the grey squirrels are correlated with phenotype, as body mass or size typically increases with age. Males which are closer in age to the switch point exhibit flexibility between the active and satellite tactics (John 1993).

Box 1 Glossary

Bourgeois tactic: the tactic yielding the highest fitness (Engqvist and Taborsky 2016).

Conditional strategy: a decision rule containing a conditional clause (Tompkins and Hazel 2007). In this strategy, an individual employs a tactic that fits its status; in other words, a tactic that would maximise the individual's fitness given its condition (e.g. age, body mass) at the time. Tactics have unequal fitness and selection is status-dependent under this strategy (Gross 1996).

Satellite/Sneaker/Parasitic tactic: a low fitness yielding tactic, often used by smaller males which exploit the reproductive investment of more competitive males (Engqvist and Taborsky 2016).

Single strategy: describes systems where the tactics employed by individuals are not genetically determined but are governed by a single set of decision rules. Under this strategy, the fitness of each tactic is not fixed but rather fluctuates with prevailing environmental conditions (Schradin and Lindholm 2011).

Strategy: a set of decision rules governing which tactic an individual will follow (Gross 1996). For example, striped mice *Rhabdomys pumilio* are considered to follow a single strategy.

Switch-point: the point at which individuals switch tactics (Schradin and Lindholm 2011).

Tactic: a behavioural phenotype generated by a decision rule (Tompkins and Hazel 2007).

Switch-points can typically be illustrated using fitness curves. In Figure 1.1 below, a satellite or parasitic tactic (Fig 1.1 "X") shows higher individual fitness than the bourgeois tactic at lower status (could be smaller size or age) while the bourgeois tactic (Fig 1 "Y") shows higher fitness than the parasitic tactic at higher status (Schradin and Lindholm 2011). The fitness functions will intersect at some value of status (Fig 1.1 "S"), where the fitness of the two tactics is equal. It is at this point of intersection that individuals are expected to switch from one tactic to another (Tompkins and Hazel 2007; Schradin and Lindholm 2011). Switching tactics at point "S" is the decision rule that maximises fitness and is consequently the decision rule around which ARTs will evolve (Gross 1996). This model is based on status dependent selection which assumes that the population is genetically monomorphic in its response to a status and that the average fitness of tactics is unequal (Gross 1996). Tactic changes before the switch point can be constrained by factors such as age. This is particularly true where status, such as body mass, increase with increasing age. In such instances, younger individuals may not be able to switch tactics before they have acquired the body mass that confers higher status (Tompkins and Hazel 2007).

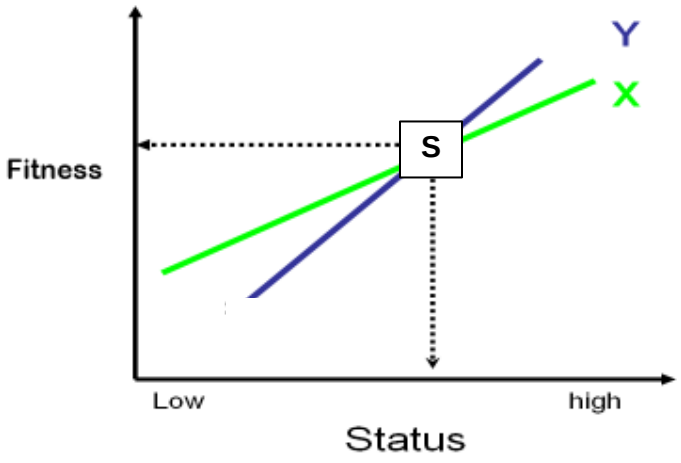

Figure 1.1. Status dependent selection model (SDS) proposed by Gross (1996) and reviewed in Tompkins and Hazel (2017). At point S (switch point), the fitness of the two tactics (i.e. the bourgeois and parasitic tactic) is equal and individuals are expected to change tactics at this point. X and Y show the parasitic and bourgeois tactic, respectively.

Male social behaviour

The social interaction between reproductive males is mainly influenced by strategies for gaining mating opportunities and hence male-male interactions are mostly competitive (Waterman 1997). Consequently, amicable male-male interactions are not widespread in animals (Waterman 1997; Chiyo *et al.* 2011). Yet, male-male tolerance exits. Examples of strong male-male associations in mammals mostly occur in species displaying: (1) male philopatry- for example, in the squirrel monkeys *Saimiri oerstedi*, philopatric males show no male-male aggression within-troops and interact amicably with each other (Boinski 1994); (2) joint dispersal of males in multi-litter siblings, such as in lions *Panthera leo* (Packer and Pusey 1982); or (3) cooperative defence of oestrous females, as occurs in the bottlenose dolphins *Tursiops trancatus* (Connor *et al.* 1992).

Several hypotheses have been proposed to explain the evolution of grouping in mammals, of which seven could explain the development and existence of all-male groups (reviewed in Waterman 1997), as listed below.

1. Males aggregate around females in oestrous. In this hypothesis, males form groups only in the breeding season but are aggressive to each other outside the breeding season (Waterman 1997), as occurs in the tree squirrel *Sciurus vulgaris* (Wauters, *et al.* 1990). In such cases, male grouping has no further adaptive function but is a reflection of a breeding system (Waterman 1997).
2. Males form groups outside the breeding season to assess their competitive abilities, as occurs in the polar bear *Ursus maritimus* (Latour 1981). This hypothesis assumes that fighting determines access to females, and the males interact in sparring ("practice" fighting) competitions (Waterman 1997).
3. Males form groups to enhance thermoregulation during cold seasons but interact aggressively in warm periods when there are no benefits of thermoregulation from grouping, such as in group sleeping males of the tree squirrel *Sciurus carolinensis* (Koprowski 1991).
4. Males form groups for reproductive alliances (Waterman 1997). This hypothesis predicts that males cooperate to obtain territories or females from other groups, as exemplified by chimpanzees *Pan troglodytes* (Wrangham 1986).
5. Satellite males may assist dominant males in territory defence, so dominant males may tolerate subordinate males in their groups (Waterman 1997) as found in impala *Aepyceros melampus* (Leuthold 1970).
6. Males form groups for information exchange, such as information about food or the location of females in oestrus. Younger and less experienced males would associate with older males

to gather such information from them, as occurs in the waterbuck *Kobus ellipsiptrymnus* (Wirtz 1982).

7. Males may benefit from grouping through enhanced predator defence because groups have better overall vigilance than solitary individuals, as occurs in the Cape ground squirrel *Xerus inaurus*. Here, time-sharing vigilance emancipated individuals to spend more time in productive activities, such as feeding or resting (Waterman 1997).

The genus *Rhabdomys*

The African striped mouse is a small (adult mass 30-80 g), murid rodent of the genus *Rhabdomys*, with a widespread distribution in southern Africa (Schumann *et al.* 2005). Mitochondrial DNA (mtDNA) analyses by Rambau *et al*. (2003) showed that the genus is comprised of two species i.e. *R. pumilio* in the western part and *R. dilectus* in the eastern part of its geographic range, with *R dilectus* further divided into two subspecies, namely *R. dilectus chakae* and *R. dilectus dilectus* in the southern and northern parts of its range respectively (Rambau *et al.* 2003). However, further genetic comparisons of *Rhabdomys* specimens from South Africa, Zambia and Namibia using mtDNA (Cytochrome Oxidase I) and nuclear interons (Eef1a1, SPTBN1, Bfib7 and MGF) by du Toit *et al.* (2012) revealed that *R. pumilio* should be divided into three species: *R. pumilio* (southern and west coast regions of South Africa and Namibia); *R. intermedius* (central South Africa, mainly occurring in the Karoo); and *R. bechuanae* (central Namibia, central parts of the Northern Cape, North-West Province and Free State Province of South Africa).

The genus exhibits a diurnal activity pattern with the main activities concentrated during the mornings and evenings and reduced during the midday period (Schumann *et al.* 2005; Schradin and Pillay 2005a). It is found in several habitats, such as grasslands, marshes, forests, semi-deserts and deserts (Kingdon 1974). Across this distribution range, it is an opportunistic omnivore, with a diet ranging from seeds, other plant material to insects, thus showing a high degree of ecological plasticity due to the influence of different habitats on its demography (Baker and Brown 2011).

Striped mice are seasonal breeders, with the breeding period varying for taxa in different geographic locations (Schradin 2005). The gestation period is 22-23 days, after which approximately five pups are produced (Brooks 1982). Pups may begin to eat solid food at 10 days old and leave the nest from 12 days old (Brooks 1982; Schradin and Pillay 2005a)

Given the wide distribution range of *Rhabdomys*, it can be expected that populations and species within the genus will exhibit differences in demography and reproductive behaviour, which can in turn, influence their social system (Schradin and Pillay 2005a). For

instance, in the grasslands of Zimbabwe (Choate 1972), female striped mice share a nest with their most recent litter, with weaned young being allowed to remain with newly born young; while males occupy separate areas. However, in the grasslands of Pretoria, the midlands of KwaZulu Natal and the semi-succulent thorny scrub of the Eastern Cape, striped mice have been observed to be solitary (Choate 1972; Brooks 1982; Schradin and Pillay 2005b).

Rhabdomys pumilio

There have been intensive and long-term field and captive studies on a population of *Rhabdomys pumilio* in the arid Succulent Karoo. This population has been characterised as a territorial, group-living, solitary forager with communal breeding, paternal care and helpers at the nest (Schradin and Pillay 2004). Moreover, *R. pumilio* demonstrates social flexibility, where individuals of both sexes change social organisation, from group living to solitary living, based on prevailing environmental conditions (Schradin *et al.* 2012). In this species, individuals of both sexes are able to switch between tactics (Schradin *et al.* 2012). Adult female striped mice may: (1) leave the natal group to start solitary breeding; (2) remain in their natal group as non-breeding adult philopatrics or breed communally; or (3) may give birth away from the natal group but later return to it (Hill *et al.* 2015). Body mass has been found to be an important predictor of tactics, governing whether or not female striped mice become solitary breeders; females adopting the solitary tactic are heavier than those which breed communally (Hill *et al.* 2015). However, stochastic extrinsic factors such as the death of all but one adult female group member may also give rise to female solitary breeders in striped mice. In such cases, the solitary tactic is not the outcome of a strategy but is an incidental consequence of extrinsic factors (Hill *et al.* 2015).

Male ARTs in this species are better understood. Male striped mice may adopt one of three tactics, which are governed by a single strategy (Box 1), with the fitness outcome of each tactic being dependent on prevailing environmental conditions (Schradin *et al*. 2012). The three ARTs include: (1) breeding males (referred to as breeders) which defend territories wherein there are communally breeding females; (2) philopatric males (referred to as philopatrics) which remain in the natal nest and show allo-parental care and may sneak out to mate with females of neighbouring groups; or (3) solitary living roaming males (referred to as roamers; Schradin *et al.* 2010). The tactic chosen by male striped mice depends on their body mass. The smallest males are philopatric (≈ 30-40 g), intermediate-sized males are solitary roamers (≈ 50-59 g) and the largest males are territorial breeders (≈ 60-80 g). In this species different tactics yield different fitness under different environmental conditions (single strategy). In conditions of high population density, breeders had 10 times and 102 times higher

reproductive success than roamers and philopatrics respectively. Under conditions of intermediate population density, the breeding and roaming tactics yielded similar fitness, while only roamers occurred under conditions of low population density (Schradin and Lindholm 2011). Recently, an unusual occurrence of bachelor groups has been observed, in which two or more males share a nest with each other without a female group member present (Schradin unpublished data). Little else is known about these bachelor groups and they occur sporadically in the study population. Therefore, the aim of my study was to investigate the composition and function of bachelor groups in *Rhabdomys pumilio*, particularly whether they represent an alternative reproductive tactic.

Objectives and predictions

Objective 1. Establish the age and body mass of bachelor males and compare these to that of territorial, roaming and philopatric males. The reproductive tactics employed by striped mice males are largely influenced by body mass.

- If bachelor groups formed as a result of reproductive competition (for instance, being expelled by the breeding male), I predicted that the average age and body mass of bachelor males at the start of the breeding season would be between that of philopatric and that of solitary living, roaming males (i.e. 3.9 - 8.4 months and ≈ 30-59 g; Schradin *et al.* 2009). In striped mice, territorial breeders have the greatest body mass amongst males as well as the highest fitness (Schradin and Lindholm 2011). Based on this, it follows that males would not have to form bachelor groups (possibly conferring lower fitness) if their body mass was high, but that they would compete for territories and adopt a tactic yielding high fitness (territorial breeding).

Objective 2. Establish the origin of males forming bachelor groups. Three possibilities may explain the formation of bachelor groups in striped mice: (1) all female members of a group disappear, leaving only males; (2) males of one group may leave their natal group to form bachelor groups due to the pressures of reproductive competition by the breeding male in their natal nest; and (3) unrelated males may form bachelor groups for thermoregulatory benefits through huddling at night.

- Striped mice groups are typically comprised of close kin. I thus predicted that bachelor groups are kin-based alliances (males that have dispersed from one natal group, i.e. philopatric males). If bachelor groups formed as a result of stochastic factors (such as the disappearance of all females in the group), it would also follow that the males left behind were kin.

Objective 3: Establish the season during which bachelor groups most frequently occur (breeding vs non-breeding season), and whether population density, sex-ratio and breeding opportunities in the population influence the number of bachelor groups occurring.

- I predicted that bachelor groups would most frequently occur during the breeding season, especially if they form as result of reproductive competition. However, in the Succulent Karoo, ubiquitous cold nights makes huddling an advantage. Temperatures in this region may fall below 10°C, even in summer, which is far below the striped mouse zone of thermoneutrality of 30°C (Scantlebury *et al.* 2006). Thus, in this species, the formation of bachelor groups for the benefit of thermoregulation may not be restricted to the breeding season only.
- Population densities may influence competition for resources (i.e. females and food). Following the habitat saturation model of Emlen (1982a), I predicted that there would be more bachelor groups under conditions of low population density, because when population density is low, there may be more vacant territories, allowing for dispersal of philopatric males, which might eventually form bachelor groups.
- I predicted that a male biased sex ratio (many more males than females) would result in more bachelor individuals.
- I predicted that a lower chance to breed (breeding opportunity) would lead to the formation of more bachelor groups because female groups are secured by territorial males.

Objective 4. Establish whether or not bachelors are reproductively active (typically scrotal or non-scrotal) in the breeding season.

- If bachelor groups formed as result of reproductive competition with dominant males, I expected that they would be scrotal (sexually mature).

Objective 5. Assess the tactics employed by males before and after they are bachelors.

- I predicted that bachelor groups may form as a tactic of decreasing thermoregulatory costs through social huddling. Males which have dispersed from their natal groups would benefit from group living. If this is the case, the previous tactic of bachelors would be more often the philopatric tactic than the roaming or breeding tactic (with the exception of bachelor groups which form as a result of the death of all female members, in which case, breeding males may accidentally become bachelors).
- I also predicted that bachelor males may switch to the roaming or territorial breeding tactic (Schradin *et al.* 2009). This may be especially the case if young males joined bachelor groups at the start of the breeding season and then gained body mass as the breeding season progressed, such that they were heavy enough to obtain and defend a territory by the end of the breeding season.

CHAPTER TWO
MATERIALS AND METHODS

Study site and period

The study was conducted at the Succulent Karoo Research Station (SKRS) in Goegap Nature Reserve, located approximately 15 km from Springbok in the Northern Cape Province (S29 41.712 E18 01.5, altitude 912 m). This area receives an average annual rainfall of approximately 160 mm, predominantly in the winter months, where temperatures can fall below 0°C (Schradin and Pillay 2005a). Summers are typically hot and dry with temperatures reaching approximately 40°C (Schradin and Pillay 2005a). I visited the study site for several months in 2017 to conduct field work for this study. However, the population density of striped mice has decreased significantly because of a severe and persistent drought in western South Africa. I therefore could not obtain sufficient data for study, despite conducting all the field techniques listed here. Instead, historical data collected from 2009 to 2016 by researchers at SKRS were used in my study.

There are more than 4000 plant species in the Succulent Karoo and the area has been identified as one of the 25 global biodiversity hotspots (Myers *et al*. 2000). In the study site, the vegetation is mostly dominated by *Zygophyllum retrofractum* and *Lycium cinerum* shrubs and different species of ephemerals in spring (Schradin and Pillay 2004). The patchy distribution of these small shrubs means that food and nesting sites for striped mice are limiting resources (Schradin 2005b).

The SKRS has been conducting long term (> 15 years) research at Goegap Nature Reserve, on a 7 ha permanent study site. In this site, striped mice are well habituated to the presence of observers due to ongoing monitoring of the population (Rimbach *et al.* 2016). The site is characterized by sandy areas and patchy bush/shrub distribution (Schradin and Pillay 2004).

Trapping, marking and monitoring of striped mice

Individuals were live-trapped using Sherman-like metal traps (26x9x9 cm; Figure 2.1 below; Schradin and Pillay 2004). Traps were baited using a mixture of bran flakes, raisins, sea salt and sunflower oil, a bait that has been successfully used in various studies involving striped mice (Schradin 2004; Schradin 2006; Rimbach *et al.* 2016). The traps were placed next to bushes containing the nesting sites of groups or roaming individuals (roamers nest

alone), and were thereafter continuously monitored. Mice were captured and handled using protocols approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC clearance number: 2007/40/01).



Figure 2.1. Sherman-like metal live-traps (26x9x9 cm) placed next to a *Zygophyllum retrofractrum* shrub, containing the nesting site of a group of striped mice.

Trapping was done in the early mornings and in the late afternoons but not during the hottest times of the day, when striped mice are mostly inactive (Schradin *et al.* 2007). Body mass measurements were taken during both the morning and afternoon trapping sessions, five times every week, but for this study, only the morning measurements were used for analysis (before mice gained body mass due to foraging). Traps were checked every 30-45 minutes and trapped mice were weighed (to 0.1g) using an electronic scale, and their reproductive status was determined. Males were categorized as either scrotal (testes descended) or non-scrotal (testes inside abdomen; Schradin and Pillay 2005b). Each mouse was marked with an ear tag (National Band and Tag, Newport, KY, USA) and with a unique colour combination using hair dye (Inecto Rapid, Pinetown, South Africa; Figure 2.2) for identification during field observations. This dye has been found to have no negative effects on the behaviour of striped mice (Schradin 2006). By marking all mice, it was possible to record the groups from which bachelor males originated. Unmarked males were assumed to have originated outside of study site (immigrants), and ear tagged and marked when they joined the study population.



Figure 2.2. Ear-tagged and painted (blond-black behind) male striped mouse during field observation. Each mouse was painted with a unique combination of colours, using hair dye, to identify individuals during direct field observations.

Observations and radio-tracking

Groups and individuals were directly observed in the mornings (sunrise) and afternoons (sunset) in front of their nests. Each group or individual was observed for 2 to 3 consecutive days (both mornings and afternoons), at least once every two weeks, and observations lasted for 30 to 45 minutes. Striped mice typically bask in the sun when they emerge from their nests at sunrise and when they return from foraging at sunset. During this time, it is possible to identify group members, and thus record group composition. Additionally, breeding, roaming and bachelor males (see determination of male tactics below) were trapped, anaesthetised with di-ethyl ether and fitted with a radio transmitter (Schradin and Pillay 2005b). Individuals were tracked twice a day (morning/afternoon and at night), five times a week, using an AOR 8000 wide range receiver and a Telonics RA-14K antenna. It has been established that radio transmitters do not cause harm or represent a cost to collared individuals (Schradin 2006). By tracking individuals to their nesting sites at night, it was possible to record group composition and the identity of males in each group.

Determination of male tactics, population density and sex ratio

A combination of trapping, radio-tracking and direct observations for the period 2009 to 2016, were used to determine the reproductive tactics followed by individual males. Male striped mice reach sexual maturity at 4-6 weeks of age with a body mass ranging from 20-30g. Thus, only males older than 4 weeks, with a body mass >30g were considered for study. If males had previously been trapped at a group as juveniles (body mass <25g) and still trapped as adults in the same group, they were considered philopatric (Schradin and Yuen 2011; Schoepf and Schradin 2012a). Breeding males were identified as the heaviest scrotal male in a non-natal group. Adult males not sharing a nest with any other mice were considered as roamers (Schradin *et al.* 2012). Additionally, some males may live in a non-natal group which already has females defended by a territorial breeding male, and their philopatric offspring. Since these males were not related to the group members, they were classified as "non-natal group living". Two or more males sharing a nest with each other, without a female group member, were identified as bachelor males. Bachelor males were assigned to one of three categories according to relatedness and how the groups were formed. Males were regarded as related if they originated from the same group. The categories were: a) unrelated males form bachelor groups nesting away from their natal groups, b) all female members of a group disappeared, leaving behind males, which are related; and c) related males of one group left their natal group to form a bachelor group.

Data Analysis

Data were analysed using the statistical software program R 2.4.1 (R Development Core Team 2006). Body mass and age were compared among the 4 male tactics at the start of the breeding season by fitting a linear mixed model using the lme4 package (Bates *et al.* 2015). The average body mass of each individual for the month September was used as the body mass for the start of breeding season. Age was calculated for each male (where data were available) at the start of breeding season (September) from their birth dates. Body mass was the response variable, age was a continuous factor, tactic was a fixed factor, and male ID, group number and year were introduced as random factors (intercepts only). The interaction of age and tactic on body mass was also examined. Since body mass residuals differed significantly from a normal distribution (Shapiro-Wilk test, $p < 0.05$), the data were normalised using a Box Cox transformation for linear models from the MASS package (Venables and Ripley 2002). The model assumptions were verified by plotting model residuals and inspecting Q-Q plots. Furthermore, to assess which variables in the model were highly

correlated, variance inflation factors (VIFs) were inspected using the car package (Fox and Weisberg 2011) and VIF value was set at <2. For pairwise body mass comparisons between all tactics, Tukey's Honest Significance Difference (HSD) test in the stats package (R Core Team 2017) was conducted *post hoc*.

A Fisher's exact test was used to establish the season (breeding versus non-breeding) during which bachelor males were most likely to occur. To analyse whether the number of bachelor groups that occurred was affected by population density, sex-ratio and breeding opportunities, a generalised linear model (GLM) with a Poisson distribution was fitted to the data using the "glm" function from the lme4 package (Bates *et al.* 2015). The response variable (number of bachelor groups occurring) were count data and differed significantly from a normal distribution ($p < 0.001$), and hence a GLM was used. Population density was estimated for each month (from 2009 to 2016) as the total number of sexually mature mice divided by the study area size in hectares. The sex ratio was estimated for each month as the total number of sexually mature females to total number of sexually mature males. Breeding opportunity was represented as the number of groups with females divided by the number of adult (sexually mature) males. To compensate for over-dispersion, I refitted the model with a quasi-Poisson distribution (Crawley 2012).

Pearson's Chi-Square test was used to establish whether males (all reproductive tactics) were more likely to be scrotal or non-scrotal at the start of the breeding season. The breeding season for each year was adjusted according to the month when striped mice initiated breeding (approximately 5-6 weeks before the first pups emerged) to when breeding terminated (5-6 weeks before last observed pups; Brooks 1982; Schradin and Pillay 2005a).

A paired t-test was used to establish whether there were differences in body mass between tactic switches (previous tactic to bachelor and bachelor to next tactic). The Fligner-Keller test was used to test for equality of variance across the 4 male reproductive tactics (breeders, roamers, philopatrics and bachelors). Then two separate one-way analysis of variance (ANOVA) models were used to establish whether 1) the previous tactic had an influence on the body mass at which individuals switched to the bachelor tactic, and 2) the subsequent tactic employed by bachelors was influenced by the body mass at which they switched.

CHAPTER THREE
RESULTS

Objective 1. Comparison of body mass and age among male tactics at the start of the breeding season (September)

For comparisons of body mass and age, I used data collected only in the month of September 2009 to 2016. Information was available for 256 males of which 39.8% were breeders, 8.6% were bachelors, 38.8% were philopatric, and 13.6% were roamers (Table 3.1). Hereafter, I refer to bachelor groups as a "tactic" for convenience and ease of reporting only and not as a way of concluding that bachelor groups are indeed a reproductive tactic.

Table 3.1. The number of individual males employing each of the reproductive tactics in striped mice at the start of the breeding season (September) from 2009 to 2016

	2009	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**Total**
Breeder	14	8	9	20	15	14	12	10	102
Bachelor	4	0	2	2	0	4	5	5	22
Philopatric	13	10	18	34	5	5	5	7	97
Roamer	5	2	8	7	5	3	2	3	35
Total	**36**	**20**	**37**	**63**	**25**	**26**	**24**	**25**	**256**

The results of the linear mixed model (Table 3.2) showed that the philopatric and bachelor tactics were significant predictors of body mass, while the breeder and roaming tactic were not. Age was not a significant predictor of body mass (Figure 3.2). The interaction between age and the bachelor and philopatric tactics significantly predicted body mass while the interaction between age and the breeding and roaming tactics was not a significant predictor of body mass. A pairwise comparison of body mass between tactics *post hoc* showed that breeders were significantly heavier than males of the other three tactics (Figure 3.1). Bachelors and roamers were significantly heavier than philopatrics, lighter than breeders, but not significantly different from each other.

Table 3.2. Results of the linear mixed model to assess the influence of tactic and age on body mass. Variables that significantly influenced body mass appear in bold

Response	Estimate	SE	t-value	P value
Intercept	27.378	2.409	11.365	< 0.001
Tactic Breeder	-1.670	5.854	-0.285	0.776
Tactic Bachelor	-18.190	5.287	-3.441	**< 0.001**
Tactic Philopatric	-20.422	3.04	-6.708	**<0.001**
Tactic Roamer	1.670	5.854	0.285	0.777
Age	0.341	0.177	1.928	0.061
Tactic breeder*age	0.501	0.568	0.881	0.374
Tactic bachelor*age	1.364	0.452	3.016	**<0.001**
Tactic philopatric*age	1.151	0.293	3.923	**<0.001**
Tactic roamer*age	-0.501	0.568	-0.881	0.384

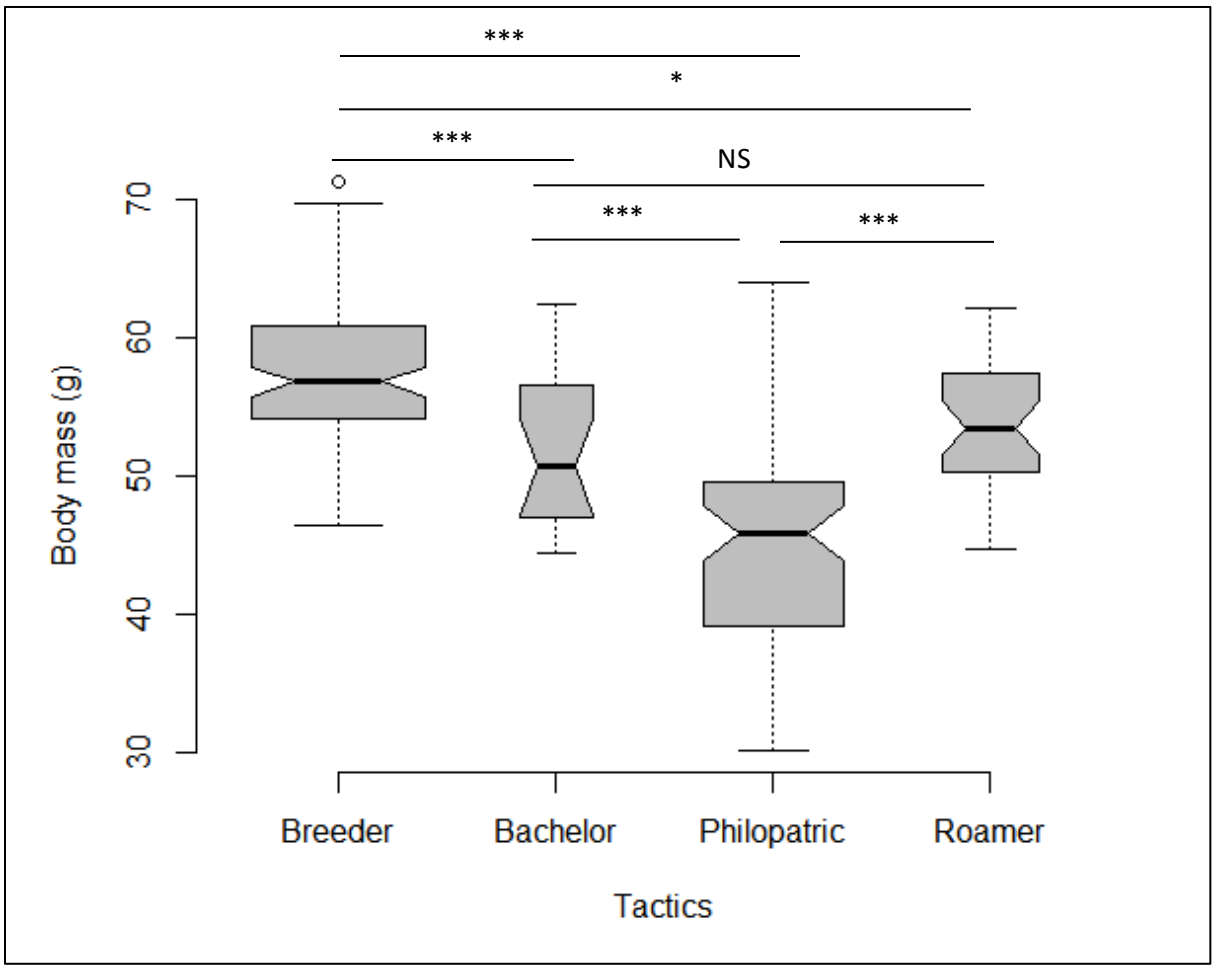

Figure 3.1. Body mass of territorial-breeding, bachelor, philopatric and roaming males at the start of the breeding season (September). Horizontal black lines represent the median, notches show the confidence interval of the median, whiskers show minimum and maximum values of non-outlier data and the open circle shows an outlier. The width of each box is proportional to the sample size (N = 256). Significant differences in body mass between tactics indicated in *post hoc* test are shown by:
*$p < 0.05$; ***$p < 0.001$

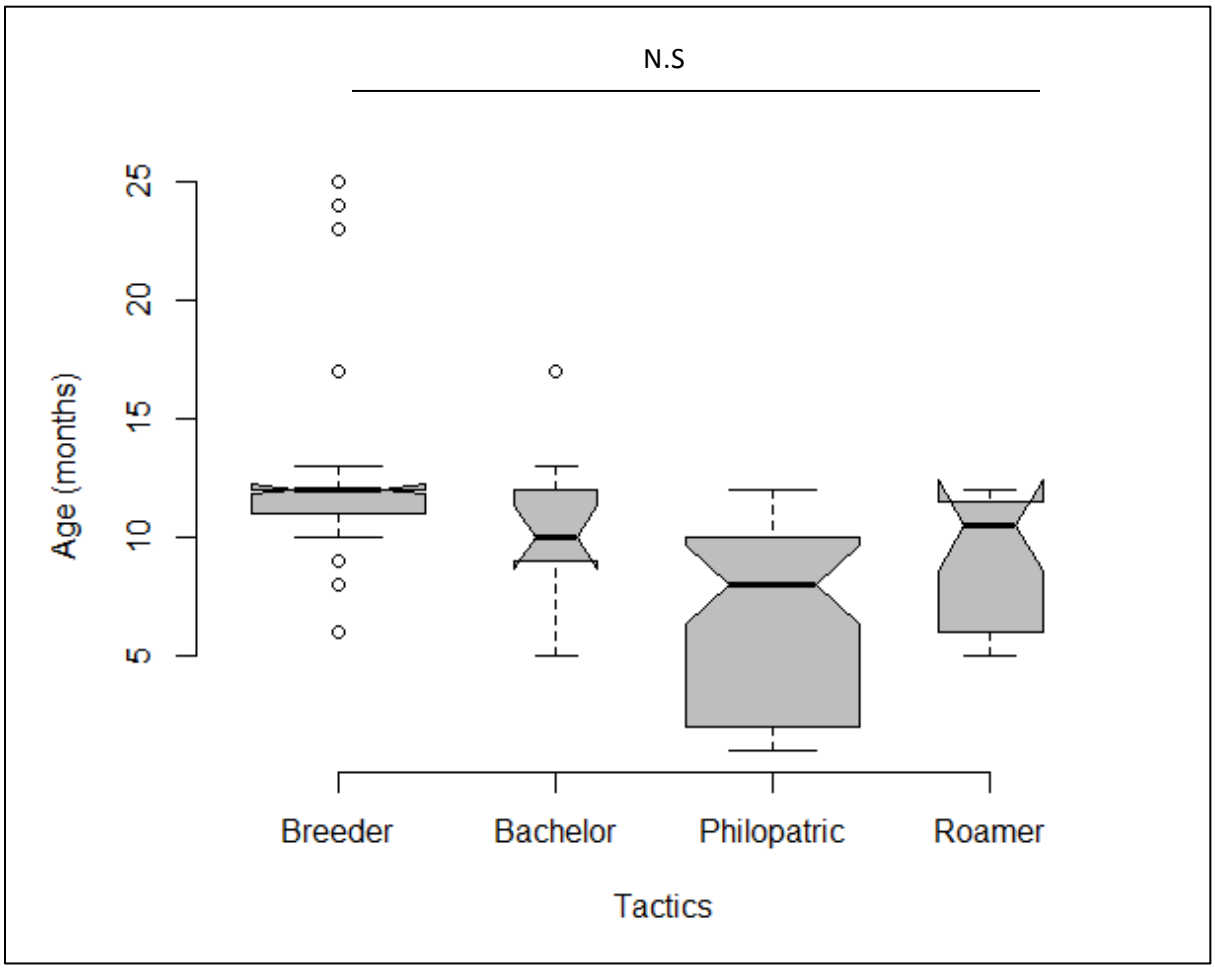

Figure 3.2. Age (months) of territorial-breeding, bachelor, philopatric and roaming males at the start of the breeding season (September). Horizontal black lines represent the median, notches show the confidence interval of the median, whiskers show minimum and maximum values of non-outlier data and open circles show outliers. The width of each box is proportional to the sample size (N = 256).

Objectives 2 and 3. The origin of males forming bachelors groups, and factors affecting occurrence

During the period 2009 to 2016, 18 bachelor groups comprising of a mean±SD of 2.67±0.69 (range: 2-5) individuals were observed (N = 49, which differs from N = 22 in Table 3.1 above, which is only for the month September). In comparison, there were 13±1.87 (range: 11-16) breeding groups per year in the same time period. Membership in bachelor groups changed frequently, with males joining and leaving the groups at different times. These groups were never maintained for a duration of more than 2.78±1.35 (range: 1-5) months, after which they disbanded. Bachelor groups were formed mostly (N = 31; 63.3%) by unrelated males away from their natal groups. In 14 instances (28.6%), bachelor groups formed when all female members of a group disappeared leaving behind related males, and in 2 cases (4.1%) related males of one group had left their natal group to form a bachelor group (Figure 3.3). Two males (4.1%) could not be assigned to one of these three categories as they were of unknown origin (indicated in Figure 3.3 as "unresolved"). Groups disbanded when all group members switched to another tactic (61.1%, N=11), when all group members died (33.3%, N=6), and when a female joined a bachelor group (5.6%, N=1).

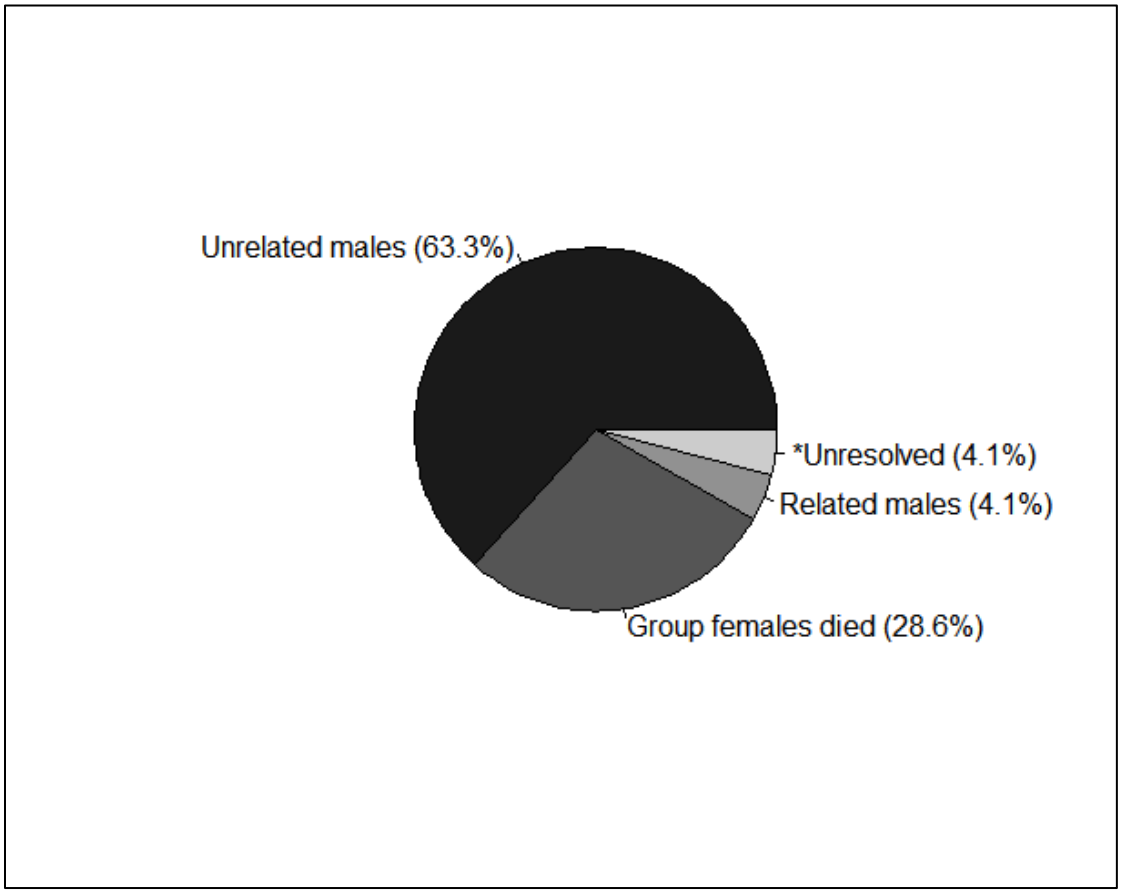

Figure 3.3. The proportion of bachelor males in each origin category (N = 49)

*The origin of two males could not be established (unresolved).

The results of the generalised linear model (GLM) showed that population density and breeding opportunity were significant predictors of the number of bachelor groups that occurred, while sex ratio and the interaction between sex-ratio and population density, did not significantly predict the number of bachelor groups that occurred (Table 3.3). Overall, more bachelor groups ocurred under conditions of low to intermediate population density, and none were observed at high population density (Figure 3.4). More bachelor groups occurred in conditions of lower breeding opportunities (i.e. as the number of groups with females divided by the number of sexually mature males; Figure 3.5). Bachelor males were significantly more likely to occur in the breeding season than in the non-breeding season ($p < 0.001$, Fisher's exact test; Figure 3.4), with of 6.5% of males (out of the total number of males) being bachelors in the breeding season and 0.61% of males (out of the total number of males) being bachelors in the non-breeding season.

Table 3.3. Results of the generalized linear model to assess the influence of population density and sex ratio on the number of bachelor groups occurring. The variable that significantly influenced the response variable appears in bold

Response (No. of bachelor groups)	**Estimate**	**SE**	**t-value**	**P value**
Intercept	-2.457	0.997	-2.465	0.016
Density	-0.047	0.020	-2.360	**0.020**
Sex Ratio	0.265	0.604	0.439	0.662
Breeding Opportunities	**5.057**	**1.061**	**4.765**	**<0.001**
Density*Sex Ratio	-0.025	0.090	-0.281	0.779
Density*Breeding opportunities	**0.301**	**0.104**	**2.898**	**0.005**

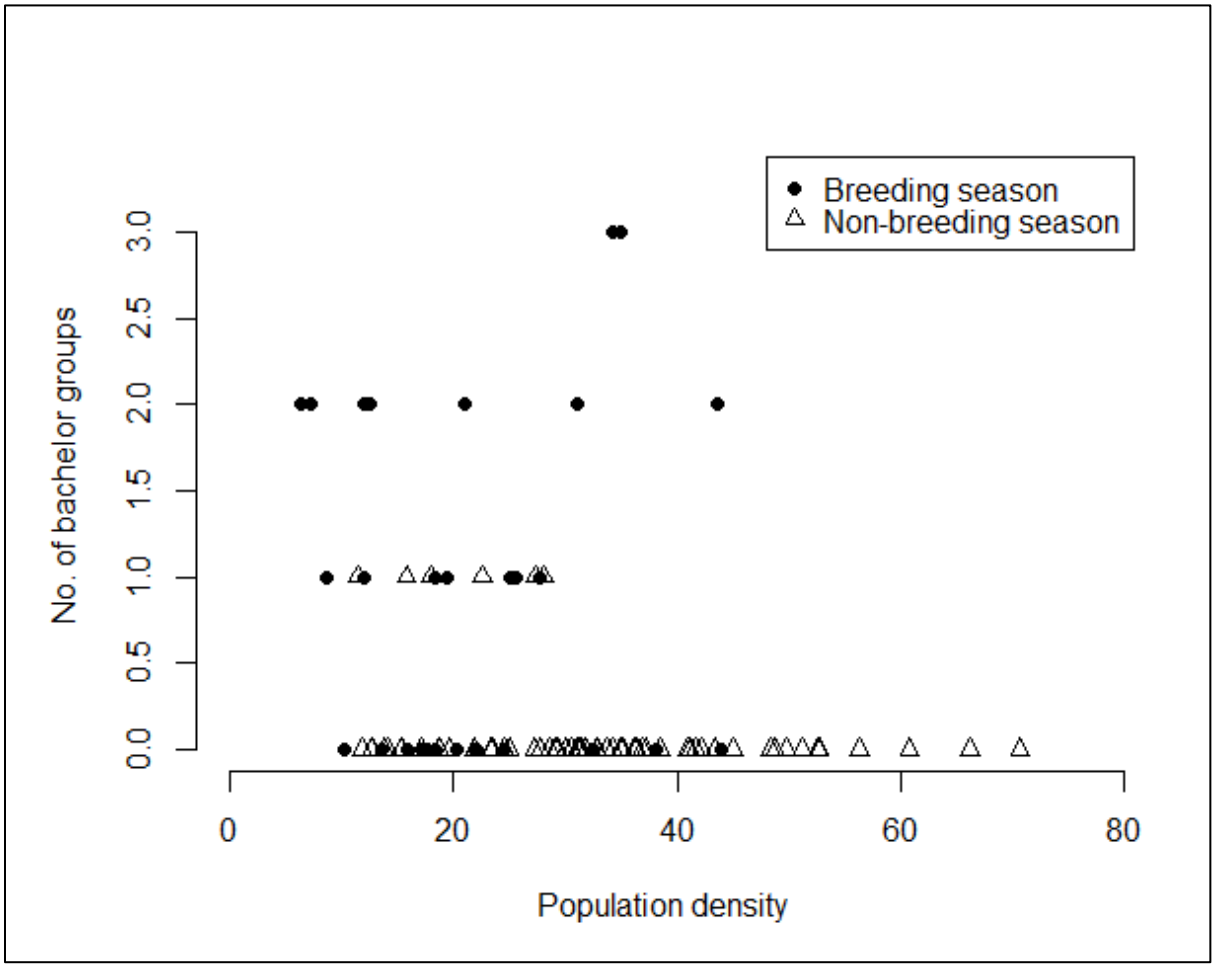

Figure 3.4. Number of bachelor groups that occurred at different population densities (total number of sexually mature mice per hectare), in the breeding (black dots) and non-breeding (open triangles) season.

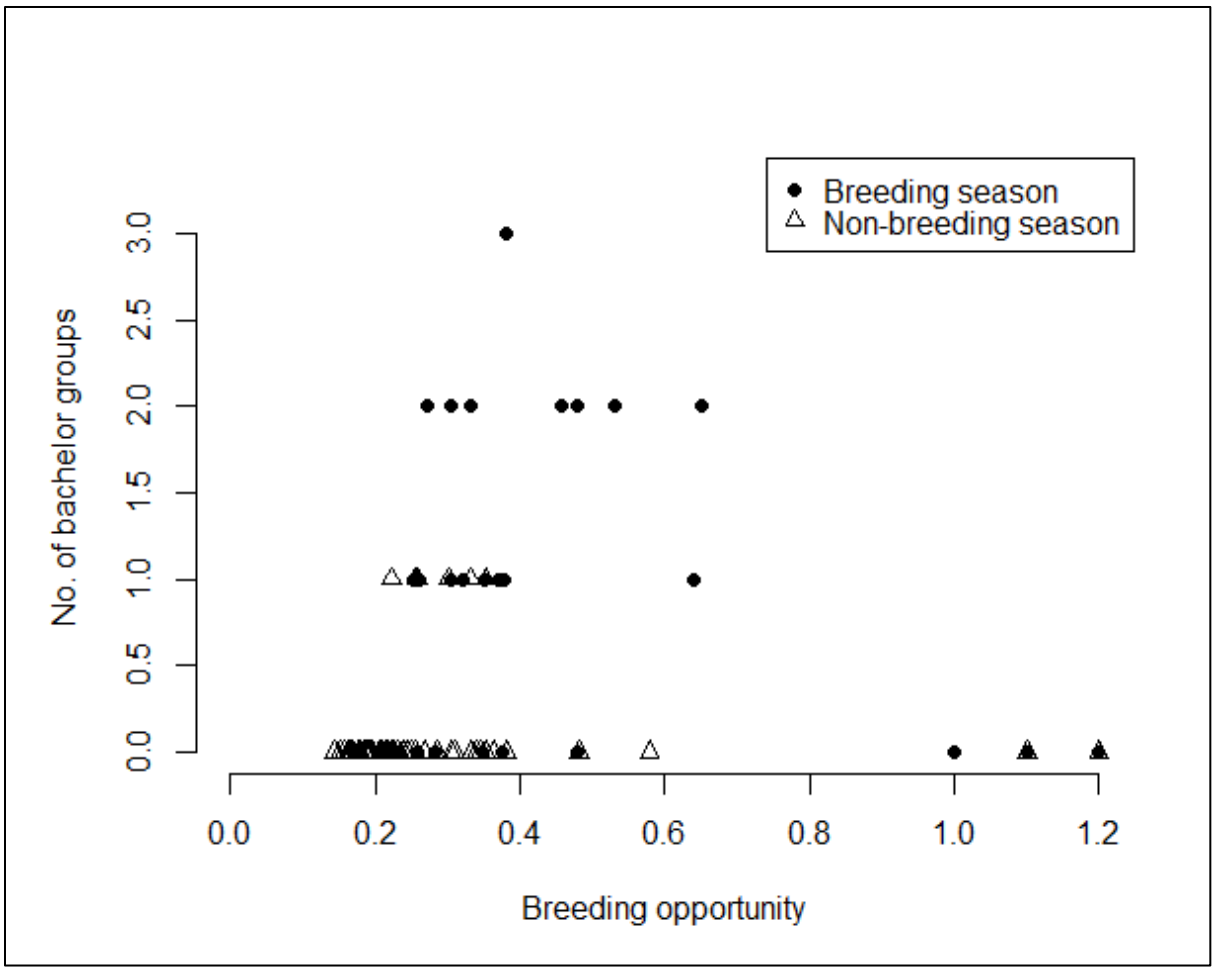

Figure 3.5. Number of bachelor groups that occurred at different breeding opportunities (number of groups with females divided by number of sexually mature males), in the breeding (black dots) and non-breeding (open triangles) season

Objective 4. Reproductive activity

At the start of the breeding season, males of all tactics were significantly more likely to be scrotal than non-scrotal (χ^2 =21.43, p < 0.001, Pearson's Chi square test; Figure 3.6). Of these, 99% of breeders were scrotal (N = 76), 89% of bachelors were scrotal (N = 19), 85% of philopatric males were scrotal (N = 89) and 100% of roamers were scrotal (N = 30).

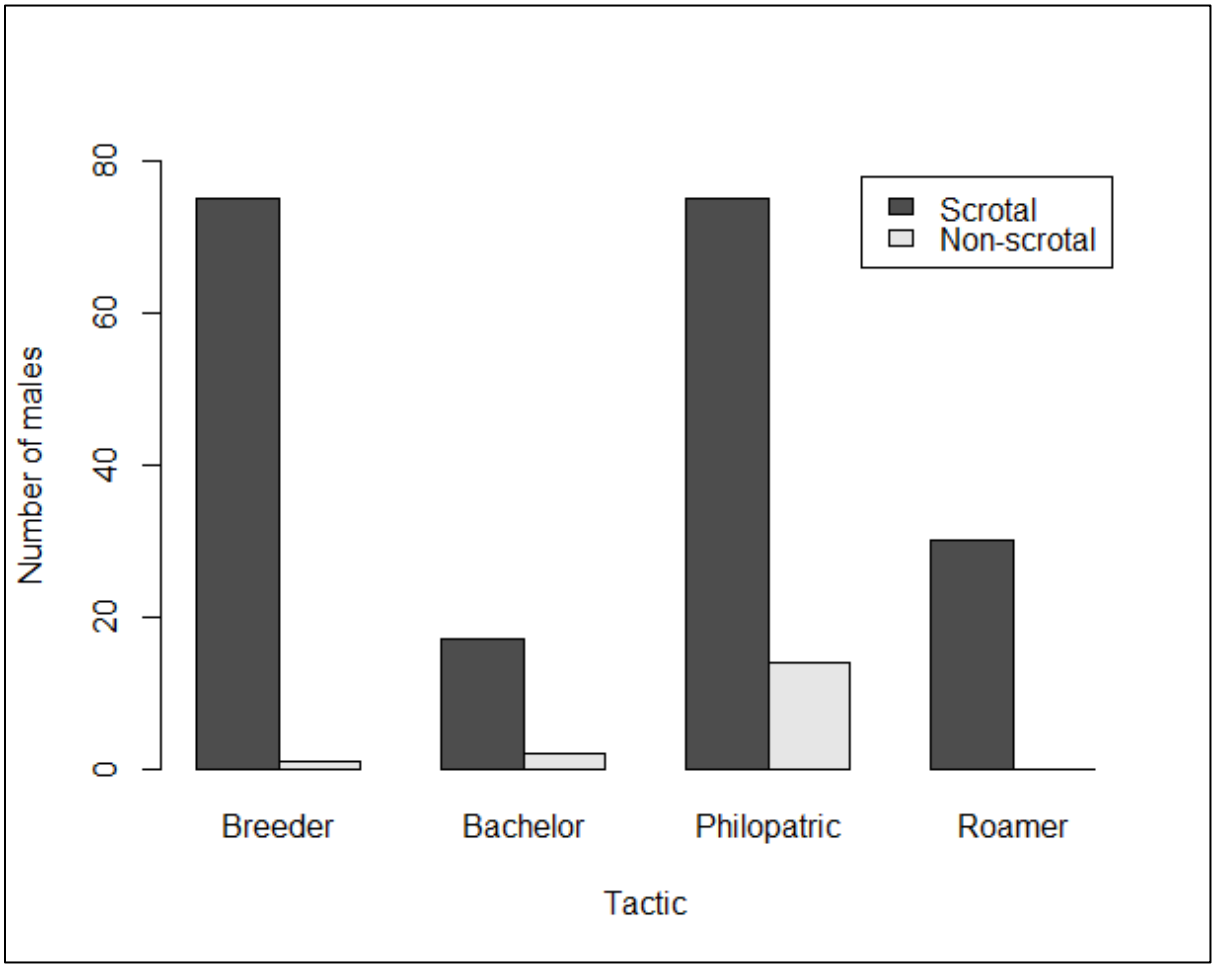

Figure 3.6. Number of scrotal (dark grey bar) and non-scrotal (light grey bar) males in 4 tactics. Males were more likely to be scrotal than non-scrotal at the start of the breeding season.

Objective 5. Tactics prior to and post the bachelor tactic

Before switching to the bachelor tactic 57.1% of males had been philopatric, 16.3% were roamers, 14.3%, were breeders and 2% had been living in a non-natal group (where there was already a breeder and females; Table 3.4). 42.9% (N=3) of breeding males were replaced in their original group by another male which became the new breeder. These new breeders were significantly heavier than the breeders which became bachelors (t= -4.91, df = 2, p = 0.039). Other breeders (57%, N=4) which became bachelors did so after the death of all female group members. The previous tactic of 8.16% of bachelors could not be established because they were immigrants into the study site.

After the bachelor tactic 42.9% of males switched to the roaming tactic, 26.5% to the breeding tactic and 2.0% went on to join a non-natal group which already had a breeder (Table 3.4). 76% of these switches to the next tactic occurred during a breeding season. Males were never observed going back to their natal groups (philopatric) after the bachelor tactic. A total of 14 (28.6%) males disappeared or died while they were bachelors.

Table 3.4. The number of males switching from different tactics to the bachelor tactic and from the bachelor tactic to different tactics

From	To	Number
Philopatric	Bachelor	28
Breeder	Bachelor	8
Roamer	Bachelor	7
Non-natal group**	Bachelor	1
Immigrant	Bachelor	5
Total		**49**
Bachelor	Roamer	21
Bachelor	Breeder*	13
Bachelor	Non-natal group**	1
Bachelor	Disappeared	14
Total		**49**

*8 out of 13 bachelors became breeders during a breeding season, while 5 out of 13 bachelors became breeders during a non-breeding season. Out of the 5 bachelors which became breeders during a non-breeding season, 3 lived long enough to reach the next breeding season and the other 2 disappeared before the next breeding season.

** The males which lived in non-natal groups did so during non-breeding seasons.

There was a significant difference between the mean body mass at which males became bachelors and the mean body mass at which males switched to the next tactic (df =29, t = 43.295, p< 0.001). On average, males gained body mass while they were bachelors (Figure 3.7). When switching to and from the bachelor tactic, there were no significant differences in body mass between males previously following different tactics *(*F=0.562, df=3 p = 0.692 Figure 3.8), nor were there significant differences in body mass between males switching to different tactics after the bachelor tactic (F=4.316, df=2, p= 0.271).

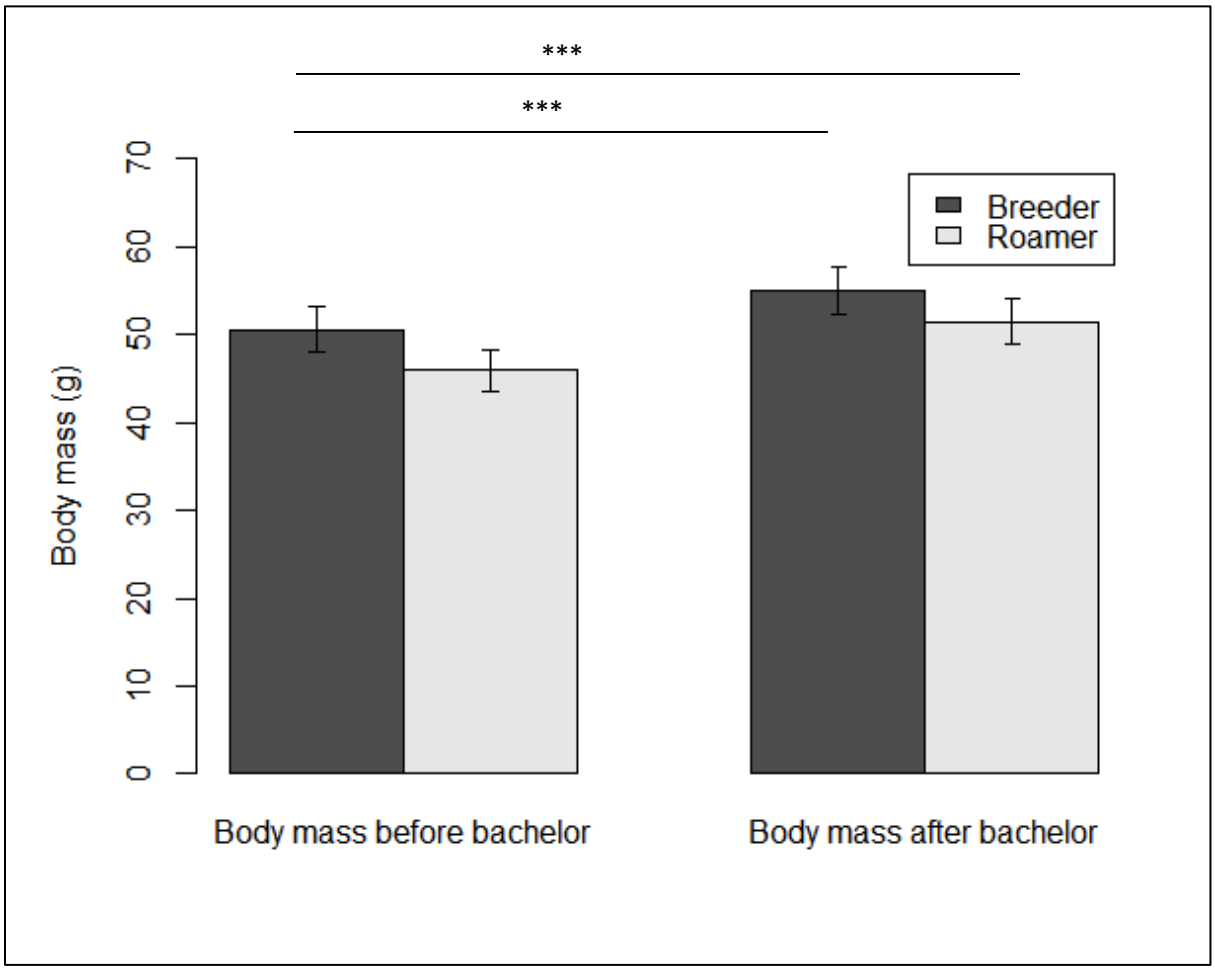

Figure 3.7. The change in body mass for males which became breeders and roamers before and after the bachelor tactic. The breeding and roaming tactic were the two main tactics employed after the bachelor tactic. Error bars represent the 95% confidence limit. Significant differences in body are shown by ***p<0.001.

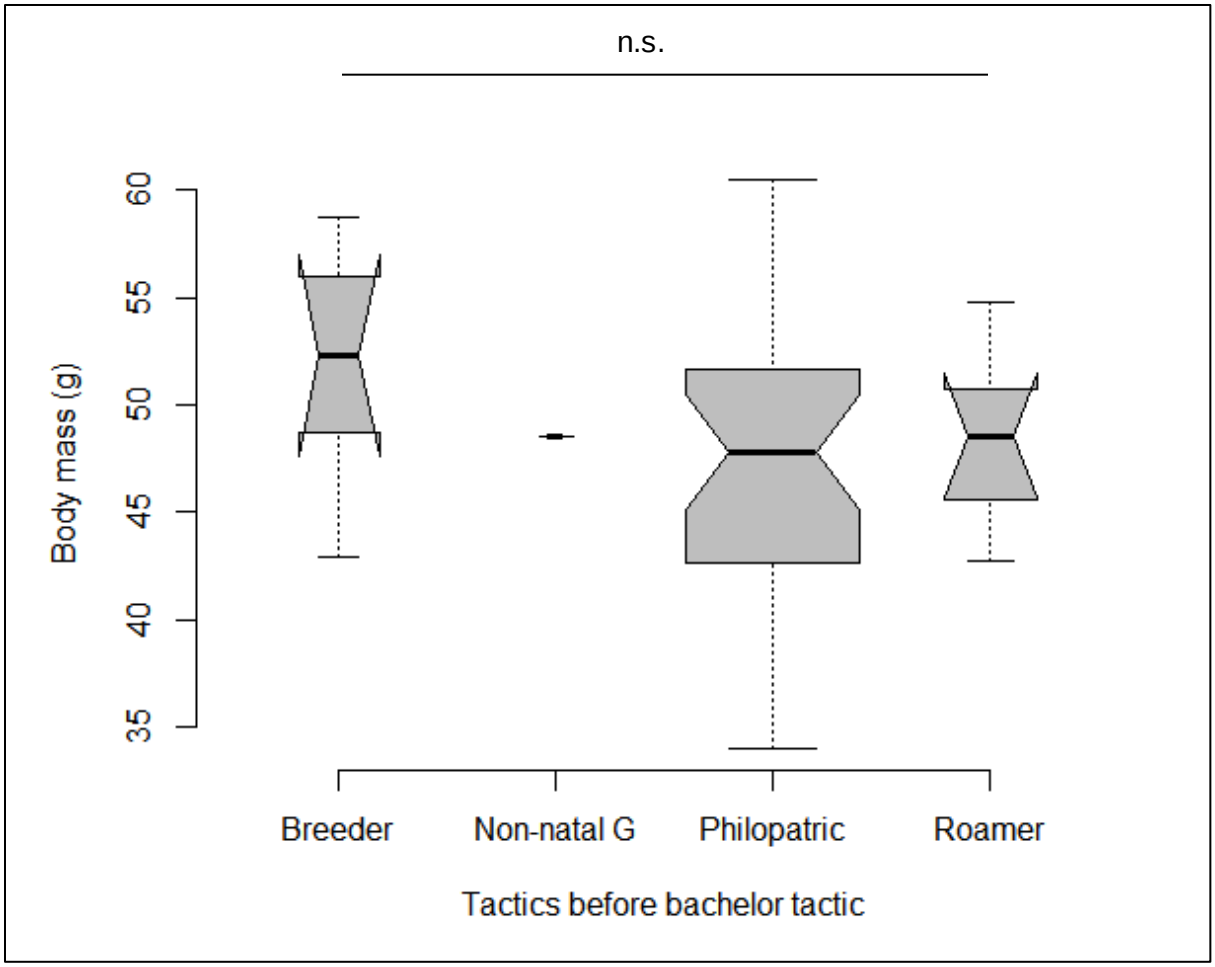

Figure 3.8. Body mass of males switching from breeder, non-natal group-living, philopatric and roamer tactics to the bachelor tactic. Horizontal black lines represent the median, notches show confidence interval of the median, whiskers show minimum and maximum values. The width of each box is proportional to the sample size (N = 49). No significant differences in mean body mass were noted (n.s., $p > 0.05$).

CHAPTER FOUR
DISCUSSION

Males in several animal species show variation in social and reproductive behaviour which is often associated with differences in morphology and physiology. Young and old, small and large males regularly make use of different behaviours and tactics in order to secure mates and increase their fitness (Emlen 1997). My study was concerned with investigating the phenomenon of bachelor males in the African striped mouse, *Rhabdomys pumilio*. Specifically, I aimed to establish the composition and function of bachelor groups, to compare these males to those using other tactics, and to establish whether the formation of bachelor groups possibly represents a fourth alternative reproductive tactic (ART) in striped mice.

Comparison of body mass across all tactics

The status of an individual, reflected in its age, body mass or size, plays an important role in determining which tactic that individual will follow (Gross 1996; Hunt and Simmons 2001). When comparing body mass among the four tactics, breeding males were the heaviest, philopatric males the lightest, and roamers and bachelors both occupied intermediate positions. These results concur with those of various other studies involving three known male tactics in striped mice (i.e. philopatrics, roamers and breeders, in order of increasing body mass; Schradin *et al.* 2009; Schradin and Lindholm 2011; Schradin *et al.* 2012).

Larger body size can be advantageous during combat and territorial encounters, thus conferring greater competitive abilities to males which are larger (Bachman and Widemo 1999). This is also the case in striped mice, where the largest males are dominant territorial breeders. In this species, individuals are more likely to attack a strange mouse that is lighter than themselves than one which is heavier within their territory, indicating the importance of body mass in territory defence and thus the maintenance of social and reproductive status (Schradin 2004). Bachelor males can thus be seen as males which are large enough to disperse, possibly due the pressures of within-group reproductive competition, but not competitive enough to obtain and defend a territory. This is common in many species, where forming bachelor groups (or herds) is an alternative reproductive tactic employed by less competitive males which may be excluded by territorial or resident males (Waterman 1997). These bachelor males form coalitions while they wait to secure a reproductive position in a group (e.g. patas monkey *Erythrocebus patas*; Gartlan 1974) or while they wait to gain a territory (e.g. white rhinoceros *Ceratotherium simum*; Owen-Smith 1975).

Interestingly, there were no significant differences in body mass between roamers and bachelors (although roamers were on average heavier than bachelors). Why then would some dispersing male striped mice live in bachelor groups instead of employing the solitary roaming tactic? In the Succulent Karoo, night temperatures can drop close to 0°C, which is far below the striped mouse thermoneutral zone of 30°C (Scantlebury *et al.* 2006). Thus, grouping for huddling may offer the benefit of warmth, thereby increasing survival chances (Schradin and Pillay 2004). According to Scantlebury *et al.* (2006), striped mice sleeping alone expend approximately 25% more energy than striped mice sleeping in groups. Similarly, white-backed mouse-birds *Colius colius*, which huddle together in winter, save up to 50% of their energy when compared to solitary birds (McKechnie and Lovegrove 2001). Bachelor groups could then be a mechanism of evading reproductive competition which is present at the natal nest, without the thermoregulatory costs associated with living solitarily.

Huddling is accompanied by a significant reduction in water consumption, which is important for desert dwelling mammals such as striped mice and other small rodents (Alberts 1978, Canals *et al.* 1989). Increased nocturnal vigilance may also be an important benefit to sleeping in a group. Previous studies have shown that at least one group member in striped mouse nests is awake during the night and any disturbance causes the group to swiftly leave the nest (Lehmann 2009). However, what is unknown, due to the lack of genetic data (paternity analyses), is whether or not chances of gaining reproductive success are lower as bachelors than as roamers. Roamers have home ranges larger than both philopatric males and territorial breeders, and they invade the home ranges of several defended female groups (Schradin *et al.* 2009). It is possible that several males nesting as one bachelor group might not be able to have such extensive home ranges without interfering with each other when looking for mating opportunities, and this might have cost implications for the reproductive success of bachelors. The trade-offs between group-living and roaming should thus play an important role in determining whether or not males join bachelor groups or employ the solitary roaming tactic.

While the benefits of group living outlined above provide ultimate explanations for the formation of bachelor groups, differences between roamers and males which become bachelors could also be explained by proximate causes. Specifically, these differences could be in testosterone levels and in resting metabolic rate (RMR). For instance, roamers have the highest testosterone levels (possibly promoting risky behaviour) and the lowest RMR (due to larger thermoregulatory costs) of all striped mice male tactics (Schradin *et al.* 2009). In addition, Schoepf and Schradin (2012b) found that males which disperse and live solitarily differ behaviourally (i.e. more aggression and more social investigation) from other males, even before they disperse, indicating that personality traits may be important in dispersal (Cote and Clobert 2007; Clobert *et al.* 2009). Further studies should thus consider physiological differences in bachelor males and males of other tactics, particularly between roamers and

bachelors. This would provide further insight into why some males would disperse and become bachelors while others become roamers, especially since there seems to be no differences in body mass between the two tactics.

Origin of males forming bachelor groups and factors affecting occurrence

My results revealed that bachelor groups were formed as a consequence of two main mechanisms: 1) when unrelated males that had left several natal groups formed bachelor groups (63%); and 2) incidentally, through the death of all female group members, leaving behind related males (29%). Only 2 males left their natal group together, forming one bachelor group. Kin selection is one of the factors explaining male-male affiliation in multi-male groups of several mammalian species, where kin members ultimately gain inclusive fitness, as occurs in the spider monkey *Ateles paniscus chamek* (Symington 1990), chimpanzees *Pan troglodytes* (Morin *et. al* 1994) and African wild dog *Lycoan pictus* (Frame *et al.* 1979). While kinship is regarded as an important factor in dispersal patterns and social behaviour, it is apparently not a prerequisite for the formation of bachelor groups in striped mice, contrary to my predictions. In other species, unrelated males have been known to form multi-male groups which exhibit coalition and affiliative behaviours, as exemplified by members the genus *Macaca* (Hill 1994), white-faced capuchin *Cebus capucinus* (Fedigan 1993) and cheetah *Acinonyx jubatus* (Caro 1994). According to Schradin *et al.* (2010), striped mice groups usually consist of close kin, but unrelated mice may form huddling groups in winter when no kin are available, indicating that while kin are preferred partners for huddling, unfavourable conditions may force striped mice to "make-do" by huddling with unrelated individuals for thermoregulatory benefits. Similarly, meadow voles *Microtus pennsylvanicus* usually form huddling groups consisting of kin, but may change to groups of unrelated individuals when population density and thus the availability of kin declines (Webster and Brooks 1981). Males which disperse from their natal groups may thus benefit from group living (forming bachelor groups) even in the absence of kin, by sharing a nest with other unrelated males.

That some bachelor groups formed due to environmental disrupters (Schradin 2013), i.e. through the death of all female group members leaving only males behind, demonstrates the important point that these all-male groups do not always reflect individual male choices (choice to disperse), and are thus not always the outcome of a strategy. Stochastic extrinsic factors may sometimes impose changes in tactics and social organisation upon individuals and this is especially the case when an important group member/s dies (Schradin *et al.* under review). In pair-living Scandinavian wolves *Canis lupus lupus*, the death of one of the pair results in the other becoming temporarily solitary (Milleret *et al.* 2017). Similarly, in striped mice, the death of all but one adult female group member gives rise to female solitary breeders

(Hill *et al.* 2015). Importantly, group-living females which became solitary of their own volition were reported to have a higher body mass and lower levels of the stress hormone corticosterone than females which became solitary via external constraints (death of all group members); indicating that females choosing to become solitary differ in individual traits from those forced to do so by environmental disrupters (Hill *et al.* 2015).

The presence of a conspecific can greatly reduce the reproductive output of an individual (Schoepf and Schradin 2012a). Reproductive competition is thus usually the unavoidable consequence of group living. However, whether or not an individual actually chooses to disperse as a result of reproductive competition may be influenced by ecological factors such as the availability of territories, which in turn, can be influenced by population density (Emlen 1982a; Hatchwell and Komdeur 2000; Kokko and Ekman 2002). In my study, at the start of the breeding season, males of all tactics (breeders, philopatrics, roamers, bachelors) were significantly more likely to be scrotal (sexually mature, thus physiologically capable of breeding; Schradin *et al.* 2012) than non-scrotal. Since male striped mice cannot obtain a breeding position within their natal groups (Schradin *et al.* 2010), reproductive competition during the breeding season may force males to disperse. This may explain the significantly higher incidence of bachelor males in the breeding season as opposed to the non-breeding season.

At a lower breeding opportunity, more bachelor groups were observed. Because there is typically one breeding male per group (Schradin and Pillay 2005b), a higher number of adult males can result in fewer breeding opportunities, leaving males which cannot obtain a breeding position in a group with one of two options: remain in the natal group with fewer chances of reproductive success; or disperse (eventually leading to the formation of bachelor groups). Population density was a significant predictor of the number of bachelor males that occurred, with more bachelors occurring in conditions of low to intermediate population density, but never at high population densities. This indicates the role of ecological constraints in whether or not individuals disperse. A high population density may result in a lack of empty territories (Emlen 1982a; Bergmuller *et al.* 2005), which hinders sexually mature individuals from choosing a dispersal tactic. Thus, reproductive competition coupled with empty territories into which males can disperse (low population density) are apparently the conditions which seem to favour dispersal leading to the eventual formation of bachelor groups.

Tactics employed by males before and after they were bachelors

Male striped mice of the Succulent Karoo start their adult life as philopatrics, and may later switch to one of two tactics, i.e. the territorial breeding tactic or the roaming tactic (Schradin *et al.* 2009). It has been demonstrated that tactic switches of male striped mice are influenced by body mass (i.e. a conditional strategy), and body mass in turn determines success in territorial encounters (Schradin 2004). My results revealed that a majority of bachelors (51%) had been philopatric before the bachelor tactic. Dominant individuals frequently reproductively supress and sometimes even evict subordinates in group living species, such as Mongolian gerbils *Meriones unguiculatus* (Saltzman *et al.* 2006), house mice *Mus musculus* (Pocock *et al.* 2005) and in members of the genus *Marmota* (Blumstein and Armitage 1999). In many species, dispersal is a tactic to avoid harassment and competition with dominant group members (Le Galliard *et al.* 2006). Eviction events have not been observed in free-living striped mice (Schoepf and Schradin 2012a) but only in captivity (Schradin, unpubl. data). At the start of the breeding season, 85% of philopatric striped mouse males were scrotal, indicating their capability to breed. This may explain why a majority of bachelors were previously philopatric males, which had left their natal group when the opportunity to change tactics became available.

That some bachelors were previously breeders (14%) was an interesting result because in a previous study, all breeders (100%) disappeared without being observed to change their tactic (Schradin *et al*. 2012). In the present study, 57% of breeders which became bachelors did so after the death of all female group members, leaving only males behind. In such a case, it can be argued that this change in tactic was incidental. However, other breeders (43%), often displaced by another heavier male, eventually joined bachelor groups. Breeders monopolize communally breeding females by defending a territory and reproductively supressing adult male offspring living in the group (Schradin *et al.* 2009b). Losing a territorial encounter may thus result in breeding males having to change their tactics to a potentially lower fitness tactic (roaming or bachelor tactic) if they cannot displace a male in another breeding group. The loss of dominance after losing in a territorial encounter is common in mammals (Gosling 1986), amphibians (Fellers 1979) and fish (Bakker *et al.* 1989). As for bachelors which previously employed the roaming tactic (16%), cooperation in social thermoregulation may possibly explain why they joined bachelor groups.

Males which did not disappear or die while they were bachelors significantly gained body mass and went on to become roamers (43%) or breeders (27%) after the bachelor tactic. Importantly, this might suggest that the bachelor tactic possibly offers lower reproductive success, making the switch to either breeder or roamer important for bachelors who have gained enough body mass to increase their competitive abilities. The breeding tactic confers

the highest fitness on males, and roamers have higher fitness than philopatric males (Schradin and Lindholm 2011). Thus, males which cannot obtain a territory after being bachelors may still gain fitness as roamers, assuming that the bachelor male tactic has low fitness outcomes. Furthermore, the fitness of different tactics in striped mice may also depend on prevailing environmental conditions, consistent with a single strategy. Specifically, under intermediate population densities, the roaming and breeder tactic yield similar fitness, while under low population densities, the roaming tactic can have very high fitness (Schradin and Lindholm 2011). Bachelor males occur in conditions of low to intermediate population densities. Perhaps the tactic they employ after the bachelor tactic is mediated by such ecological factors.

Schradin *et al.* (2006) attributed the instability of non-kin sleeping groups in striped mice to conflict, which is higher between non-kin than between kin. Since most bachelor groups were mainly comprised of non-kin, the same explanation is probably applicable in my study. In support, bachelor groups had dynamic and unstable membership, with members joining and leaving the groups at different times. Nonetheless, this might be a function of being a bachelor rather than kinship. For instance, even in the case of bachelor groups which comprised of related males after the death of all female group members, the groups disbanded within 1 to 5 months as a result of one or more m embers leaving the group and thus changing tactics. Similarly, bachelor groups in feral horses *Equus ferus* were reported to be inherently unstable (Feist and McCullough 1975).

Another interesting finding in my study was the unusual occurrence of non-natal group living males. These were males which lived in a group that already had a breeder defending communally breeding females, with their adult philopatric offspring of both sexes, but were not related to the group members. I found that a few males lived in such groups before becoming bachelors. Importantly, this was only observed in the non-breeding season. At the start of the breeding season, these males left these groups to join bachelor groups. Whether or not they were evicted by the resident breeding male is unknown. One of these males was observed living in a non-natal group after the bachelor tactic, but this was only after the breeding season. It is significant that this occurrence was observed only in non-breeding seasons, and points to the absence of reproductive competition, reducing within group conflict.

CONCLUSION

My study revealed important information about a phenomenon that has not been studied in striped mice previously. Bachelor males occupy the intermediate position (i.e. heavier than philopatrics, lighter than breeders) in the body mass spectrum of male striped mice and they do not differ in body mass from solitary living roamer males. This is significant since the tactics employed by male striped mice are largely influenced by body mass, which is consistent with conditional strategies. While the benefits of group living via decreased thermoregulatory costs (Scantlebury *et al.* 2006) and nocturnal vigilance (Shradin and Pillay 2004) provide some explanation as to why some males would be become bachelors and not roamers, possible reproductive costs associated with group-living may deter some males from adopting this tactic. Further studies regarding physiological differences could provide deeper insight into the adoption of this tactic.

Bachelor groups were mainly comprised of unrelated philopatric males which had dispersed from their natal nests, possibly due to reproductive competition. This is further supported by the higher incidence of bachelor males in the breeding season than in the non-breeding season, and by the fact that bachelor males are typically scrotal, thus capable of breeding. Nonetheless, the environment plays a role in the formation of bachelor groups. Stochastic factors (such as the death of all female group members, leaving only males) may give rise to bachelor groups and in such instances, groups can comprise of related males. Ecological factors such as population density affect the occurrence of bachelor groups, with low population densities seemingly favouring the formation of these groups. This can be attributed to the availability of territories under conditions of low population density which provide places into which males can disperse (Emlen 1982a).

The prior tactic before becoming bachelors was predominantly the philopatric tactic, which further indicates that philopatrics are making the “best-of-a-bad-job” and are likely to disperse as soon as another tactic becomes appropriate for them, as suggested by Schradin *et al.* (2009). The dynamic and unstable membership of bachelor groups, usually disbanding in less than five months, may be explained by possible conflict within these groups since they consist of non-kin conspecifics (Schradin *et al.* 2006). That all bachelor males, which did not die or disappear, changed to another tactic suggests that the bachelor tactic might also be a “best-of-a-bad-job” tactic. After the bachelor tactic, males mainly become solitary living (roamers), suggesting that this tactic probably has higher fitness than the bachelor tactic.

In sum, I suggest that the bachelor tactic is a “transitional tactic”. Such a tactic facilitates the change from a low fitness tactic (philopatric) to a high fitness tactic by allowing relatively small males to cooperate in social thermoregulation, until they get the opportunity to

employ a higher fitness tactic. Whether or not males sire any offspring while they are bachelors remains a question open to investigation by genetic (paternity) analyses. Without such analyses, I cannot conclusively state that bachelor groups in striped mice represent an alternative reproductive tactic.

REFERENCES

Adams, E.S. 1994. Territory defence by the ant *Azteca trigona*: maintenance of an arboreal ant mosaic. *Oecologia*, ***97*****,** pp.202-208.

Alberts, J.R. 1978. Huddling by rat pups: group behavioural mechanisms of temperature regulation and energy conservation. *Journal of Comparative and Physiological Psychology* ***92*****,** p.231.

Bachman, G. and Widemo, F. 1999. Relationships between body composition, body size and alternative reproductive tactics in a lekking sandpiper, the ruff (*Philomachus pugnax*). *Functional Ecology* ***13*****,** pp.411-416.

Baker, M.A.A. and Brown, J.S. 2011. Variation of within-day foraging costs in the striped mouse (*Rhabdomys pumilio*). *Mammalian Biology-Zeitschrift für Säugetierkunde* **76,** pp.654-656.

Bakker, T.H., Bruijn, E. and Sevenster, P. 1989. Asymmetrical effects of prior winning and losing on dominance in sticklebacks (*Gasterosteus aculeatus*). *Ethology*, ***82*****,** pp.224-229.

Bates, D., Maechler, M., Bolker B., Walker, S. 2015. Fitting Linear Mixed-Effect Models Using lme4. *Journal of Statistical Software* **67,** pp.1-48.

Beach, F.A. and Jaynes, J. 1954. Effects of early experience upon the behaviour of animals. *Psychological Bulletin*, ***51*****,** p.239.

Bergmuller, R., Heg, D. & Taborsky, M. 2005. Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proceedings of the Royal Society of London, Series B*, **272,** pp.325–331.

Blumstein, D.T. and Armitage, K.B. 1999. Cooperative breeding in marmots. *Oikos*, pp.369-382.

Boinski, S. 1994. Affiliation patterns among male Costa Rican squirrel monkeys. *Behaviour* **130,** pp.191-209.

Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E.V., Järvinen, A. and Metcalfe, N.B. 2004. Large–scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London B: Biological Sciences* ***271*****,** pp.1657-1662.

Brooks, P.M. 1982. Aspects of reproduction, growth and development of the four striped mouse, *Rhabdomys pumilio* (Sparrman 1974). *Mammalia* **46,** pp.52-64

Canals, M., Rosenmann, M. and Bozinovic, F. 1989. Energetics and geometry of huddling in small mammals. *Journal of Theoretical Biology* ***141*****,** pp.181-189

Candolin, U. and Wong, B.B. eds. 2012. *Behavioural responses to a changing world: mechanisms and consequences*. OUP Oxford.

Caro, T. 1994. Cheetahs of the Serengeti Plains: group living in an asocial species. University of Chicago Press.

Chaine AS, Clobert J. 2012. Dispersal. In: Candolin U, Wong BBM, editors. Behavioural responses to a changing world: mechanisms and consequences. Oxford: Oxford University Press, pp.63–79.

Chiyo, P.I., Archie, E.A., Hollister-Smith, J.A., Lee, P.C., Poole, J.H., Moss, C.J. and Alberts, S.C. 2011. Association patterns of African elephants in all-male groups: the role of age and genetic relatedness. *Animal Behaviour* **81,** pp.1093-1099.

Choate, T.S. 1972. Behavioural studies on some Rhodesian rodents. *Zoologica Africana* **7,** pp.103-118.

Clobert, J., Le Galliard, J. F., Cote, J., Meylan, S. & Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* **12,** pp.197-209.

Connor, R.C., Smolker, R.A. and Richards, A.F. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences* **89,** pp.987-990.

Cote, J. & Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B*, **274,** pp.383-390.

Crawley, M.J. 2012. The R book. John Wiley & Sons.

Danforth, B.N. 1991. The morphology and behaviour of dimorphic males in *Perdita portalis* (Hymenoptera: Andrenidae). *Behaviour, Ecology, Sociobiology* **29,** pp235-247.

Davies, N.B. 1992. Dunnock Behaviour and Social Evolution (Vol. 3). Oxford University Press.

Day, T., Pritchard, J. and Schluter, D. 1994. A comparison of two sticklebacks. *Evolution* ***48***, pp.1723-1734.

Dodson, S. 1989. Predator-induced reaction norms. *Bioscience* ***39,*** pp.447-452.

Dominey, W.J. 1984. Alternative mating tactics and evolutionarily stable strategies. *American Zoologist* **1,** pp.385-396.

Doody, J.S., Guarino, E., Georges, A., Corey, B., Murray, G. and Ewert, M. 2006. Nest site choice compensates for climate effects on sex ratios in a lizard with environmental sex determination. *Evolutionary Ecology* ***20*****,** pp.307-330.

du Toit, N., van Vuuren, B.J., Matthee, S. and Matthee, C.A. 2012. Biome specificity of distinct genetic lineages within the four-striped mouse *Rhabdomys pumilio* (Rodentia:

Muridae) from southern Africa with implications for taxonomy. *Molecular Phylogenetics and Evolution* **65,** pp.75-86.

Eggert, A.K. 1992. Alternative male mate-finding tactics in burying beetles. *Behavioural Ecology* **3**, pp.243-254.

Emlen, D.J. 1997. Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behavioural Ecology and Sociobiology* **41,** pp.335-341.

Emlen, S.T. 1982a. The evolution of helping. I. An ecological constraints model. *American Naturalist* **119,** pp.29–39.

Emlen, S.T. 1982b.The evolution of helping. II. The role of behavioural conflict. *American Naturalist* **119,** pp.40–53.

Engqvist, L. and Taborsky, M. 2016. The evolution of genetic and conditional alternative reproductive tactics. *Proceedings of the Royal Society of London B: Biological Sciences* **283,** pp.2945.

Faulkes, C.G., Abbott, D.H. and Jarvis, J.U.M. 1990. Social suppression of ovarian cyclicity in captive and wild colonies of naked mole-rats, *Heterocephalus glaber*. *Journal of Reproduction and Fertility*, ***88*****,** pp.559-568.

Fedigan, L. 1993. Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology* ***14*****,** pp.853-877.

Feist, J.D. and McCullough, D.R. 1975. Reproduction in feral horses. *Journal of Reproduction and Fertility. Supplement*, **23,** pp.13-18.

Fellers, G.M. 1979. Aggression, territoriality, and mating behaviour in North American treefrogs. *Animal Behaviour*, ***27*****,** pp.107-119.

Forsyth, A. and Montgomerie, R.D. 1987. Alternative reproductive tactics in the territorial damselfly *Calopteryx maculata*: sneaking by older males. *Behavioural Ecology and Sociobiology* **21,** pp.73-81.

Fox, J., and Weisberg, S. 2011. An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage.

Frame, L.H., Malcolm, J.R., Frame, G.W. and Lawick, H. 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania 1967–1978. *Ethology* ***50*****,** pp.225-249.

Frankenhuis, W.E. and Del Giudice, M. 2012. When do adaptive developmental mechanisms yield maladaptive outcomes? *Developmental psychology*, ***48*****,** pp.628.

Fraser, B.A., Janowitz, I., Thairu, M., Travis, J. and Hughes, K.A. 2014. Phenotypic and genomic plasticity of alternative male reproductive tactics in sailfin mollies. *Proceedings of the Royal Society of London B: Biological Sciences* **281,** pp.2310.

Gartlan, J.S. 1974. Adaptive aspects of social structure in *Erythrocebus patas*. In Proceedings from the Symposia of the 5th Congress of the International Primatological Society 17-161 Tokyo, Japan Science Press.

Godfrey, S.S., Bull, C.M., James, R. and Murray, K. 2009. Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. *Behavioural Ecology and Sociobiology* ***63***, pp.1045-1056.

Gosling, L.M. 1986. Economic consequences of scent marking in mammalian territoriality. In *Chemical Signals in Vertebrates* ***4,*** pp.385-395. Springer, Boston, MA.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology & Evolution* **11,** pp.92-98.

Hansen, M.M., Olivieri, I., Waller, D.M. and Nielsen, E.E. 2012. Monitoring adaptive genetic responses to environmental change. *Molecular Ecology* ***21*****,** pp.1311-1329.

Hartle, D.L., Clark, A.G. and Clark, A.G. 1997. Principles of population genetics (Vol. 116). Sunderland: Sinauer associates.

Hatchwell, B.J. and Komdeur, J. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour* ***59*****,** pp.1079-1086.

Hill, D.A. 1994. Affiliative behaviour between adult males of the genus Macaca. *Behaviour* ***130*****,** pp.293-308.

Hill, D.L., Pillay, N. and Schradin, C. 2015. Alternative reproductive tactics in female striped mice: heavier females are more likely to breed solitarily than communally. *Journal of Animal Ecology* **84,** pp.1497-1508.

Hunt, J. and Simmons, L.W. 2001. Status-dependent selection in the dimorphic beetle *Onthophagus taurus*. *Proceedings of the Royal Society of London B: Biological Sciences* ***268*****,** pp.2409-2414.

Jackson, T.P. 1999. The social organisation and breeding system of Brants' whistling rat (*Parotomys brantsii*). *Journal of Zoology* **247,** pp.323–331.

Jenkins, M. 1928. The effect of segregation on the sex behaviour of the white rat as measured by the obstruction method. *Genetic Psychology Monographs*.

John, L.K. 1993. Alternative reproductive tactics in male eastern grey squirrels: "making the best of a bad job". *Behavioral Ecology* **4,** pp.165-171.

Kingdon, J. 1974. East African Mammals. London: Academic Press.

Kokko, H. and Ekman, J. 2002. Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *The American Naturalist* ***160*****,** pp.468-484.

Komers, P.E. 1997. Behavioural plasticity in variable environments. *Canadian Journal of Zoology* ***75***, pp.161-169.

Koprowski, J.L. 1991. The evolution of sociality in tree squirrels: the comparative behavioural ecology of fox squirrels and eastern grey squirrels (Doctoral dissertation, University of Kansas, Systematics and Ecology).

Kraus, C., Heistermann, M. and Kappeler, P.M. 1999. Physiological suppression of sexual function of subordinate males: a subtle form of intrasexual competition among male sifakas (*Propithecus verreauxi*). *Physiology & Behaviour*, ***66***, pp.855-861.

Latour, P.B. 1981. Interactions between free-ranging, adult male polar bears (*Ursus maritimus* Phipps): a case of adult social play. *Canadian Journal of Zoology* **59,** pp.1775-1783.

Le Galliard, J.F., Gundersen, G., Andreassen, H.P. and Stenseth, N.C. 2006. Natal dispersal, interactions among siblings and intrasexual competition. *Behavioural Ecology*, ***17*****,** pp.733-740.

Lee, P.C. 1991. Adaptations to environmental change: an evolutionary perspective. In *Primate Responses to environmental change,* pp.39-56. Springer, Dordrecht.

Lehmann, D. 2009. Does nest sharing in striped mice (*Rhabdomys pumilio*) increase vigilance towards nocturnal predators? MSc thesis, University of Zurich.

Leuthold, W. 1970. Observations on the social organization of impala (*Aepyceros melampus*). *Ethology*, *27*(6), pp.693-721.

López-Maury, L., Marguerat, S. and Bähler, J. 2008. Tuning gene expression to changing environments: from rapid responses to evolutionary adaptation. *Nature Reviews Genetics* ***9*****,** pp.583-593.

Lott, D.F. 1991. Intraspecific variation in the social systems of wild vertebrates (Vol. 2). Cambridge University Press.

Majolo, B., de Bortoli Vizioli, A. and Schino, G. 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. *Animal Behaviour* ***76***, pp.1235-1247.

McCarthy, M.M. and Vom Saal, F.S. 1985. The influence of reproductive state on infanticide by wild female house mice (*Mus musculus*). *Physiology & Behaviour* ***35*****,** pp.843-849.

McFarland, R., Barrett, L., Boner, R., Freeman, N.J. and Henzi, S.P. 2014. Behavioural flexibility of vervet monkeys in response to climatic and social variability. *American Journal of Physical Anthropology* **154,** pp.357-364.

McKechnie, A.E. and Lovegrove B.G. 2001. Thermoregulation and the energetic significance of clustering behaviour in the white-backed mousebird (*Colius colius*). *Physiological and Biochemical Zoology*, ***74*****,** pp.238-249.

Mery, F. and Burns, J.G. 2010. Behavioural plasticity: an interaction between evolution and experience. *Evolutionary Ecology **24*,** pp.571-583.

Milleret, C., Wabakken, P., Liberg, O., Åkesson, M., Flagstad, Ø., Andreassen, H. P. and Sand, H. 2017. Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. *Journal of Animal Ecology* **86**, pp.43-54.

Montgomerie, R., Lyon, B. and Holder, K. 2001. Dirty ptarmigan: behavioural modification of conspicuous male plumage. *Behavioural Ecology **12***, pp.429-438.

Morin, P.A., Moore, J.J., Chakraborty, R., Jin, L., Goodall, J. and Woodruff, D.S. 1994. Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science-New York Then Washington*, pp.1193-1193.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403,** pp.853-858.

Noble, G.K. and Curtis, B. 1935. Sexual selection in fishes. *Anatomical Record*, ***64*,** pp.84-85.

Owen-Smith, R.N. 1975. The social ethology of the white rhinoceros *ceratotberium simum* (Burchell 1817). *Ethology* **38,** pp.337-384.

Packer, C. and Pusey, A.E. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* **296,** pp.740-742.

Piersma, T. and Drent, J. 2003. Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution* **18,** pp.228-233.

Pocock, M.J., Hauffe, H.C. and Searle, J.B. 2005. Dispersal in house mice. *Biological Journal of the Linnean Society ***84*,** pp.565-583.

Pulido, F. 2007. Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. *Climate Research ***35*,** pp.5-23.

R Core Team. 2017. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org

Rambau, R.V., Robinson, T.J. and Stanyon, R. 2003. Molecular genetics of *Rhabdomys pumilio* subspecies boundaries: mtDNA phylogeography and karyotypic analysis by fluorescence in situ hybridization. *Molecular phylogenetics and evolution* **28,** pp.564-575.

Randall, J.A., Hekkala, E.R., Cooper, L.D. and Barfield, J. 2002. Familiarity and flexible mating strategies of a solitary rodent, *Dipodomys ingens*. *Animal Behaviour* **64,** pp.11-21.

Randall, J.A., Rogovin, K., Parker, P.G. and Eimes, J.A. 2005. Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. *Behavioral Ecology* ***16*****,** 961-973.

Refsnider, J.M. and Janzen, F.J. 2012. Behavioural plasticity may compensate for climate change in a long-lived reptile with temperature-dependent sex determination. *Biological Conservation* ***152*****,** pp.90-95.

Rimbach, R., Willigenburg, R., Schoepf, I., Yuen, C.H., Pillay, N. and Schradin, C. 2016. Young but not old adult African striped mice reduce their activity in the dry season when food availability is low. *Ethology* **122,** pp.828-840.

Ronald, N.O.Ë. and Sluijter, A.A. 1990. Reproductive tactics of male savanna baboons. *Behaviour* **113,** pp.117-169.

Rymer, T.L., Pillay, N. and Schradin, C. 2016. Resilience to droughts in mammals: a conceptual framework for estimating vulnerability of a single species. *The Quarterly Review of Biology* **91,** pp.133-176

Saltzman, W., Ahmed, S., Fahimi, A., Wittwer, D.J. and Wegner, F.H. 2006. Social suppression of female reproductive maturation and infanticidal behaviour in cooperatively breeding Mongolian gerbils. *Hormones and Behavior*, ***49*****,** pp.527-537.

Scantlebury, M., Bennett, N.C., Speakman, J.R., Pillay, N. and Schradin, C. 2006. Huddling in groups leads to daily energy savings in free-living African Four-Striped Grass Mice, *Rhabdomys pumilio*. *Functional Ecology* **20,** pp.166-173.

Scheiner, S.M. and Lyman, R.F. 1991. The genetics of phenotypic plasticity. II. Response to selection. *Journal of Evolutionary Biology* **4,** pp.23-50.

Schew, W.A. and Ricklefs, R.E. 1998. Developmental plasticity. *Oxford Ornithology Series* **8,** pp.288-304.

Schoepf, I. and Schradin C. 2012a. Better off alone! Reproductive competition and ecological constraints determine the sociality in the African striped mouse (*Rhabdomys pumilio*). *Journal of Animal Ecology* ***81*****,** pp.649-656

Schoepf, I. and Schradin, C. 2012b. Differences in social behaviour between group-living and solitary African striped mice, Rhabdomys pumilio. *Animal behaviour* ***84*****,** pp.1159-1167.

Schradin C. 2013. Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Phil. Trans. R. Soc. B.* **368**

Schradin, C. 2004. Territorial defense in a group-living solitary forager: who, where, against whom? *Behavioral Ecology and Sociobiology* **55,** pp.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,** pp.77-82.

Schradin, C. 2006. Whole-day follows of striped mice (*Rhabdomys pumilio*), a diurnal murid rodent. Journal of *Ethology* **24,** pp.37-43.

Schradin, C. and Lindholm, A.K. 2011. Relative fitness of alternative male reproductive tactics in a mammal varies between years. *Journal of Animal Ecology* **80,** pp.908-917.

Schradin, C. and Pillay, N. 2004. The striped mouse (*Rhabdomys pumilio*) from the succulent karoo, South Africa: a territorial group-living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology* **118,** p.37.

Schradin, C. and Pillay, N. 2005a. Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent karoo. *Mammalian Biology-Zeitschrift für Säugetierkunde* **70,** pp.84-92.

Schradin, C. and Pillay, N. 2005b. Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy* **86,** pp.99-107.

Schradin, C. and Yuen, C.H. 2011. Hormone levels of male African striped mice change as they switch between alternative reproductive tactics. *Hormones and behaviour* **60,** pp.676-680.

Schradin, C., Hayes L.D., Pillay, N., and Bertelsmeier, C. under review. The evolution of intra-specific variation in social organization. *Ethology*.

Schradin, C., König, B. and Pillay, N. 2010. Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology*, **79,** pp.515-521.

Schradin, C., Krackow, S., Schubert, M., Keller, C., Schradin, B. and Pillay, N. 2007. Regulation of activity in desert-living striped mice: The importance of basking. *Ethology* **113,** pp.606-614.

Schradin, C., Lindholm, A.K., Johannesen, J.E.S., Schoepf, I., Yuen, C.H., Koenig, B. and Pillay, N. 2012. Social flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*). *Molecular Ecology* **21,** pp.541-553.

Schradin, C., Scantlebury, M., Pillay, N. and König, B. 2009. Testosterone levels in dominant sociable males are lower than in solitary roamers: physiological differences between three male reproductive tactics in a sociably flexible mammal. *The American Naturalist* **173,** pp.376-388.

Schradin, C., Schubert, M. and Pillay, N. 2006. Winter huddling groups in the striped mouse. *Canadian Journal of Zoology* **84,** pp.693-698

Schumann, D.M., Cooper, H.M., Hofmeyr, M.D. and Bennett, N.C. 2005. Circadian rhythm of locomotor activity in the four-striped field mouse, *Rhabdomys pumilio:* a diurnal African rodent. *Physiology & Behaviour* **85,** pp.231-239.

Shuster, S.M. 1989. Male alternative reproductive strategies in a marine isopod crustacean (Paracerceis sculpta): the use of genetic markers to measure differences in fertilization success among α-, β-, and γ-males. *Evolution*, pp.1683-1698.

Sih, A., Ferrari, M.C. and Harris, D.J. 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications **4**,* pp.367-387.

Smith-Gill, S.J. 1983. Developmental plasticity: developmental conversion versus phenotypic modulation. *American Zoologist* **23,** pp.47-55.

Snell-Rood, E.C. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour **85**,* pp.1004-1011.

Spitze, K. 1992. Predator-mediated plasticity of prey life history and morphology: *Chaoborus americanus* predation on *Daphnia pulex*. *The American Naturalist* **139,** pp.229-247.

Stephens, D.W. 1991. Change, regularity, and value in the evolution of animal learning. *Behavioural Ecology **2**,* pp.77-89.

Symington, M.M. 1990. Fission-fusion social organization in Ateles and Pan. *International Journal of Primatology **11,*** pp.47-61.

Taborsky, M. 1994. Sneakers, satellites, and helpers – parasitic and cooperative behaviour in fish reproduction. *Advances in the Study of Behaviour* **23,** pp.1–100.

Taborsky, M. and Brockmann, H.J. 2010. Alternative reproductive tactics and life history phenotypes. In Animal behaviour: evolution and mechanisms (pp. 537-586). Springer Berlin Heidelberg.

Thompson, D.C. 1977. Reproductive behaviour of the grey squirrel. *Canadian Journal of Zoology* **55,** pp.1176-1184.

Tollrian, R. 1995. Predator-induced morphological defences: costs, life history shifts, and maternal effects in *Daphnia pulex*. *Ecology* **76,** pp.1691-1705.

Tomkins, J.L. and Hazel, W. 2007. The status of the conditional evolutionarily stable strategy. *Trends in Ecology & Evolution* **22,** pp.522-528.

Tuomainen, U. and Candolin, U. 2011. Behavioural responses to human-induced environmental change. *Biological Reviews **86**,* pp.640-657.

Venables, W.N., and Ripley, B. D. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York.

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S.M., Schlichting, C.D. and Van Tienderen, P.H. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology & Evolution* **10,** pp.212-217.

Waterman, J.M. 1997. Why do male Cape ground squirrels live in groups? *Animal Behaviour* **53,** pp.809-817.

Wauters, L., Dhondt, A.A. and De Vos, R. 1990. Factors affecting male mating success in red squirrels (*Sciurus vulgaris*). *Ethology Ecology & Evolution* **2,** p.204.

Weber, A. and Declerck, S. 1997. Phenotypic plasticity of Daphnia life history traits in response to predator kairomones: genetic variability and evolutionary potential. *Hydrobiologia* **360,** pp.89-99.

Webster, A.B. and Brooks, R.J. 1981. Daily movements and short activity periods of free-ranging meadow voles *Microtus pennsylvanicus*. *Oikos*, pp.80-87.

West-Eberhard, M.J. 2003. Developmental plasticity and evolution. Oxford University Press.

Willmer, P., Stone, G. and Johnston, I. 2009. *Environmental physiology of animals*. John Wiley & Sons.

Wingfield, J.C. and Kenagy, G.J. 1991. Natural regulation of reproductive cycles. *Vertebrate Endocrinology: Fundamentals and Biomedical Implications*, ***4*(**Part B), pp.181-241.

Wirtz, P. 1982. Territory holders, satellite males and bachelor males in a high density population of waterbuck (*Kobus ellipsiprymnus*) and their associations with conspecifics. *Ethology* **58,** pp.277-300.

Wrangham, R.W. 1986. Ecology and social relationships in two species of chimpanzee. *Ecological aspects of social evolution: Birds and mammals*, pp.352-378.