

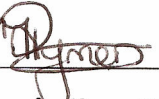
**Paternal care in the striped mouse *Rhabdomys*  
*pumilio*: ontogeny and function**

Tasmin Lee Rymer

A thesis submitted to the Faculty of Science,  
University of the Witwatersrand, Johannesburg,  
in fulfilment of the requirements for the  
degree of Doctor of Philosophy.

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I declare that this thesis is my own unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



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Tasmin Lee Rymer

20<sup>th</sup> day of April 2009

## ABSTRACT

Paternal care is rare and its development is poorly studied. I studied the ontogeny and function of paternal care in captive striped mice *Rhabdomys pumilio* from the succulent karoo, South Africa. Male striped mice show extensive parental care, displaying all behaviours (e.g. huddling and retrieving pups) shown by mothers, except nursing. In a first set of experiments, I studied non-genetic and genetic influences on the development of paternal care. The experimental design involved studying the development of paternal care in sons raised by the mother alone, both parents, and parents separated by a barrier. Sons raised by mothers alone were better fathers (i.e. displayed greater levels of paternal care behaviour) than sons from the other treatments; in contrast, daughters always showed higher levels of maternal care behaviour, regardless of treatment. Parent-offspring regressions indicated a partial patrilineal genetic influence of maternal (daughters), but not paternal (sons), care behaviour. Finally, sons raised by the mother and a second care-giver (older female sibling) also displayed better paternal care. My results indicate that fathers do not influence the development of paternal care in their sons genetically or non-genetically. Instead, an unanticipated finding was that mothers overcompensated in their maternal care behaviour in the absence of a male and the presence of a second care-giver, which correlated strongly with the greater levels of paternal care behaviour shown by their sons.

In a second set of experiments, I investigated the role of the father in offspring learning, and female mate choice for males with different levels of paternal care behaviour. Using two populations of striped mice (succulent karoo and grassland), my results indicated that mothers were more reliable demonstrators of information about novel food in both populations, but fathers were more reliable demonstrators for young succulent karoo striped mice only. In mate choice tests for olfactory cues of males with different levels of paternal care ability and experience, and for visual cues from males showing either paternal or no care, females preferred experienced males to inexperienced males, but showed no other preferences.

In conclusion, my results indicate that fathers are reliable demonstrators about novel food, at least in the succulent karoo, and supports previous findings that fathers are important for offspring development and survival in this population. However, the development of paternal care does not appear to be transmitted from fathers to sons

(i.e. good fathers do not necessarily produce sons that are better fathers). This, together with the inability of females to distinguish between better and poor quality fathers, suggests that the level of paternal care is not as important as its mere occurrence, so that any paternal care would be beneficial to offspring.

## DEDICATION

For my family whose patience and understanding have been inexhaustible

“The great tragedy of Science: the slaying of a beautiful hypothesis by an  
ugly fact.”

*Biogenesis and Abiogenesis* – Thomas Henry Huxley

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## CHAPTER ONE

### Introduction

#### Maternal care

Maternal care in mammals is vital for offspring survival (Ziegler et al. 2004) as the early nutritional requirements of the young are obtained from the mother (i.e. through her milk). The mother may also influence offspring survival in other ways. For example, small rodent pups, such as in prairie voles *Microtus ochrogaster*, require exogenous heat for thermoregulation (Wang & Novak 1994), while maternal care in larger species, such as sheep *Ovis* sp., promotes mother-offspring bonding (Grandinson 2005).

During the early postnatal period, mammalian mothers can influence offspring behavioural development through the quality and quantity of care they provide (Fleming et al. 2002). For example, impaired maternal care leads to increased neophobia and decreased exploratory behaviour in young laboratory mice *Mus musculus* (Curley et al. 2008), while maternal abuse (e.g. high rejection rates and contact-breaking behaviour) of young by rhesus macaque *Macaca mulatta* mothers results in delayed independence and increased anxiety in offspring (McCormack et al. 2006). In addition, mothers may also influence offspring cognitive development. Liu et al. (2000) demonstrated that young rats *Rattus norvegicus* that receive high levels of maternal care (licking and grooming) during infancy show enhanced spatial learning and memory ability compared to rats that receive low levels of maternal care, indicating that maternal care influences development of the hippocampus. Variations in maternal care behaviour also influence the development of the hypothalamic-pituitary-adrenocortical (HPA) system, which affects, for example, behavioural fearfulness in novel environments and later responsiveness to offspring (Macrí et al. 2004). For example, female Long-Evans hooded rats that receive high levels of maternal care when young show lower levels of plasma adrenocorticotrophic hormone and corticosterone (Liu et al. 1997) and higher levels of maternal care when they reach adulthood (Francis et al. 1999).

Mammalian mothers, through provision of maternal care, may also shape the development and later expression of maternal care behaviour in their daughters. Francis et al. (1999) found that female Long-Evans hooded rats showed higher levels of licking and grooming of their offspring if they received high levels of licking and grooming from their own mothers. In addition, Kikusui et al. (2005) found a negative influence of early weaning on later maternal care behaviour in female mice (Balb/cA strain). Since mothers have the ability to influence various aspects of the physical, behavioural and cognitive development of their offspring, it is not surprising that many studies have focused on the importance of maternal care on the development of young.

### **Paternal care**

Paternal care, defined as any direct or indirect nongametic investment made by the father post-fertilization that benefits his offspring (Dewsbury 1985; Woodroffe & Vincent 1994), is uncommon in mammals, occurring in only 5-10% of species (Wright 2006). Direct paternal care includes those behaviours performed in the presence of young that directly influence offspring survival, growth and/or development, such as huddling, grooming, retrieving and carrying, food provisioning, predator defence, babysitting and socializing (Malcolm 1985). For example, male California mice *Peromyscus californicus* (Dudley 1974; Gubernick & Teferi 2000) and male Djungarian hamsters *Phodopus campbelli* (Wynne-Edwards 1995) enhance offspring survival primarily through huddling of young. Indirect paternal care, in contrast, includes those behaviours performed in the absence of young that indirectly influence offspring survival, growth and/or development, such as den construction, alarm calling, caring for females and territory maintenance (Malcolm 1985). For example, male rock-haunting possums *Petropseudes dahli* display tail beating, a type of alarm signal, which serves to warn young of approaching predators (Runcie 2000).

Paternal care has only been demonstrated in six mammalian orders (Carnivora, Cetacea, Diprotodontia, Lagomorpha, Primates and Rodentia), with the majority of studies focusing on carnivores (e.g. bat-eared foxes *Otocyon megalotis*, Wright 2006), primates (e.g. common marmosets *Callithrix jacchus*, Schradin et al. 2003; humans *Homo sapiens*, Quinlan 2003) and rodents (e.g. California mice, Gubernick & Teferi 2000).

### **The evolution and importance of paternal care**

A male mammal's lifetime reproductive success is mainly determined by the number of matings achieved and not by the number of offspring he helps raise, since males are unable to provide direct care during the prenatal period (Orians 1969; Queller 1997). However, the occurrence of paternal care in some mammals suggests that this behaviour has evolved because the benefits of providing care outweigh the costs associated with lost mating opportunities (Gubernick & Teferi 2000).

Smuts & Gubernick (1992) proposed the "male care hypothesis" to explain the evolution of paternal care. This hypothesis predicts that males should provide care when: 1) males can exchange paternal care for future reproductive opportunities if certainty of paternity is low; 2) the certainty of paternity is high; and 3) the development, growth and survival of young is enhanced by the provision of care. Furthermore, paternal care may also have evolved because males are constrained ecologically and/or socially from securing additional mating opportunities ("mating constraints hypothesis", Orians 1969; Queller 1997). It is important to realise that these hypotheses (discussed below) are not necessarily mutually exclusive.

When certainty of paternity is low, there should be selection for males not to invest in young that are potentially unrelated to them (Møller & Cuervo 2000). Provision of care requires a high level of energy expenditure, which could have an impact on the physical condition of a male, thereby influencing his probability of breeding in the following season (Houston et al. 2005). However, by remaining with the resident female and investing in her current young, males may develop a bond with the female and ensure future reproductive opportunities, as seen in newly formed owl monkeys *Aotus azarai* pairs (Fernandez-Duque et al. 2008). After pair bonding, certainty of paternity increases and investment in current young may offset the costs associated with decreased body condition through enhanced offspring survival and/or growth (e.g. *A. nancymae* and *A. azarai*, Wolovich et al. 2008).

Paternal care is most likely to evolve when offspring survival is enhanced by the provision of male care (Woodroffe & Vincent 1994). Young rodent pups are unable to thermoregulate and require exogenous heat (through huddling) to ensure better growth and metabolism (Wang & Novak 1994). Provision of care by males during low temperatures may therefore reduce heat loss from young, thereby enhancing their

survival and growth, as seen in meadow voles *Microtus pennsylvanicus* (Parker & Lee 2002), Djungarian hamsters (Wynne-Edwards 1995) and California mice (Dudley 1974; Gubernick & Teferi 2000). Young mammals are also dependent on their mother's milk for a period of time after birth, which places large energetic demands on the female (Gittleman & Thompson 1988; Roulin 2002). Males may reduce the workload of the female by providing care, allowing the female more time to engage in other activities, such as foraging, as seen in European ground squirrels *Spermophilus citellus* (Huber et al. 2002).

Paternal care may evolve when males are constrained from securing additional mating opportunities (Orians 1969; Queller 1997). Social conditions, such as population density, may regulate mating behaviour, influencing whether males remain with females or desert them. For example, under high population density, male hoary marmots *Marmota caligata* maximise their reproductive success by adopting a roaming strategy and visiting many females (Barash 1975). However, under low population density, males may associate with only one female, decreasing the need for mate guarding, due to reduced male-male competition. This frees males to increase their level of paternal investment in offspring (Barash 1975).

Male mammals influence offspring survival in many ways. For example, male California mice huddle young (Gubernick & Teferi 2000), while male bat-eared foxes increase offspring survival by remaining at the den while the female is away foraging (Wright 2006). Male mammals also influence offspring behavioural development; for example, young southern grasshopper mice *Onychomys torridus* females are more active and males more aggressive when raised by both parents, compared to young raised by mothers alone (McCarty & Southwick 1977). The importance of paternal care on offspring cognitive development has also been identified. In trumpet-tailed rats *Octodon degus*, lack of paternal care influences synaptic development in the anterior cingulate cortex (Otscharoff et al. 2006), an area of the brain involved with problem-solving and error recognition, by reducing the density of synaptic shaft synapses (Allman et al. 2001). The influence of this reduction on behaviour, however, remains to be shown. In contrast, spatial learning does not appear to be influenced by paternal care in California mice, suggesting that paternal care, at least under laboratory conditions, may not necessarily influence development of the hippocampus (Bredy et al. 2004).

### **The development of paternal care**

Few studies have investigated the role fathers play in the development and transmission of paternal care behaviour in their sons. Bester-Meredith & Marler (2003) have provided some evidence that reductions in the level of paternal care behaviour by California mouse fathers can influence the subsequent development of paternal care behaviour in sons, possibly because a lack of paternal care influences the expression of vasopressin in the bed nucleus of the stria terminalis (BNST) (Bester-Meredith & Marler 2003). However, their study used a cross-fostering paradigm, in which young were raised by the less paternal white-footed mice *Peromyscus leucopus* (Bester-Meredith & Marler 2003), which could have introduced other confounding effects into the study. Vasopressin is secreted in the hippocampus, an area known to be influenced by acute stress in male rats (Conrad et al. 2004). Although Bester-Meredith & Marler (2003) found increased vasopressin expression in the BNST in California mice experiencing high levels of paternal care, Bredy et al. (2004) found no apparent influence of paternal care on the development of the hippocampus. Therefore, it is possible that the results obtained by Bester-Meredith & Marler (2003) were influenced by factors other than paternal care, such as stress. It is imperative that more studies investigate if, and how, paternal care is transmitted from fathers to sons and it is important to consider the mechanisms underpinning the transmission of behaviour.

The development of behaviour is influenced by both genetic and non-genetic (e.g. learning, Cushing & Kramer 2005) factors, although the expression of a behaviour may be influenced more strongly by either environment or genetic components. For example, MacColl & Hatchwell (2003) found that offspring feeding rate in long-tailed tits *Aegithalos caudatus*, a measure of paternal investment, is not strongly influenced by environmental effects but has a significant heritable component, whereas paternal state in meadow voles, a species that rarely shows paternal care, is strongly regulated by environmental cues (Parker & Lee 2001). Unfortunately, researchers in this field have tended to focus solely on either genetic or non-genetic (environmental) influences when examining the development of paternal care. For example, Bester-Meredith & Marler (2003) focused on the influence of the environment in shaping young California mouse behaviour, while Freeman-Gallant & Rothstein (1999), working with savannah sparrows *Passerculus sandwichensis*, found male feeding rate



to be under apparent genetic control. A small number of studies have investigated how paternal care in rodents is non-genetically influenced (e.g. Bester-Meredith & Marler 2003), but I am unaware of any studies that have investigated genetic influences on paternal care. It is therefore important to investigate further those factors underlying the development of paternal care in rodents.

## Study species

### *Description*

The striped mouse *Rhabdomys pumilio* is a small ( $\pm 40$  g) diurnal rodent belonging to the family Muridae (de Graaff 1981). It is characterised by four dark stripes on the dorsal surface running from the back of the neck to the base of the tail (Skinner & Chimimba 2005). Pelage colour, body mass and tail length can vary between geographical areas (Coetzee 1970). There is no distinct dimorphism between the sexes in terms of body size or mass (Skinner & Chimimba 2005).

The striped mouse has a widespread, although discontinuous (Brooks 1982), distribution, occurring throughout southern Africa and parts of east Africa (Skinner & Chimimba 2005). It occupies a variety of habitat types in southern Africa, from the dry semi-desert of the succulent karoo in the Northern Cape to the moist grasslands of KwaZulu-Natal. It favours areas with good vegetation cover, particularly grass (Skinner & Chimimba 2005), but uses other vegetation types when these are present (e.g. in the succulent karoo, striped mice nest in *Zygophyllum retrofractum* bushes, which is the predominant vegetation type; Schradin & Pillay 2004a).

Striped mice are opportunistic omnivores and the diet varies both seasonally and geographically, with striped mice in scrub habitat types, such as the Fish River Valley (Eastern Cape, South Africa), feeding predominantly on *Acacia* pods, snails, worms, eggs, roots and fibres (Perrin 1980a), while striped mice in semi-arid habitat types, such as the succulent karoo (Northern Cape, South Africa) feed primarily on succulents (e.g. *Zygophyllum retrofractum*) and *Acacia* tree seeds (Schradin & Pillay 2004a).

In the grassland regions of South Africa, the striped mouse is solitary (Brooks 1974). Females raise young alone and males only associate with females for mating. In the arid succulent karoo, striped mice are group-living (Schradin & Pillay 2004a).

Groups consist of 3-4 communally breeding females, 1-2 breeding males and their overwintering sexually mature philopatric young, which forgo reproduction until the next breeding season and remain at the nest, helping to raise their siblings in the subsequent litter (Schradin & Pillay 2004a). Striped mouse males in the succulent karoo show a flexible mating strategy (Schradin 2008): 1) Newly mature philopatric males remain in the natal nest and help their parents raise the next litter. 2) Under periods of low population density, males older than one year become solitary roamers, seeking mating opportunities and providing no care. 3) Under periods of high population density, males older than one year become group-living breeders and provide paternal care.

Striped mice are seasonal breeders, producing five pups per litter on average during spring (Perrin 1980b; Willan & Meester 1989), following a gestation period of approximately 25 days (Brooks 1982), and females show a post-partum oestrous. Under optimal conditions in captivity, striped mice can produce as many as 12 offspring (personal observation). The young are altricial and are born naked (Brooks 1982). Young are completely mobile by 8 days of age (personal observation) but are unable to fully regulate their body temperature until at least day 10 (Couture 1980). They will start eating solid food from this time (Pillay 2000). Offspring are weaned at 16 days and sexual maturity is usually attained by two months of age (Brooks 1982).

### ***Phylogeny and taxonomy.***

There are two karyotypic forms ( $2n = 46$  and  $2n = 48$ ) of *Rhabdomys* in southern Africa (Ducroz et al. 1999). Rambau et al. (2003) conducted a phylogenetic analysis of the mtDNA of *Rhabdomys pumilio* and reported two main clades: one from the dry, western parts of southern Africa and the other from the moist, eastern and northern parts of the subregion. They proposed the existence of two species, namely *Rhabdomys pumilio* representing the western form, occurring in semi-desert to desert areas, and *Rhabdomys dilectus* representing the eastern form, occurring in grasslands (Rambau et al. 2003). They found that striped mice from the semi-desert/desert areas are basal to these lineages, indicating a more ancestral origin to striped mice from the eastern grassland regions. They further divided the eastern form into two subspecies, *R. d. dilectus* ( $2n = 46$ ) and *R. d. chakae* ( $2n = 48$ ), based on chromosomal and mtDNA data. Despite these pronouncements about the taxonomy of *Rhabdomys*, the findings are not conclusive due to limited sample sizes and the occurrence of shared

lineages (Rambau et al. 2003). Due to these uncertainties regarding the phylogenetic relationships among populations, I treat the genus as monotypic and will consider all populations as *Rhabdomys pumilio* in this study.

### ***Paternal care***

Although paternal care in captive striped mice was first reported by Choate (1972), the first experimental study to describe paternal care in striped mice was conducted by Schradin & Pillay (2003). They studied two populations – one from the succulent karoo and the other from a grassland locality – in captivity. Both populations displayed paternal care in captivity, but only the succulent karoo population showed paternal care in nature. During paternal care, males showed all the behavioural characteristics of females (e.g. huddling and grooming pups), apart from lactation (Schradin & Pillay 2003). The striped mouse from the succulent karoo is currently the only African murid known to show paternal care in nature and, therefore, offers a unique opportunity for investigating the role of the father in the development and transmission of paternal care in their sons. Paternal care in this population could be a male mating strategy, since males provide care to improve the development and survival of their own offspring, thereby increasing the males' own reproductive fitness (Schradin 2008). Winter and early spring night time temperatures in the succulent karoo can fall below 0 °C and direct paternal care by males in the form of huddling is known to significantly enhance offspring development under these conditions (Schradin & Pillay 2005a). Pups from the succulent karoo were found to grow faster when fathers were present than when fathers were absent (Schradin & Pillay 2005a). These results were compared to striped mice from a grassland population, in which pups grew at similar rates regardless of whether the father was present or absent. This suggests that low night time temperatures in the succulent karoo may have selected for paternal care in this population (Schradin & Pillay 2005a). Schradin & Pillay (2004a) also demonstrated that striped mice from the succulent karoo live in territorial groups characterised by the presence of young philopatric helpers.

The hormone prolactin is associated with both maternal (Wynne-Edwards & Timonin 2007) and paternal care behaviour (Gubernick & Nelson 1989) in rodents. Prolactin promotes “pup-contact-induced” paternal care behaviours (Sakaguchi et al. 1996) and is considered to be the “hormone of paternity” (Schradin & Anzenberger

1999). Prolactin has also been associated with paternal care in desert striped mouse males. Unlike other mammals species, such as common marmosets (Schradin & Anzenberger 2004), male striped mice do not show fluctuating levels of prolactin coinciding with the presence or absence of pups, but rather exhibit an “all or none” response, with experienced males showing consistently high levels of prolactin (and consequently high levels of paternal care, Schradin 2008) and inexperienced males showing low prolactin levels (Schradin & Pillay 2004b). This could be the result of the short life span (i.e. 1-2 years) and short breeding period (i.e. three months) of striped mice in the succulent karoo (Schradin & Pillay 2004a).

Levels of prolactin also vary with the male mating strategies (see above) of striped mice (Schradin & Pillay 2005b; Schradin 2008). Prolactin levels are predictably lower in roaming males, whereas group living, dominant, paternal males have higher prolactin levels (Schradin 2008). Breeding males never revert to a roaming strategy (Schradin et al. in press), suggesting that prolactin may regulate differences in paternal care and thus could be a mechanism driving male reproductive strategies in this population of striped mice (Schradin 2008). For photographs of desert striped mice and the study area, visit [www.stripedmouse.com](http://www.stripedmouse.com).

### **Motivation for the study**

Mammalian fathers, like mammalian mothers, have the ability to influence the survival, growth and development of their offspring (e.g. Gubernick et al. 1993). In addition, fathers may play an important role in shaping the behaviour of their offspring (e.g. Bester-Meredith & Marler 2003). However, it is apparent that little is known about the role mammalian fathers play in shaping the development of behaviour in their offspring generally, and the development of paternal care behaviour in their sons particularly. In addition, because of the rarity of paternal care behaviour in mammals, more information is needed to determine its importance in shaping developmental trajectories, survival and reproductive success of offspring.

I studied paternal care in a captive population of striped mice, derived from the succulent karoo (hereafter termed “desert” striped mice) from August 2005 to August 2007. I chose this population because these striped mice display paternal care under both natural and captive conditions, and the relevance of the behaviour in a broader, behavioural and ecological context would be apparent in this population but not in

grassland population which only show paternal care in captivity. The objectives of this study were to investigate: 1) the development and transmission of paternal care in male striped mice; and 2) the function of paternal care in striped mice. This resulted in two broad aims. The first aim was to investigate how genetic and non-genetic factors influence the development and transmission of paternal care. Since behaviour is influenced by both genetic and non-genetic factors, both components should be investigated in studies of behavioural transmission. My study, therefore, has been designed to tease apart the direct (non-genetic) from the indirect (genetic) influences of the father on the development and expression of paternal care in his sons. The second aim was to investigate the role of paternal care in other aspects of behaviour, such as learning and female mate choice.

The study was divided into two sections. In the first section, I focused on the ontogeny of paternal care (Chapters 2-5). Initially, I investigated whether paternal care in desert striped mice is mainly a genetically acquired behaviour or is mainly influenced by the early experience of associating with the father (Chapter 2). From this, it became apparent that mothers play an important role in shaping the expression of paternal care behaviour in their sons. Therefore, I decided to investigate whether this same pattern also exists between mothers and daughters (Chapter 3). I then investigated whether parental care (i.e. both paternal and maternal care) has a heritable component and whether this behaviour (if genetic) is transmitted matrilineally or patrilineally (Chapter 4). In addition, as desert striped mice are characterised by helpers at the nest (fathers, sisters (i.e. aunts) and philopatric young) (Schradin & Pillay 2004a), I investigated whether any care-giver (i.e. older sibling from a previous litter), could influence the development of paternal care in young males (Chapter 5).

In the second section, I focused on the function of paternal care (Chapters 6-7). Desert striped mouse fathers influence offspring survival and development (Schradin & Pillay 2005a), and they may also provide learning opportunities for their young. In Chapter 6, I used striped mice from two different populations (succulent karoo and grassland) to investigate how fathers influence the responses of young mice to novel foods. In the final experimental chapter (Chapter 7), I investigated whether desert striped mouse females prefer mates based on the paternal quality of males because mating with good fathers (i.e. mates that provide high levels of paternal care to young) should potentially ensure that genes for good quality parenting are transmitted

to the next generation, and/or better paternal care would improve offspring growth and development.

### Arrangement of the thesis

This thesis consists of the introductory chapter (Chapter 1), six experimental chapters (Chapters 2-7) comprising the main body of the thesis and a general discussion chapter (Chapter 8). The experimental chapters are written as manuscripts for publication, with Chapter 6 (Social transmission of information about novel food in two populations of the African striped mouse, *Rhabdomys pumilio*) having already been published in the journal *Animal Behaviour* (Vol. 76, pp. 1297-1304). Because of the format of this publication, which includes an abstract, background information, methods section and separate reference list, the other chapters in this thesis have been formatted in the same manner. The tables and figures are numbered sequentially for each chapter and the pages of this thesis are numbered in sequence. A separate reference list is provided for each chapter and thus there may be repetition of references between chapters.

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## CHAPTER TWO

### **Mothers, not fathers, influence the development of paternal care in African striped mice *Rhabdomys pumilio***

#### ABSTRACT

The mode of transmission (genetic and non-genetic) of paternal care behaviour between generations is poorly documented. I investigated the transmission of paternal care behaviour in African striped mice *Rhabdomys pumilio*, from the succulent karoo, in which males display high levels of paternal care. Adults and unweaned young were assigned to one of three treatments in captivity: 1) both parents raised young together; 2) the mother raised young alone; and 3) the parents were physically separated by a barrier and the mother raised young alone. I studied paternal care behaviour in sons (at sexual maturity) from all treatments. If paternal care is mainly influenced by social factors (i.e. is transmitted non-genetically), I expected that the expression of paternal care in sons would be positively influenced by the presence of the father. If paternal care is under strong genetic determination, I expected that the presence/absence of the father would not influence the development of paternal care in their sons. My data showed that sons raised by mothers alone displayed the greatest levels of care, sons raised by both parents showed the lowest levels of care and sons physically separated from their fathers showed intermediate levels of care. My results do not provide evidence for or against the genetic or non-genetic transmission of paternal care from fathers to sons. Instead, mothers increased maternal care for their offspring when fathers were absent (treatments 2 and 3), which significantly and positively correlated with paternal care behaviour displayed by their sons. I suggest that the non-genetic transmission of information by mothers, possibly as a consequence of increased suckling, is important for the ontogeny of paternal care in their sons.

*Keywords:* African striped mouse, behavioural transmission, maternal care, ontogeny, paternal care, *Rhabdomys pumilio*

## INTRODUCTION

Paternal care is uncommon in mammals, occurring in only 5-10% of species (Wright 2006). The rarity of this behaviour can be explained by: 1) the inability of males to provide direct care during the prenatal period, thereby providing males with an opportunity to desert their mates and seek additional mating opportunities (Gubernick & Teferi 2000); and 2) the male's lifetime reproductive success, which is mainly determined by the number of matings achieved and not by the number of offspring he helped raise (Gomendio et al. 2008).

Paternal care is predicted to occur when social conditions reduce the ability of a male to secure additional mating opportunities (Orians 1969; Queller 1997). For example, hoary marmot *Marmota caligata* males show increased paternal investment when social interactions with other males are low (i.e. males live in relative isolation from each other and therefore do not have to invest much energy in mate guarding; Barash 1975). In addition, environmental conditions, such as weather (Hayes & Robertson 1989), can influence paternal care behaviour by altering a male's response to his offspring. Male meadow voles *Microtus pennsylvanicus* exhibit significantly more paternal care behaviour during a shortened photoperiod, possibly because short day length reflects a time of limiting resource availability and decreased temperatures (Parker & Lee 2002). This could cause males to cohabit with females and offspring to minimize thermoregulatory costs. Under such conditions, paternal care may evolve as the benefits of providing care significantly increase offspring survival (Wynne-Edwards 1995) and lead to a higher male fitness than mate searching.

Active paternal care is known to influence offspring survival in some species (e.g. California mice *Peromyscus californicus*, Gubernick & Teferi 2000), thereby increasing the reproductive fitness of the father. If the benefits accrued from providing care are higher than the benefits obtained from additional mate searching, paternal care should be favoured by selection and transmitted across generations (Gomendio et al. 2008). This transmission can have both a genetic (Hunt & Simmons 2002) and a non-genetic (e.g. learning; Cushing & Kramer 2005) basis, as behaviours are the result of gene-environment interactions (Goodenough et al. 2001). While a variety of studies have investigated the non-genetic (e.g. Francis et al. 1999; Weaver et al. 2004) and genetic (Hunt & Simmons 2002) transmission of maternal care behaviour between generations, few studies have explored how paternal care behaviour can be

transmitted. Bester-Meredith & Marler (2003) demonstrated that male California mice, which are retrieved less often as pups, show lower levels of retrieval behaviour themselves as adults, suggesting that the development of paternal care behaviour may be non-genetically transmitted in this species. In contrast, Freeman-Gallant & Rothstein (1999) used offspring feeding rates in savannah sparrows *Passerculus sandwichensis* as a measure of paternal investment and found that feeding rates of fathers and sons closely corresponded, maintaining that this is indicative of genetic determination.

The African striped mouse *Rhabdomys pumilio* is a small ( $\pm 40$  g) diurnal murid rodent with a widespread distribution in southern Africa (de Graaff 1981). This species offers a unique opportunity to investigate the influence of the father on the development and transmission of paternal care behaviour in male offspring, as striped mice from the succulent karoo of South Africa (hereafter termed “desert” striped mice) show high levels of direct paternal care in both the field and captivity, displaying all the behaviours shown by females (e.g. huddling and retrieving pups) apart from lactation (Schradin & Pillay 2003). In the succulent karoo, striped mice live in groups of 3-4 adult females and 1-2 adult males (Schradin & Pillay 2004a). Offspring typically remain philopatric for a number of months because of the limited availability of suitable nesting sites, high population density and the benefits of group living, such as reduced energy expenditure due to group huddling (Schradin 2005; Scantlebury et al. 2006).

Male desert striped mice typically show a nearly three-fold increase in time spent in the natal nest when pups are present (Schradin & Pillay 2003) and offspring development is faster when the father is present (Schradin & Pillay 2005). What is not clear is whether a male must experience direct care from his own father in order to display appropriate levels of paternal care to his own offspring. Therefore, the aim of this study was to determine whether paternal care in desert striped mice is mainly influenced by the early experience of paternal care. To test this, I studied paternal care behaviour in desert striped mice in captivity, using males raised under three treatments: 1) by both parents; 2) by the mother only; or 3) by the mother physically separated from the father. I predicted that, if paternal care is mainly influenced by the early experience of paternal care (non-genetic transmission), sons raised by their mothers only would show lower levels of paternal care behaviour than sons raised by both parents. Alternatively, if paternal care is merely an instinctive response to the

presence of young, neither the presence nor the absence of fathers would influence the level of paternal care behaviour displayed by their sons. The treatment in which the parents were physically separated and the offspring were raised by the mother only was designed to test whether the mere presence of the father, even though he could not directly interact with his offspring, influences the expression of paternal care behaviour in his sons.

## METHODS

Striped mice used in this study were F1–F4 generation individuals derived from Goegap Nature Reserve in the succulent karoo (Northern Cape Province, South Africa; 29.40 S, 17.53 E). All individuals were captive born and were at least 3 months old at the time of testing. Captivity does not appear to influence parental care behaviour (Schradin & Pillay 2003). They were housed in the Milner Park Animal Unit at the University of the Witwatersrand, under partially controlled environmental conditions (14:10 h light: dark regime, lights on at 0500 hours; 20–24 °C; 30–60% relative humidity).

Fifteen breeding pairs were established and housed in glass tanks (46 x 30 cm and 32 cm high). The floor of the tanks was covered with a layer of wood shavings for bedding. A plastic nest box (13 x 9 cm and 10 cm high) was provided. Nesting material comprised a handful of dry grass provided weekly and approximately 5 g of paper towel provided twice weekly. One cardboard toilet roll/paper cup was provided weekly per mouse for behavioural enrichment. Subjects had access to water *ad libitum* and each mouse was fed approximately 5 g of mixed seed (sunflower, millet, oats, linseed, horse cubes) and approximately 10 g of fresh fruit or vegetables daily. The seed was sprinkled throughout the cage to stimulate foraging behaviour (C. Schradin, pers. comm.).

The intention in this study was to obtain three consecutive litters per breeding pair and randomly assign each litter to one of three different treatments (see below). Nine pairs produced the required three litters, three pairs each produced two litters and three pairs each produced one litter only. Data from an additional seven pairs (two pairs produced two litters each and five pairs produced one litter each) were used to achieve the required sample size.



Experiments involved two phases. In Phase 1, breeding pairs were subjected to three treatments in random sequence: 1) Mother + father (M+F) – both parents raised the young together until weaning at 21 days of age; 2) Mother alone (M-F) - the father was removed from the mother a few days prior to parturition and housed in a separate opaque holding cage (42 x 26 cm and 14 cm high) in a separate room. Thus, males had no contact with the female and the offspring post-partum; 3) Mother + father separated (M/F) – the father was separated from the mother and offspring a few days prior to parturition by inserting a wire mesh barrier (30 x 32 cm, 1 x 1 cm squares) into the breeding tank and placing the female with young, and the male on opposite sides. The father had visual, olfactory and auditory contact with the female and offspring, but no physical contact. At weaning, offspring from all three treatments were housed individually or in same-sex sibling pairs in opaque holding cages under the conditions described above.

The maternal care behaviour of mothers in all breeding treatments and the paternal care behaviour of fathers in the M+F treatment was video recorded for 15 min every second day, starting on DAY 1 (DAY 0 = day of birth) until DAY 11. These data were used to assess the contribution of parental care of the mother only or both parents to the development of paternal care behaviour in sons. Recordings were made until DAY 11 since young striped mice start eating solid food at this time (Pillay 2000), are often outside the nest and paternal care decreases after this time. Recordings were made between 0700 and 1100, coinciding with the peak activity period of striped mice. No observers were present in the room during taping sessions. Using continuous sampling, I scored the behaviour of test subjects for the 15 min taping session and summed the time spent in paternal care for the six days of taping. Paternal care was scored using the following behaviours (after Schradin & Pillay 2003): huddling and licking pups and time spent in close proximity (< 2 cm of pups). However, for maternal care, I could not distinguish between nursing and huddling pups, so the data were grouped and collectively classified as huddling (as described by Schubert et al. in press).

In Phase 2, at sexual maturity (approximately 90 days of age), one male (son) from each litter per treatment was randomly selected and paired with an unrelated female (obtained from the breeding colony) of approximately the same age, resulting in three treatments: SM+F, SM-F and SM/F (son from M+F, M-F and M/F, respectively). Pairs were housed in opaque holding cages and kept under the same

husbandry conditions as described above. A few days prior to parturition, pairs were transferred into glass tanks and males and females were housed together until offspring were weaned (i.e. as described for M+F). The paternal care behaviour of males from all three treatments (SM+F, SM-F, SM/F) was recorded as for Phase 1 males (see above).

A retrieval test was conducted for males in Phase 2. For this, nine litters per treatment were studied when pups were three days old. In the retrieval tests, both parents were removed from the breeding tank and four pups from the litter were randomly selected and placed as far away from the nest box as possible; in litters comprising less than four pups, all pups in the litter were used in tests. In litters of more than four pups, those pups not used in tests were housed with their mother in a holding cage in a separate room for the duration of the test.

The father was returned to the breeding tank and placed directly into the nest box. The tank was videotaped for 10 min (no observers were present in the room) and the latency to retrieve offspring to the nest was recorded in seconds. A retrieval score was allocated for the number of pups retrieved: 0 = no pups retrieved; 1 = 1 pup retrieved; 2 = 2 pups retrieved, and so on. In four cases, litter size was less than 4 pups (2 pups in 2 litters; 3 pups in 2 litters). The retrieval score was thus adjusted based on the number of pups used. For example, if both pups were retrieved (in 2 litter pups) the equivalent score was 4. Once the session ended, the female and remaining offspring were placed back into the breeding tank. All pups were retrieved either by the mother or father within five minutes of returning the mother to the breeding tank. Males, females and pups (whether or not they were used in tests) did not experience any obvious ill effects.

I also determined the growth rate of pups in litters produced in Phase 2. For this, litter mass was recorded to the nearest 0.1 g every day after birth for the first seven days, and every three days thereafter until weaning. These values were then used to calculate growth rates for litters between DAY 1 and DAY 21 (at weaning). Growth rates were calculated using the formula:  $(\text{LN mass DAY 21} - \text{LN mass DAY 1})/20$  days.

### **Statistical Analysis**

For all analyses I used Statistica 7.1 (Statsoft Inc, [www.statsoft.com](http://www.statsoft.com)). All parental care data met the assumptions of normality (Shapiro–Wilk’s test) and homogeneity of

variances (Levene's test), but the datasets for growth rate and retrieval tests had to be square root transformed prior to analyses. Maternal care behaviour, paternal care behaviour and growth rate were analysed with mixed models, using the general linear model (GLM) module. In all analyses, treatment and litter order (i.e. the first to third litter produced by a pair, to account for their previous breeding experience) were entered as fixed categorical predictors. Breeding pair identity was included as a random effect since not all pairs produced three litters in Phase 1 and I used one or two litters each from some other breeding pairs to achieve the required sample size. Litter size was included as a continuous predictor (covariate) in the analyses. Maternal care behaviour was also included as a covariate for analysis of their sons' paternal care behaviour. Similarly, mixed models were used in the analysis of retrieval behaviour (latency to retrieve and retrieval score) but I also included the number of pups tested in the retrieval tests as another covariate. Tukey honest significant difference (HSD) post hoc tests were used to identify specific differences. The model-level significance was determined at  $\alpha = 0.05$ . All tests were two-tailed. Bonferroni sequential adjustments were applied for the two retrieval behaviours ( $\alpha' = 0.025$ ). A linear regression was used to compare the parental care behaviour of mothers (Phase 1) and sons (Phase 2).

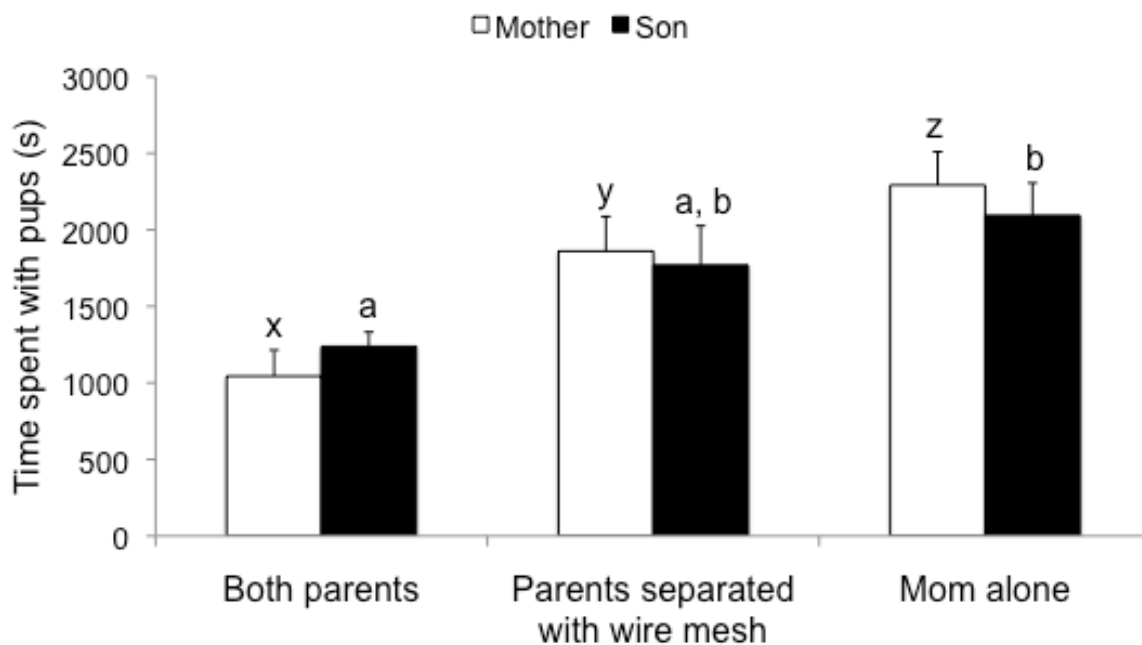
## RESULTS

### Maternal Care Behaviour (Phase 1)

Treatment ( $F_{2, 13.22} = 12.95, P < 0.001$ ) was a significant predictor of maternal care behaviour. Post hoc tests revealed a graded response, with mothers in the absence of the father (M-F) displaying more care than mothers separated from their mates with a wire mesh barrier (M/F), and females housed with their mates (M+F) showed the lowest levels of care (Fig. 1). Litter order ( $F_{3, 32.63} = 0.03, P = 0.992$ ), breeding pair identity ( $F_{31, 7.00} = 0.44, P = 0.947$ ) and litter size ( $F_{1, 7.00} = 1.26, P = 0.299$ ) did not significantly influence maternal care.

### Total Parental Care Behaviour (Phase 1)

I compared the total parental care provided by both parents in the M+F treatment and mothers in the M-F and M/F treatments. Treatment ( $F_{2, 12.46} = 3.00, P = 0.087$ ) was



**Figure 1.** Parental care displayed by desert striped mouse mothers and their adult sons. Mean + SE time spent with pups (seconds) by females in three treatments and by their sons resulting from these treatments. Tukey post hoc tests are provided separately for mothers and sons, and bars with the same letters indicate non-significant differences.

not a significant predictor of total parental care behaviour: mean ( $\pm$  SE) seconds – M+F = 2663.93 (193.97) s; M-F = 2338.25 (163.96) s; M/F = 1879.47 (185.90) s. The following variables did not influence total parental care behaviour: litter order ( $F_{3, 30.92} = 0.26, P=0.851$ ); breeding pair identity ( $F_{31, 7.00} = 0.39, P=0.969$ ); and litter size ( $F_{1, 7.00} = 0.94, P=0.365$ ).

### Paternal Care Behaviour (Phase 2)

Treatment ( $F_{2, 35.53} = 6.15, P=0.005$ ) was a significant predictor of paternal care behaviour. Post hoc tests revealed that males in the SM-F treatment showed the most care, those in the SM+F treatment showed the least care, and males in the SM/F treatment occupied an intermediate position (Fig. 1). Maternal care behaviour was a significant covariate for paternal care behaviour of their sons ( $F_{1, 6.00} = 12.37, P=0.013$ ). A linear regression revealed that there was a significant and strongly positive relationship between the parental care provided by mothers (Phase 1) and their sons (Phase 2) ( $R^2 = 0.64; F_{1, 43.00} = 9.25, P=0.004$ ). The following variables did

not affect paternal care: litter order ( $F_{3, 32.17} = 2.25, P=0.102$ ); breeding pair identity ( $F_{31, 6.00} = 1.75, P=0.249$ ); and litter size ( $F_{1, 6.00} = 1.71, P=0.239$ ).

### **Paternal Care Behaviour (Phase 1 versus Phase 2)**

Treatment ( $F_{3, 48.80} = 2.98, P=0.040$ ) was a significant predictor of paternal care behaviour. Post hoc tests revealed that males in the SM-F treatment showed the most care, those in the SM+F treatment showed the least care, and males in the SM/F treatment and fathers (M+F) occupied an intermediate position. Litter order ( $F_{3, 36.94} = 0.81, P=0.497$ ), breeding pair identity ( $F_{31, 21.00} = 1.20, P=0.051$ ) and litter size ( $F_{1, 21.00} = 0.01, P=0.908$ ) did not affect paternal care.

### **Retrieval Behaviour (Phase 2)**

The results of the retrieval tests performed by males from the three treatments are provided in Table 1. Neither of the two parameters - latency to retrieve pups and retrieval score – was influenced by the categorical predictors (treatment, litter order, breeding pair identity) nor the covariates (number of pups used in tests, litter size).

### **Offspring Growth (Phase 2)**

Treatment ( $F_{2, 17.90} = 0.09, P=0.936$ ) was not a good predictor of pup growth rate: mean ( $\pm$  SE) – SM+F = 0.079 (0.002); SM-F = 0.080 (0.003); SM/F = 0.079 (0.002). In addition, litter order ( $F_{3, 37.40} = 0.21, P=0.888$ ), breeding pair identity ( $F_{31, 7.00} = 0.74, P=0.737$ ) and litter size ( $F_{1, 7.00} = 0.17, P=0.697$ ) did not significantly influence growth rate.

## **DISCUSSION**

My results do not support the prediction that paternal care in desert striped mouse sons is positively influenced by the presence of their fathers, as sons raised by both parents (M+F) showed the lowest levels of paternal care behaviour compared to treatments in which the father was absent (M-F, M/F). In addition, my results do not indicate that the amount of paternal care behaviour shown is genetically transmitted from fathers to sons, as sons from treatments in which the father was absent (M-F, M/F) showed considerably higher than predicted levels of paternal care behaviour. If paternal care behaviour was mainly genetically transmitted, I would have expected

**Table 1.** Retrieval tests performed using desert striped mouse males from three treatments. Values are presented as mean ( $\pm$  SE). Description of the retrieval score is presented in the text.

Treatment	Latency to retrieve pups (s)	Retrieval score
SM+F	214.56 (67.82)	3.13 (0.49)
SM/F	359.18 (87.07)	2.38 (0.56)
SM-F	318.50 (100.58)	3.13 (0.49)
Statistics		
Treatment	$F_{2, 18.12} = 0.64, P=0.541$	$F_{2, 17.09} = 2.26, P=0.135$
Litter order	$F_{3, 16.00} = 0.42, P=0.742$	$F_{3, 16.00} = 0.19, P=0.904$
Breeding pair identity	$F_{16, 16.78} = 1.49, P=0.211$	$F_{16, 16.78} = 1.28, P=0.311$
Number of pups in retrieval test	$F_{1, 17.28} = 0.36, P=0.556$	$F_{1, 17.32} = 0.34, P=0.570$
Litter size	$F_{1, 18.04} = 0.63, P=0.436$	$F_{1, 18.10} = 0.85, P=0.368$

that neither the presence nor the absence of the father would have influenced the development of paternal care in their sons.

In the absence of the father, female desert striped mouse mothers doubled the time spent with young. Similarly, rock cavies *Kerodon rupestris* (Tasse 1986) increased the amount of time spent with young over 1.5 fold when males were absent. My data indicate that there was a strong, significant correlation between maternal care behaviour and later paternal care behaviour by their sons, and the absence of the father resulted in a higher level of paternal care behaviour being shown by their sons. Therefore, the mother appears to have a strong influence on the development of paternal care behaviour in her sons.

It has been suggested that decreased maternal care in the presence of a male may be the result of reduced maternal workload (McGuire 1997). However, increased sexual motivation to mate by both parents during post-partum oestrous could also disrupt maternal care (McGuire 1997). As demonstrated in my study, female desert striped mice may decrease maternal care in the presence of the male because the father reduces the maternal workload by helping raise the young (e.g. by huddling). If maternal care was disrupted due to sexual motivation, I would have expected maternal care behaviour to be lower when females were physically separated from their mates

by a barrier, as females still had visual, olfactory and auditory contact with males through the barrier. This, however, was not the case.

Paternal care behaviour can change as a result of experience. Prolactin is known to be associated with paternal care in rodents (e.g. Gubernick & Nelson 1989), including the striped mouse (Schradin & Pillay 2003; Schradin 2008). Levels of prolactin increase with experience in male desert striped mice (Schradin & Pillay 2004b); therefore I expected that all sons from all treatments would show lower levels of care and that older males in the M+F (Phase 1) treatment would show higher levels of care. This was not the case, implying that the lack of experience in sons cannot explain why sons raised by mothers alone showed higher levels of care.

The retrieval test has been used previously to assess paternal motivation to offspring in desert striped mice (Schradin & Pillay 2003). Interestingly, treatment did not influence paternal retrieval behaviour. In the succulent karoo, males will retrieve experimentally displaced pups outside their nests, regardless of their genetic relationship (Schradin & Pillay 2004a). Since small pups may crawl from the nest when disturbed, retrieval behaviour may be an instinctive response to minimize predation risk to pups (C. Schradin, pers. comm.) and is possibly under genetic control. It would thus be predictably independent of treatment effects in my study.

Schradin & Pillay (2005) have shown in free-living desert striped mice that fathers are beneficial for offspring development when spring night time temperatures are low, sometimes even below 0 °C. In contrast, I did not find any influence of paternal absence on the growth of juvenile striped mice from this population. My study was performed under controlled laboratory conditions with temperatures never below 18 °C. Brown (1993) maintained that the laboratory environment may not be appropriate for offspring to show a developmental response to increased parental provisioning because laboratory conditions are optimal for adults, thus minimizing the energetic constraints usually associated with parental care.

The results of my study are surprising in light of empirical evidence from at least one study on a rodent suggesting that early social interactions with fathers may influence the development of paternal care in their offspring (Bester-Meredith & Marler 2003). In contrast to the results of that study, the similarity of the data from the SM-F and SM/F in this study strongly suggests that the expression of paternal care in striped mice is influenced by the absence of the father and increased investment by the mother.

In many species, mothers are reliable demonstrators for young. Young chimpanzees *Pan troglodytes schweinfurthii* learn termite-fishing behaviour by observing their mothers (Lonsdorf 2006), while house mice *Mus domesticus* (Valsecchi et al. 1989) and golden hamsters *Mesocricetus auratus* (Lupfer et al. 2003) prefer the same flavoured food that their mothers have eaten. Similarly, I have shown that young striped mice (from grassland and desert localities) are more likely to learn about novel food from their mothers than their fathers, because mothers provide multiple channels (e.g. olfactory cues on the breath and gustatory cues in milk) for information transfer (Rymer et al. 2008, Chapter 6). Therefore, I suggest that females may also be reliable demonstrators of parental care for their sons, because the increased association with their mothers during the preweaning phase allows sons to access information via multiple maternal channels, such as through physical contact and suckling.

Suckling behaviour stimulates production of the hormone prolactin (Lupoli et al. 2001), which is known to be associated with both maternal (e.g. rats *Rattus norvegicus*, Bridges et al. 1985; hamsters, McCarthy et al. 1994) and paternal care behaviour in rodents (e.g. California mice, Gubernick & Nelson 1989). Increased maternal investment may result in increased circulating plasma prolactin, which can then be transferred to the milk (Pahwa & Pandey 1984; Ellis et al. 1996). Ingestion of this prolactin could result in increased circulating prolactin in sons, resulting in the development of higher levels of paternal care behaviour later in the SM-F and SM/F males.

Alternatively, the expression of higher levels of paternal care behaviour in sons raised in the absence of their fathers could be the result of a potential stress suffered by their mothers. As female desert striped mice rarely raise young alone due to the presence of philopatric helpers, sisters (i.e. aunts) and fathers, increased maternal care in the absence of a male could be a response to stress induced by raising young alone. For example, juvenile female rhesus macaques *Macaca mulatta*, which show elevated cortisol levels due to stress, also show greater interest in their infants (Maestriperi 2005). The early mother-young relationship is known to influence the development of the hypothalamic-pituitary-adrenocortical (HPA) system in offspring, which affects, for example, behavioural fearfulness in novel environments and later responsiveness to offspring (Macrí et al. 2004). Long-Evans hooded rats that receive higher levels of maternal care as pups show lower levels of plasma adrenocorticotrophic hormone and



corticosterone when they reach adulthood (Liu et al. 1997) and consequently display higher levels of maternal care behaviour (Francis et al. 1999). Taken together, the studies of rats and macaques suggest that, at least for my study, the stress incurred by female desert striped mice raising offspring alone would result in greater maternal care. This may then have lowered the level of corticosterone (i.e. lower stress) in sons, which then display greater levels of paternal care behaviour to their offspring. In addition, as corticosterone can be transferred to offspring via milk (Yeh 1984), I also expect sons to show increased stress paternal care, as in the case of macaques (Maestriperi 2005). Clearly, untangling the proximate factors influencing the development of paternal care in striped mice requires rigorous examination in future.

A female desert striped mouse, which increases maternal investment in the absence of her mate, will produce sons that display higher levels of care for her descendants (i.e. grand-offspring). The selective advantage of this maternal effect is condition-dependent, occurring in the absence of the male or possibly any other caregiver. Although females sometimes raise offspring alone (C. Schradin, pers. comm.), they often nest in groups (Schradin & Pillay 2004a) because of the benefits associated with allo-parenting (Schubert et al. in press), such as reduced thermoregulatory costs (Scantlebury et al. 2006) and improved offspring growth under challenging environmental conditions (Schradin & Pillay 2005). Therefore, it appears that the benefits of communal nesting in desert striped mice outweigh the delayed benefits of improved paternal care in sons raised by their mothers alone. In the absence of helpers however, increased maternal care may reflect a contingency strategy to allow females to trade off between current and future investment in their offspring.

While studies of parental overcompensation (i.e. when one parent increases its parental investment in an effort to overcome a loss of investment by its mate, Osorno & Székely 2004) by either females or males are relatively common in the bird literature (e.g. magnificent frigatebirds *Fregata magnificens*, Osorno & Székely 2004; rock sparrows *Petronia petronia*, Griggio & Pilastro 2007), only a few studies have investigated this type of overcompensation in mammals (e.g. female coyotes *Canis latrans*, Sacks & Neale 2001). In addition, the only study alluding to this phenomenon in rodents was conducted by Tasse (1986) in rock cavies. I thus propose an overcompensation hypothesis for biparental female rodents in which females should increase their level of maternal investment when nesting alone so as to enhance their own life time reproductive success. While the predictions about the transmission of

paternal care from fathers to sons were not supported in my study, my data show that mothers are important for the development of paternal care behaviour in their sons. Future studies in this population of striped mice should test whether daughters also show increased parental care in response to increased maternal investment by their mothers, and should also consider the proximate mechanisms of information transfer about parental care from mothers to sons and the potential fitness consequences of this transmission.

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## CHAPTER THREE

### **The development of maternal care in African striped mice *Rhabdomys pumilio* is not influenced by the mother**

#### **ABSTRACT**

Maternal care can be transmitted from mothers to daughters via genetic and non-genetic means. In a previous study (Chapter 2), paternal care behaviour in a desert population of African striped mice *Rhabdomys pumilio* was found to be influenced by the level of maternal care that sons received during early development: sons raised by their mothers alone displayed higher levels of paternal care behaviour than sons raised by both parents. The aim of the present study was to assess whether maternal care behaviour in this population is also influenced by the level of maternal care received during early development. I predicted that daughters raised by their mothers alone would show higher levels of maternal care behaviour when they reached adulthood than daughters raised by both parents. Offspring were raised under three treatments: 1) both parents raised young together; 2) mothers raised young alone; and 3) mothers and young were separated from fathers with a wire mesh barrier. At sexual maturity, the maternal care behaviour (e.g. huddling and licking pups) shown by daughters (from each treatment) was investigated. Contrary to expectations, maternal care in daughters was not influenced by rearing condition or the level of maternal care received, with daughters from all rearing conditions showing equivalently high levels of maternal care behaviour to their own offspring. I conclude that the transmission of parental care behaviour is condition-dependent in male but not female desert striped mice, since females are constrained physiologically and morphologically to care for their offspring.

*Keywords:* African striped mouse, behavioural transmission, development, maternal care, *Rhabdomys pumilio*

## INTRODUCTION

The transmission of maternal care in female rodents has both genetic and non-genetic components, although individual studies tend to report on either one or the other modes of transmission. For example, Peripato & Cheverud (2002) found that impaired maternal performance in laboratory mice *Mus musculus* of the inbred strains LG/J and SM/J has a complex genetic basis, while Kikusui et al. (2005) highlighted that early weaning of female mice (Balb/cA strain) negatively influences later maternal care behaviour (non-genetic effect).

I investigated the non-genetic transmission of maternal care from mothers to daughters in a population of African striped mice *Rhabdomys pumilio* from the succulent karoo (hereafter termed “desert striped mice”), in which males show high levels of paternal care in captivity and nature (Schradin & Pillay 2003). In a previous study, paternal care behaviour in this population of striped mice was found to be influenced by the amount of maternal care received by sons during early development: sons raised by mothers alone displayed higher levels of paternal care behaviour than sons raised by both parents (Chapter 2). These findings provide support for the influence of the non-genetic transmission of paternal care behaviour from mothers to sons. Therefore, I asked whether the level of maternal care provided by mothers also influences the expression of maternal care behaviour in their daughters.

Using the same experimental protocol described in Chapter 2, female desert striped mice raised litters: 1) together with the male; 2) alone, without male assistance; and 3) alone, but separated from the male with a wire mesh barrier, thus facilitating visual, olfactory and auditory contact, but not physical contact. Under these experimental conditions, females show higher levels of maternal care behaviour when their mates are absent (i.e. they overcompensate care in the absence of the male), which apparently improves the level of paternal care displayed by their sons (Chapter 2). Thus, I predicted that maternal care behaviour in female desert striped mice, like paternal care behaviour, would be influenced by increased maternal care received when fathers are absent and that daughters raised by mothers only would show higher levels of maternal care behaviour than daughters raised by both parents.

## METHODS

Striped mice (F1–F4 generation individuals) were derived from Goegap Nature Reserve (Northern Cape Province, South Africa; 29.40 S, 17.53 E), which is situated in the succulent karoo. They were housed in the Milner Park Animal Unit at the University of the Witwatersrand, under partially controlled environmental conditions (14:10 h light: dark regime, lights on at 0500 hours; 20–24 °C; 30–60% relative humidity).

Details of animal maintenance and husbandry are provided in Chapter 6 (Rymer et al. 2008). I used the same animals and a similar protocol to that described in Chapter 2. Briefly, 15 breeding pairs were established and each pair raised three litters. Each litter was then randomly assigned to one of three treatments: 1) Mother + father (M+F) – both parents raised young together until weaning (21 days of age); 2) Mother alone (M-F) – the male was removed from the female a few days prior to parturition and housed separately; and 3) Mother + father separated (M/F) – the male was separated from the female and young by inserting a wire mesh barrier into the breeding tank a few days prior to parturition. This allowed visual, olfactory and auditory communication between the male and the female and pups, but no physical contact. This treatment was designed to test whether the presence of the father, even without direct female interaction, influences the female's maternal care behaviour and the subsequent parental care behaviour of the developing offspring.

Litters were weaned at 21 days of age. Thereafter, a female (daughter) from each treatment was randomly selected at sexual maturity (approximately 90 days of age) and paired with an unrelated male, resulting in three treatments: DM+F, DM-F and DM/F (daughter from M+F, M-F and M/F, respectively). Each pair was maintained as for M+F. The maternal care behaviour of females in all treatments (M+F, M-F, M/F, DM+F, DM-F and DM/F) was video recorded for 15 min (between 0700 and 1100) every second day, starting on DAY 1 (DAY 0 = day of birth) until DAY 11. Using continuous sampling, I scored the behaviour of test subjects for the 15 min taping session and summed the time spent in maternal care behaviour for the six days of taping. Maternal care was scored using the following behaviours (after Schradin & Pillay 2003): huddling (includes nursing; after Schubert et al. in press), licking and time spent in close proximity (< 2 cm of pups). Maternal care behaviour shown by



daughters was then compared to that of their mothers in the M+F, M-F and M/F treatments.

### Statistical analysis

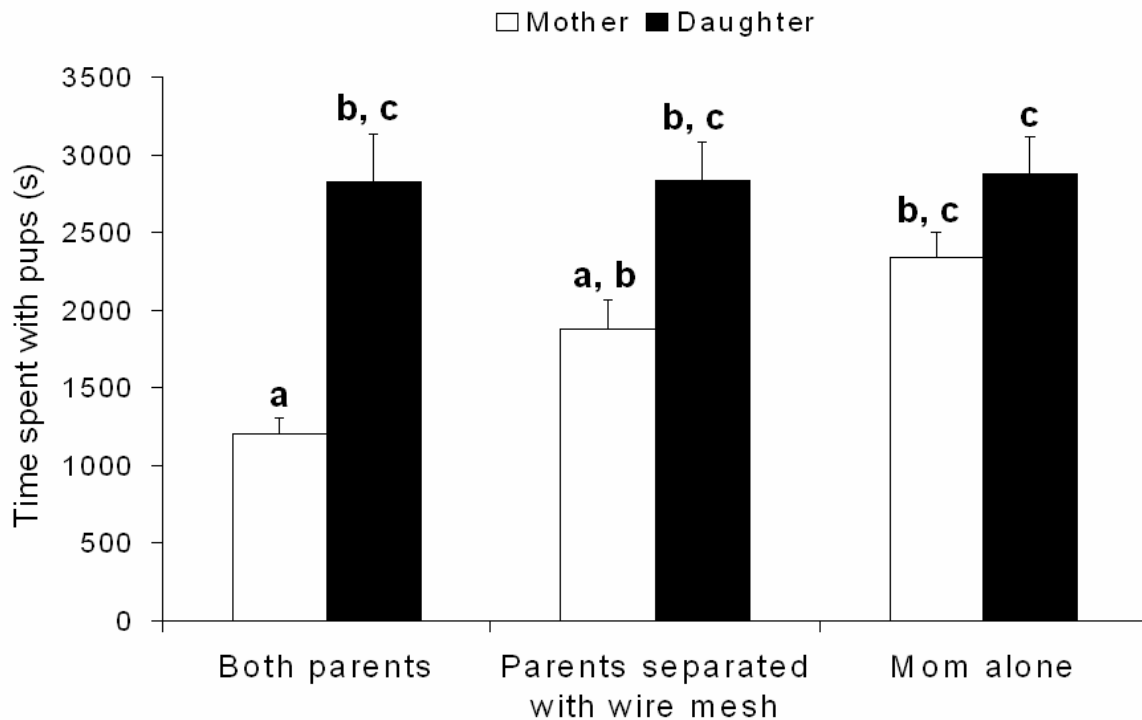
For all analyses, I used Statistica 7.1 (Statsoft Inc, [www.statsoft.com](http://www.statsoft.com)). All data met the assumptions of normality (Shapiro–Wilk’s test) and homogeneity of variance (Levene’s test). Maternal care behaviour (mothers and daughters) was analysed with a mixed model, using a general linear model (GLM) module. In all analyses, treatment and litter order (i.e. the first to third litter produced by a pair, to account for previous breeding experience) were entered as fixed categorical predictors. Breeding pair identity was included as a random effect since not all pairs produced three litters in the M+F, M-F and M/F treatments. Litter size was included as a continuous predictor (covariate). Tukey honest significant difference (HSD) post hoc tests were used to identify specific differences. The model-level significance was determined at  $\alpha = 0.05$ . All tests were two-tailed.

## RESULTS

Treatment ( $F_{5, 27.00} = 3.69, P=0.011$ ) was a significant predictor of maternal care behaviour with mothers raising young with a mate (M+F) showing the lowest levels of maternal care behaviour and daughters from mothers raising alone (DM-F) showing the highest levels of maternal care behaviour (Fig. 1). A graded response in maternal care behaviour was found in order of increasing maternal care: M+F, M/F, M-F, DM+F, DM/F and DM-F. The following variables did not affect maternal care: litter order ( $F_{3, 27.00} = 2.45, P=0.085$ ); breeding pair identity ( $F_{53, 27.00} = 1.37, P=0.188$ ); and litter size ( $F_{1, 27.00} = 0.94, P=0.340$ ).

## DISCUSSION

My results indicate that the expression of maternal care behaviour in female desert striped mice is not influenced by the amount of care received from the mother. Daughters from all treatments (DM+F, DM-F and DM/F) showed equivalently high levels of maternal care behaviour to their own offspring, regardless of the level of care they received during development. This is contrary to the findings of another study in



**Figure 1.** Maternal care displayed by desert striped mouse mothers and their adult daughters. Mean  $\pm$  SE time spent with pups (seconds) by females in three treatments and by their daughters resulting from these treatments. Bars with different letters indicate significant differences (Tukey post hoc tests)

desert striped mice, where males showed increased paternal care when they received higher levels of maternal care (Chapter 2). In the latter study, maternal care was greater when mothers raised offspring alone compared to mothers that jointly raised offspring with their mates, indicating that the absence of the father resulted in overcompensation of maternal care and concomitantly greater paternal care in their sons. A similar outcome, absence of the father and overcompensation by the mother, was not evident in the present study.

My study contrasts with other research investigating the non-genetic transmission of maternal care in rats *Rattus norvegicus* (Francis et al. 1999) and laboratory mice (Kikusui et al. 2005), which shows that higher levels of licking and grooming by mothers results in higher levels of licking and grooming in their daughters. The reasons for this difference are currently not understood. However, the expression of maternal care behaviour in desert striped mice may not be influenced during early development (i.e. phenotypically plastic) but rather females may be physiologically

and morphologically predisposed to provide care to ensure offspring survival under the harsh environmental conditions of the succulent karoo (Schradin & Pillay 2004). The very high level of maternal care in daughters suggests a possible ceiling effect and that daughters may be influenced more by the total amount of care received as opposed to the care received by either mothers or fathers. This requires investigation in the future.

Interestingly, desert striped mouse daughters did not show decreased levels of maternal care behaviour when housed with a male (DM+F), unlike that seen for their mothers (M+F). It has been suggested that, in general, females become better mothers as they gain parenting experience (e.g. reindeer *Rangifer tarandus*, Weladji et al. 2006). However, this was not the case in this study, as daughters from all treatments were naïve, yet all showed similar, or higher, levels of maternal care to their mothers. As suggested in Chapter 2 for the expression of paternal care behaviour, the expression of high levels of maternal care behaviour in daughters could be the result of a potential stress suffered by their mothers. However, this does not explain why daughters did not show a similar response to females of the M+F treatment (i.e. show decreased maternal care in the presence of her mate). Recent studies suggest that experienced, but not naïve, female desert striped mice, decrease the maternal care that they provide when helpers are present (Pillay pers. comm.). Clearly, untangling the proximate factors influencing the expression of maternal care in striped mice requires rigorous examination in future.

The results of this study demonstrate that increased maternal care by desert striped mouse mothers does not influence parental care behaviour in daughters, like it does in sons (Chapter 2). This suggests that paternal care behaviour is more behaviourally plastic than maternal care behaviour in first-time striped mouse parents. Male desert striped mice show flexibility in mating strategies (Schradin 2008), and paternal care behaviour, which is also phenotypically plastic, can be altered by the amount of maternal care received (Chapter 2). Females, on the other hand, appear to be physiologically and morphologically constrained to care for their offspring, at least when they first start reproducing.

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## CHAPTER FOUR

### **Transmission of parental care in African striped mice *Rhabdomys pumilio*: genetic influences?**

#### **ABSTRACT**

The transmission of behaviour from one generation to the next is influenced by both genetic and non-genetic components. Although evidence of non-genetic transmission of parental care exists, evidence for genetic transmission of either maternal or paternal care is meagre at best. In previous studies, paternal care behaviour, but not maternal care behaviour, in a population of African striped mice *Rhabdomys pumilio* from the succulent karoo was found to have a significant non-genetic maternal component. Sons raised in the absence of their fathers showed higher levels of paternal care behaviour compared to sons raised by both parents. This was a result of increased maternal care when fathers were absent. In contrast, daughters showed consistently high levels of maternal care to their own offspring, regardless of rearing condition. In the present study, I investigated whether there is also a genetic component influencing the transmission of parental care behaviour from parents to sons and daughters. Paternal and maternal care behaviour were documented in pairs raising litters together and was then investigated in sons and daughters derived from these litters. The transmission of parental care behaviour from fathers to sons, mothers to sons and mothers to daughters did not appear to have a strong genetic component. However, there was evidence for a strong patrilineal genetic component for parental care in daughters. The results, together with findings from previous studies, reinforce that paternal care behaviour in sons is influenced non-genetically by the mother, while maternal care behaviour in daughters is not strongly influenced non-genetically, but is rather under partial patrilineal genetic control.

*Keywords:* African striped mouse, behavioural transmission, genetics, maternal care, paternal care, *Rhabdomys pumilio*

## INTRODUCTION

The transmission of behaviour between generations may be important for the survival (Thornton 2008) and future reproductive success (Heyer et al. 2005) of individuals within a species. Behaviour is transmitted between generations via genetic and non-genetic means, although the expression of the behaviour may be influenced more strongly by either the environment, or a genetic component (Shutler et al. 2005). For example, MacColl & Hatchwell (2003) demonstrated that offspring feeding rate in long-tailed tits *Aegithalos caudatus* is not strongly influenced by environmental effects but does have a significant heritable component.

Research on the transmission of maternal care behaviour in rodents has generally focused on either genetic or non-genetic mechanisms. For example, some aspects of maternal care behaviour have a strong genetic basis (e.g. pup retrieval, Gandelman et al. 1971; nest-building behaviour, Lefebvre et al. 1998), while others have a strong non-genetic basis (licking and grooming behaviour, Francis et al. 1999; Champagne & Meaney 2007). In contrast, few studies have investigated the genetic or non-genetic transmission of paternal care behaviour between generations, even though paternal care may be as important for offspring growth and survival as maternal care (e.g. Djungarian hamsters *Phodopus campbelli*; Wynne-Edwards 1995). Bester-Meredith & Marler (2003) identified that paternal care can be non-genetically transmitted in mice of the genus *Peromyscus*, but I am unaware of any studies investigating whether paternal care behaviour has a significant genetic component in rodents.

The African striped mouse *Rhabdomys pumilio* is an appropriate model for studying the transmission of maternal as well as paternal care, as males from a desert population (succulent karoo – hereafter termed “desert” striped mice) show high levels of direct paternal care (e.g. huddling and retrieving pups) in both the field and captivity (Schradin & Pillay 2003). Previously, I found that paternal care behaviour in this population appears to be influenced by non-genetic factors (Chapter 2). Mothers increase their level of parental care behaviour when fathers are absent (i.e. they overcompensate), resulting in higher levels of paternal care in their sons. The opposite was found when mothers and fathers raised their young together. Sons raised by both parents displayed lower levels of paternal care behaviour. In contrast, daughters showed consistently high levels of care, regardless of rearing condition, suggesting

that maternal care behaviour in daughters is not influenced by non-genetic components, as was the case for their brothers.

However, as behaviour is influenced by both genetic and non-genetic factors, it is important to consider both components in studies of behavioural transmission. Chapter 2 focused on the non-genetic transmission of paternal care but did not consider genetic influences. Therefore, the aim of the present study was to investigate whether parental care behaviour (maternal and paternal) has a genetic basis in desert striped mice. To test this, I compared the paternal care behaviour of fathers and sons (when they reached adulthood) and predicted that, if paternal care has a genetic basis, the paternal care behaviour of sons will correspond significantly and positively with the behaviour of their fathers. As mothers are already known to influence the development of paternal care behaviour in their sons non-genetically, I also asked whether paternal care behaviour could have a maternal genetic basis. Further, in the absence of non-genetic influences of maternal care (Chapter 3), I investigated the genetic transmission of maternal care in daughters, and predicted that, if maternal care has a genetic basis, the expression of maternal care behaviour in daughters will correspond significantly and positively with the behaviour of the mother.

## METHODS

Desert striped mice (F1–F4 generation individuals) were derived from Goegap Nature Reserve (Northern Cape Province, South Africa; 29.40 S, 17.53 E), in the succulent karoo, and were housed in the Milner Park Animal Unit at the University of the Witwatersrand, under partially controlled environmental conditions (14:10 h light: dark regime, lights on at 0500 hours; 20–24 °C; 30–60% relative humidity).

Twenty breeding pairs were established and housed in glass tanks (46 x 30 cm and 32 cm high). Details of the husbandry and maintenance of captive populations are described elsewhere (Rymer et al. 2008, Chapter 6). Experiments involved two phases. In Phase 1, parental care behaviour of both adults was recorded (see below). In Phase 2, the parental care behaviour of sons and daughters from litters produced in Phase 1 were examined. These litters (Phase 1) were weaned at 21 days of age, and one son and one daughter from each litter was paired with an unrelated mate at sexual maturity (approximately 90 days). Parental care behaviour (by both adults) in both phases was video recorded for 15 min (between 0700 and 1100 hours) every second

day, starting on DAY 1 (DAY 0 = day of birth) until DAY 11 (young striped mice start eating solid food at this time, Pillay 2000). No observers were present in the room during taping sessions. Using continuous sampling, I scored the behaviour of test subjects for the 15 min taping session and summed the time spent in parental care for the six days of taping, for each parent separately. Parental care was scored using the following behaviours (after Schradin & Pillay 2003): huddling and licking pups and time spent in close proximity (< 2 cm of pups). For maternal care, I could not distinguish between nursing and huddling, so the data for these behaviours were collectively classified as huddling (as described by Schubert et al. in press).

### **Statistical analysis**

All analyses were performed using Statistica 7.1 (Statsoft Inc, [www.statsoft.com](http://www.statsoft.com)). The dataset met the assumptions of normality (Shapiro–Wilk’s test) and homogeneity of variances (Levene’s test) after the behavioural variables were square root transformed. Data were analysed with simple regression models, using the General Regression Model (GRM) module. For the analysis, the amount of parental care provided to offspring by either a male or female (hereafter termed “son” or “daughter” parental contribution, respectively) in Phase 2 was entered as the dependent variable. The amount of parental care provided by each of their parents (hereafter termed “father” or “mother” parental contribution, respectively) in Phase 1 was entered as the fixed categorical predictor.

When the parental contribution of sons and daughters (Phase 2) is regressed against the mid-parental contribution of their parents (Phase 1), the slope of the regression ( $\beta$ ) represents  $h^2$  (the narrow sense heritability, here defined as the proportion of phenotypic variance due to additive (heritable) genetic effects, Hoffmann & Merilä 1999). When the parental contribution of Phase 2 individuals is regressed against the parental contribution of their parents, the slope ( $2 \times \beta$ ) of the regression then equals  $h^2$  (after Falconer & Mackay 1996). As there is no general consensus of what values constitute low or high heritability (e.g. Stead et al. (2006) report heritability values between 0.5 and 0.6 as “high”, whereas Aguado et al. (2008) describe 0.52 – 0.69 narrow sense heritability values as “moderate”), the measures used here are considered relative to each other. The model-level significance was determined at  $\alpha = 0.05$ .



## RESULTS

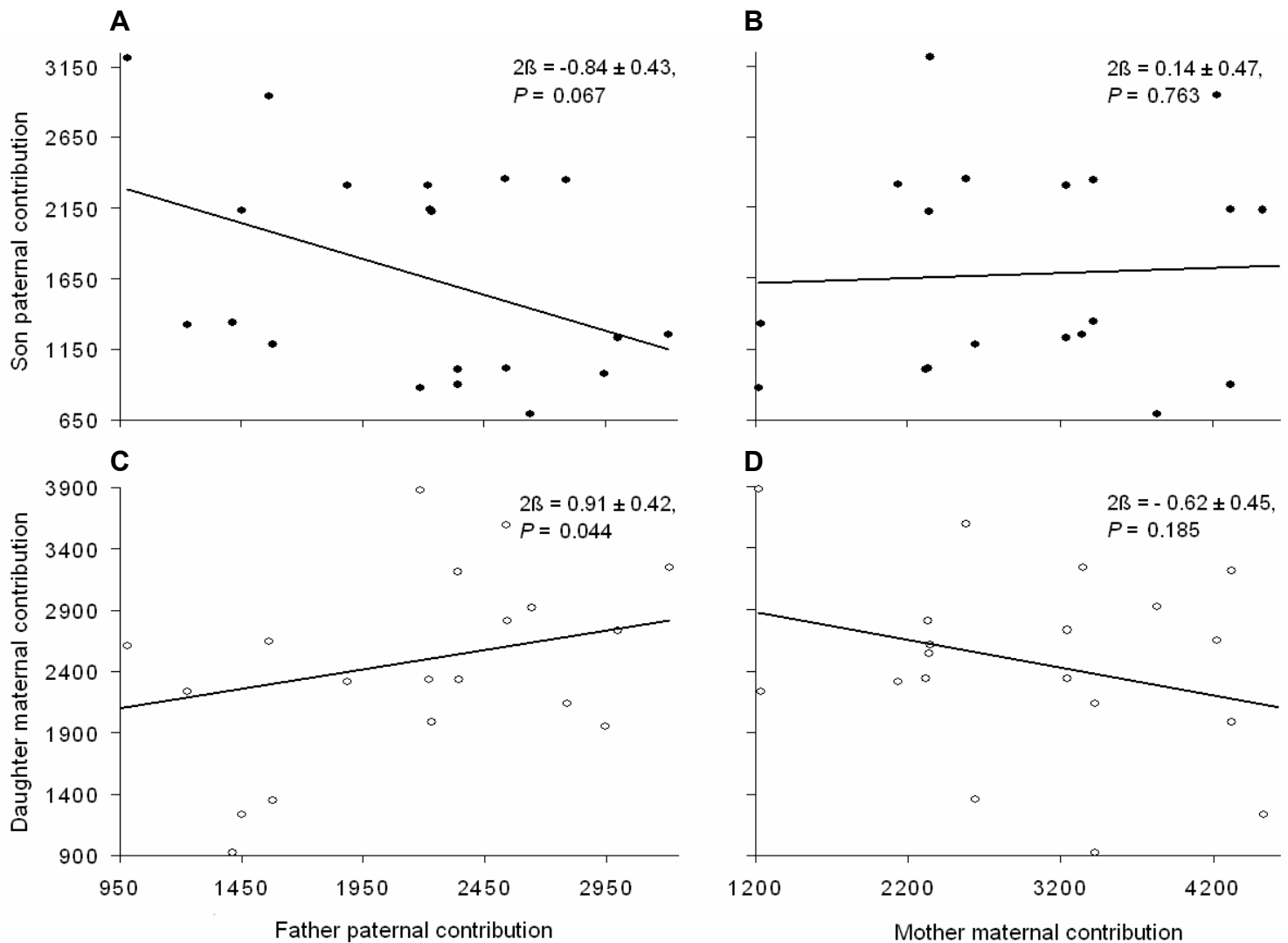
There was a strong negative correlation between the level of paternal care provided by sons (Phase 2) and the level of paternal care provided by their fathers (Phase 1), although this marginally failed to reach significance ( $2\beta = -0.84 \pm \text{SE } 0.43$ ,  $P=0.067$ ; Fig. 1A). In contrast, there was a positive, non-significant correlation between paternal contribution of sons (Phase 2) and the maternal contribution of their mothers (Phase 1) ( $2\beta = 0.14 \pm \text{SE } 0.47$ ,  $P=0.763$ ; Fig. 1B). A significant and strongly positive correlation was found when daughter parental contribution (Phase 2) was regressed against father parental contribution (Phase 2) ( $2\beta = 0.91 \pm \text{SE } 0.42$ ,  $P=0.044$ ; Fig. 1C), but there was a strongly negative (non-significant) correlation between daughters and mothers ( $2\beta = -0.62 \pm \text{SE } 0.45$ ,  $P=0.185$ ; Fig. 1D).

There was no significant correspondence between either son ( $\beta = -0.14 \pm \text{SE } 0.23$ ,  $P=0.567$ ) or daughter ( $\beta = -0.03 \pm \text{SE } 0.24$ ,  $P=0.905$ ) parental contribution when regressed against mid-parent parental contribution.

## DISCUSSION

My study provides evidence that paternal care behaviour in a desert population of striped mice is not influenced by genetic transmission from fathers to sons, as the father-son regression showed a strong negative relationship ( $2\beta = -0.84$ ). Furthermore, the results suggest a small matrilineal genetic component to paternal care behaviour. While non-zero heritability ( $2\beta = 0.14$ ) implies that there is some level of genetic influence on care-giving behaviour, non-genetic factors, such as learning could overestimate heritability (Freeman-Gallant & Rothstein 1999). In desert striped mice, there is some indication that increased maternal care, as a consequence of experimentally removing a second care-giver (i.e. the father), results in sons providing greater paternal care. This suggests that non-genetic factors influence the overall direct parental care behaviour over, at least, the first eleven days post-partum (Chapter 2). However, when sons are raised jointly by both parents, as was the case in the present study, sons provide comparatively less direct paternal care behaviour when reaching adulthood. This suggests minimal non-genetic influence on the development of overall paternal care behaviour under bi-parental conditions.

Interestingly, my results indicate that maternal care has a strong patrilineal genetic component (strongly positive daughter-father regression,  $2\beta = 0.91$ ). The heritability



**Figure 1.** Offspring-parent regressions for parental care in a desert population of striped mice. Closed circles represent sons, and open circles represent daughters. (A) Sons and fathers show a strong, marginally non-significant relationship; (B) Sons and mothers show a marginally positive relationship; (C) Daughters and fathers show a significant and strongly positive relationship; (D) Daughters and mothers show a strongly negative relationship.

may have been overestimated by paternal effects via learning, as young desert striped mice are known to learn from their fathers (Rymer et al. 2008, Chapter 6). However, absence of a similar pattern in sons supports the finding that parental care behaviour is genetically transmitted from fathers to daughters. Further study is needed to determine whether fathers also have a non-genetic influence on the expression of parental care

behaviour in their daughters, which will establish if the heritability found in this study ( $2\beta = 0.91$ ) is overestimated.

The mid-parental regression results suggest that there is no genetic component to either maternal or paternal care in desert striped mice (son  $\beta = -0.14$ , daughter  $\beta = -0.03$ ). Midparent values average the absolute values of parental care of adults (Freeman-Gallant & Rothstein 1999) and is likely to be the best estimate of effective heritability (defined as heritability on the original scale, Yazdi et al. 2002) as it takes into account the contribution made by both parents (Saxton et al. 2004). However, midparent regression assumes that the means and variances of both parents are equal (Saxton et al. 2004). In the case of mammals, the mean and variance of maternal care is always higher than that of paternal care as offspring are dependent on milk provided by mothers and females are therefore predisposed to provide care to their young. Therefore, the assumption that both parents contribute equally (equal means and variances) is not met and midparent regression is not an appropriate method for calculating heritability for this trait in mammals.

This study shows that the expression of paternal care behaviour in male desert striped mice is not under strong genetic control. However, this study showed that the expression of maternal care behaviour in daughters is strongly correlated with paternal care behaviour in their fathers, suggesting a strong genetic influence. If this is the case, I would expect females to select for good fathers (i.e. mates that provide high levels of paternal care behaviour), because of genetic advantages accrued by their daughters (i.e. displaying high levels of maternal care). Mate choice studies should be conducted to examine whether or not females can distinguish between males differing in levels of paternal care-giving ability (e.g. between good and bad fathers).

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## CHAPTER FIVE

### **The influence of a helper on the development of paternal care in African striped mice *Rhabdomys pumilio***

#### ABSTRACT

The presence of helpers in group-living species can influence the amount of parental care provided by parents to offspring, which may then influence the development of the young. I investigated the influence of a young female helper on the development of paternal care behaviour in group living African striped mice *Rhabdomys pumilio* from the succulent karoo, a desert population characterised by paternal males and philopatric helpers. Mothers raised pups with a young daughter from a previous litter. Thereafter, the paternal care behaviour was investigated in sons at sexual maturity. As a previous study showed that the sons raised by both parents displayed lower levels of paternal care than sons raised by mothers alone (Chapter 2), I expected that sons raised by mothers and helpers would also show lower levels of paternal care than sons raised by mothers alone, as helpers should share parental duties (like fathers, Chapter 2) and thus enable females to reduce their level of maternal investment. Contrary to expectations, my data showed that sons raised by mothers and helpers displayed similarly high levels of paternal care as sons raised by mothers alone, while sons raised by both parents showed the lowest levels of paternal care. My results suggest that mothers may not perceive young helpers as adequate care-givers and consequently show overcompensation of maternal care, resulting in the increased expression of paternal care in their sons.

*Keywords:* African striped mouse, helper, maternal care, parental care, paternal care, *Rhabdomys pumilio*

## INTRODUCTION

In some social mammals, females are unable to successfully raise young without the aid of conspecific helpers (e.g. marmosets *Callithrix* spp. and tamarins *Saguinus* spp., Snowdon & Cronin 2007). These helpers are usually relatives of the breeding adults (Clutton-Brock 2002), being offspring from a previous litter (e.g. cottontop tamarins *Saguinus oedipus oedipus*, Ginther et al. 2001) or siblings which have been reproductively suppressed (e.g. house mice *Mus domesticus*, König 1993); however some studies have documented allo-parental care by non-kin (e.g. superb fairy-wrens *Malurus cyaneus*, Dunn et al. 1995; meerkats *Suricata suricatta*, Clutton-Brock et al. 2000).

When offspring remain in the natal nest for a period of time after weaning, they may gain indirect and/or direct benefits by assisting their parents. For example, cottontop tamarins gain parenting experience (Tardif et al. 1984) and Florida scrub jays *Aphelocoma c. coerulescens* can gain access to a breeding territory (Woolfenden & Fitzpatrick 1978). The younger siblings of these philopatric helpers also receive direct and/or indirect benefits. Direct benefits include exogenous heat for thermoregulation (e.g. prairie voles *Microtus ochrogaster*, Wang & Novak 1994), guarding and food provision (e.g. meerkats, Clutton-Brock et al. 2001a), while indirect benefits include social transmission of information from the surrounding environment (e.g. meerkats, Thornton 2008) and burrow maintenance (e.g. tuco-tucos *Ctenomys sociabilis*, Lacey 2004). Increased offspring survival and growth also enhances the inclusive fitness of the helpers themselves (Hamilton 1963, König 1997).

Helpers can influence the amount of parental care provided by the parents. For example, the presence of helpers results in dominant female meerkats reducing investment in their litters (Clutton-Brock et al. 2001b). Reductions in investment by mothers can then influence the later expression of parental care behaviour in daughters. Francis et al. (1999) demonstrated that decreased maternal investment by female Long-Evans rats *Rattus norvegicus* in their daughters resulted in the daughters showing a corresponding decrease in maternal investment in their own offspring later. This suggests that the presence of a helper can influence the transmission of parental care from adults to offspring. To my knowledge, the influence of a helper on the development of parental care behaviour has not been investigated.

The African striped mouse *Rhabdomys pumilio* from the succulent karoo of South Africa (hereafter termed “desert” striped mouse) is a small ( $\pm 40$  g) group-living murid rodent. The social system of this population comprises 3-4 breeding females, 1-2 breeding males and over-wintering philopatric young that act as helpers for a number of months after weaning (Schradin & Pillay 2004). Helpers participate in territorial defence, nest building (Schradin & Pillay 2004) and group huddling (Schradin 2005; Scantlebury et al. 2006). Females seem to require additional help raising offspring in winter and early spring, when night time temperatures often fall below 0 °C, since young pups grow and develop faster when two adults are present than when mothers nest alone (Schradin & Pillay 2005). Under these conditions, fathers, sisters (i.e. aunts) or philopatric young can provide the help required. Under both captive and natural conditions, males from this population exhibit extensive amounts of direct paternal care, displaying all the behaviours shown by females (e.g. huddling and retrieving pups) apart from lactation (Schradin & Pillay 2003).

In a previous study, I showed that the expression of paternal care behaviour in male desert striped mice is influenced by the amount of maternal care received from mothers (Chapter 2): sons that experienced higher levels of maternal care because of the absence of the father (experimentally removed) showed higher levels of paternal care when adult than sons raised by both parents who shared parental care duties. I did not find the same response for female desert striped mice, which showed similar amounts of maternal care, behaviour regardless of rearing condition (Chapter 3).

Under natural conditions, female desert striped mice rarely raise young alone (Schradin & Pillay 2004). In a previous study, Schubert et al. (in press) showed that female desert striped mice show consistently higher levels of parental care than fathers or aunts, but there was no difference in the amount of care provided by fathers and aunts. The aim of the present study was to determine if the presence of a philopatric helper (i.e. a younger female from a previous litter) has an influence on the development of paternal care behaviour in desert striped mice. Since sons raised by both parents show lower levels of paternal care than sons raised by mothers alone (Chapter 2), I predicted that sons raised by mother and a helper would show lower levels of paternal care behaviour (i.e. similar to the level shown in sons raised by both parents, Chapter 2), since I expected that helpers would share parental duties (like fathers) with the mother. This would result in mothers reducing their level of maternal care in sons, a known determinant of the development of paternal care behaviour.



## METHODS

Striped mice used in this study were F1–F4 generation individuals derived from Goegap Nature Reserve in the succulent karoo (Northern Cape Province, South Africa; 29.40 S, 17.53 E). They were housed in the Milner Park Animal Unit at the University of the Witwatersrand, under partially controlled environmental conditions (14:10 h light: dark regime, lights on at 0500 hours; 20–24 °C; 30–60% relative humidity).

Experiments involved two phases. In Phase 1, 10 breeding pairs were established and housed in glass tanks (46 x 30 cm and 32 cm high). The floor of the tanks was covered with a layer of wood shavings for bedding and a plastic nest box (13 x 9 cm and 10 cm high) was provided. Nesting material comprised a handful of dry grass provided weekly and approximately 5 g of paper towel provided twice weekly. One cardboard toilet roll/paper cup was provided weekly per mouse for behavioural enrichment. Subjects had access to water *ad libitum*. Each mouse was fed approximately 5 g mixed seed (sunflower, millet, oats, linseed, horse cubes) and approximately 10 g fresh fruit or vegetables daily. The seed was sprinkled throughout the cage to stimulate foraging behaviour (C. Schradin, pers. comm.). Males and females raised young together until weaning at 21 days of age.

At weaning, one daughter from each litter was randomly selected and kept with the mother in the breeding tank. The father and all other offspring were removed and housed individually or in same-sex sibling pairs in opaque holding cages (42 x 26 cm and 14 cm high) under the conditions described above. As striped mice show a post-partum oestrous, mothers were pregnant when fathers and offspring were removed. The mother and older daughter then raised the next litter of young together (M+H). The parental care behaviour of the mother and helper for the next litter was video recorded for 15 min every second day, starting on DAY 1 (DAY 0 = day of birth) until DAY 11. Recordings were only made until DAY 11 as young striped mice start eating solid food at this time (Pillay 2000) and are often outside the nest. Recordings were made between 0700 and 1100 hours, coinciding with the peak activity period of striped mice. No observers were present in the room during taping sessions. Using continuous sampling, I scored the parental care behaviour of test subjects (mothers and helpers) for the 15 min taping session and summed the time spent in parental care

for the six days of taping. Parental care was scored using the following behaviours (after Schradin & Pillay 2003): huddling and licking pups and time spent in close proximity ( $< 2$  cm of pups). For maternal care, I could not distinguish between nursing and huddling pups, so the data were classified as huddling (as described by Schubert et al. in press) and as young helpers were sexually immature and not lactating, no nursing behaviour was expected for these subjects. Females never showed aggressive behaviour to helpers and rarely to their mates. The data obtained here were compared with data obtained for parental care behaviour of fathers and mothers collected in an identical fashion in a series of tests in which fathers and mothers raised young together (M+F) or mothers raised young alone (M-F) (Chapter 2). These data were used to assess the contribution of parental care of the mother only, both parents raising young together, or the mother and helper raising young together, on the development of paternal care behaviour in sons.

In Phase 2, at sexual maturity (approximately 90 days of age), one male (son) from each litter (M+H) was randomly selected and paired with an unrelated mate (obtained from the breeding colony) of approximately the same age, resulting in an SM+H treatment (son from M+H). Pairs were housed in opaque holding cages and kept under the same husbandry conditions described above. A few days prior to parturition, pairs were transferred into glass tanks and males and females were housed together until offspring were weaned (i.e. as described for M+H). The paternal care behaviour of sons was measured in the same manner as for mothers and helpers (described above). The data were compared with sons obtained from other treatments (SM+F and SM-F) from a previous experiment (Chapter 2).

I also determined the growth rate of pups in litters produced in Phase 2. For this, litter mass was recorded to the nearest 0.1 g every day after birth for the first 7 days, and every 3 days thereafter until weaning. These values were then used to calculate growth rates for litters between DAY 1 and DAY 21 (at weaning). Growth rates were calculated using the formula:  $(\text{LN mass DAY 21} - \text{LN mass DAY 1})/20$  days. Growth rate of pups (SM+H) was then compared to growth rates of pups from other litters (SM+F and SM-F) from a previous experiment (Chapter 2).

### **Statistical analysis**

All analyses were performed using Statistica 7.1 (Statsoft Inc, [www.statsoft.com](http://www.statsoft.com)). All parental care data met the assumptions of normality (Shapiro–Wilk’s test) and

homogeneity of variances (Levene's test), but the dataset for growth rate had to be square root transformed prior to analyses. All data were analysed with mixed models, using the general linear model (GLM) module. In all analyses, treatment and litter order (i.e. the first to third litter produced by a pair, to account for their previous breeding experience) were entered as fixed categorical predictors. Breeding pair identity was included as a random effect since not all pairs produced three litters in Phase 1 and I used one or two litters each from some other breeding pairs to achieve the required sample size. Litter size was included as a continuous predictor (covariate) in the analyses. Maternal care behaviour (Phase 1) was also included as a covariate for the analysis of paternal care behaviour of their sons. Tukey honest significant difference (HSD) post hoc tests were used to identify specific differences and the model-level significance was determined at  $\alpha = 0.05$ . All tests were two-tailed. A linear regression was used to compare the parental care behaviour of mothers (Phase 1) and sons (Phase 2).

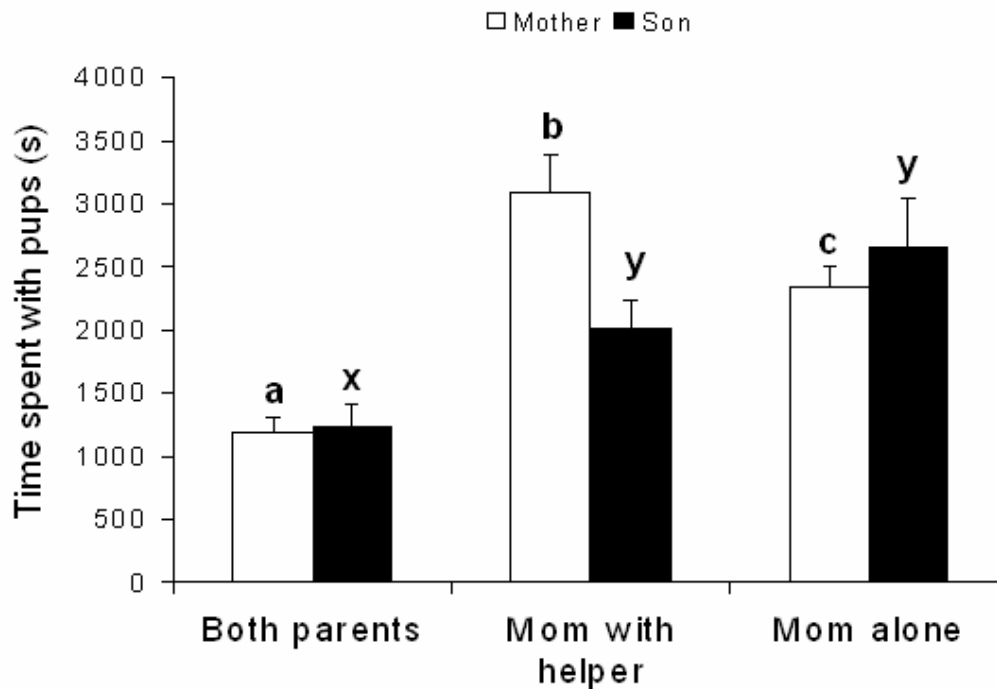
## RESULTS

### Maternal care behaviour (Phase 1)

Treatment ( $F_{2, 32.87} = 31.11, P < 0.001$ ) was a significant predictor of maternal care behaviour. Post hoc tests revealed a graded response, with mothers raising young with helpers (M+H) displaying more care than mothers raising young in the absence of their mates (M-F) and mothers housed with their mates (M+F) showed the lowest levels of care (Fig. 1). Litter order ( $F_{3, 30.40} = 0.84, P = 0.481$ ), breeding pair identity ( $F_{27, 6.00} = 3.62, P = 0.057$ ) and litter size ( $F_{1, 6.00} = 0.23, P = 0.649$ ) did not significantly influence maternal care.

### Helper and father parental care behaviour (Phase 1)

Treatment ( $F_{2, 19.00} = 21.09, P < 0.001$ ) was a significant predictor of parental care behaviour. Post hoc tests revealed that mothers in the M+H treatment showed the highest levels of care, while fathers (M+F) and helpers (M+H) showed lower, but similar, levels of care: mean ( $\pm$  SE) – M+F = 1435.83 (121.53) s; M+H = 2063.11 (383.30) s. Litter order ( $F_{4, 38.00} = 1.39, P = 0.257$ ) and litter size ( $F_{2, 19.00} = 0.39, P = 0.682$ ) did not affect parental care behaviour of helpers or fathers.



**Figure 1.** Parental care displayed by desert striped mouse mothers and their adult sons. Mean  $\pm$  SE time spent with pups (seconds) by females in three treatments and by their sons resulting from these treatments. Tukey post hoc tests are provided separately for mothers and sons, and bars with the same letter indicate non-significant differences.

### Paternal care behaviour (Phase 2)

Treatment ( $F_{2, 26.42} = 15.78$ ,  $P < 0.001$ ) was a significant predictor of paternal care behaviour. Post hoc tests revealed that males in the SM+F treatments showed the least care while males in the SM+H and SM-F treatments showed the most care (Fig. 1).

Maternal care behaviour was a significant covariate for paternal care behaviour of their sons ( $F_{1, 3.00} = 10.82$ ,  $P = 0.046$ ). A linear regression revealed that there was a significant and positive relationship between the parental care provided by mothers in Phase 1 and their sons in Phase 2 ( $R^2 = 0.44$ ;  $F_{1, 37.00} = 29.42$ ,  $P < 0.001$ ). The following variables did not affect paternal care: litter order ( $F_{3, 29.33} = 2.22$ ,  $P = 0.107$ ); breeding pair identity ( $F_{30, 1.00} = 2.62$ ,  $P = 0.459$ ); and litter size ( $F_{1, 1.00} = 1.94$ ,  $P = 0.396$ ).

### Offspring growth (Phase 2)

Treatment ( $F_{2, 22.00} = 0.87$ ,  $P = 0.435$ ) was not a significant predictor of pup growth rate: mean  $\pm$  SE – SM+F = 0.077 (0.003); SM+H = 0.082 (0.004); SM-F = 0.082

(0.003). In addition, litter order ( $F_{1, 22.00} = 3.38, P=0.080$ ), breeding pair identity ( $F_{22, 1.20.00} = 5.66, P=0.321$ ) and litter size ( $F_{1, 22.00} = 4.11, P=0.055$ ) did not significantly influence growth rate.

## DISCUSSION

My results do not support the prediction that the development of paternal care behaviour in sons is negatively influenced by the presence of a helper, as sons raised by the mother and helper (M+H) showed higher levels of paternal care, similar to the treatment in which mothers raised their young alone (M-F).

When a helper was present, mothers more than doubled the time spent with young, compared to mothers raising young with their mates. My data indicate that there was a significant correlation between maternal care behaviour shown by mothers and later paternal care behaviour shown by their sons, with sons raised by mothers alone (SM-F) and mothers with helpers (SM+H) showing the highest levels of care compared to sons raised by both parents. Therefore, in support of findings from a previous experiment (Chapter 2), mothers have a strong influence on the development of paternal care behaviour in their sons.

I did not find any treatment effect on the growth of juvenile desert striped mice, which is similar to previous findings (Chapter 2; Schubert et al. in press). This is possibly a result of optimal conditions in the laboratory, which may not be appropriate to elicit a growth response (Brown 1993).

The results of my study are unexpected, as recent reviews of cooperatively breeding bird (e.g. Hatchwell 1999) and mammal (e.g. Clutton-Brock et al. 2001b) species suggest that mothers should react to the presence of helpers by either reducing the amount of care they provide, or by maintaining the same level of care. I am aware of only one other study, in azure-winged magpies *Cyanopica cyanus*, which showed that parents increase parental investment in the presence of helpers, although the reasons for the increase are not known (Valencia et al. 2006).

Females display greater care when a young daughter helper is present rather than her male partner, suggesting that the helper may not be providing the same level of care as fathers and is possibly an inadequate care-giver. However, fathers and helpers in this study provided similar levels of care (mean ( $\pm$  SE) – helper = 2063.11 (383.30) s; father = 1435.83 (121.53) s), which suggests that daughters are, at least, spending

similar amounts of time in the nest with young as fathers. If mothers perceived these young helpers as adequate care-givers, I would expect females to show lower levels of maternal care, similar to that shown when females raised young together with fathers (M+F). Since this was not the case, it is likely that, regardless of any care provided by young helpers, females perceive the young ( $\pm$  25 days old) helper as part of the extended litter, and not as a care-giver. Alternatively, or in addition, the amount of care provided by helper desert striped mice may have been overestimated in this study. Young philopatric helpers are known to save energy by huddling in groups (Scantlebury et al. 2006), so newly weaned helpers may not be providing direct care, but may merely be benefiting from associating with the mother and pups.

Schubert et al. (in press) showed that desert striped mouse mothers spend approximately 43% of their time engaged in parental care behaviours (less than the 63% reported by Schradin & Pillay (2003)), while aunts spent only 24% of their time caring for young. They suggested that the presence of allo-parents may enable mothers to reduce their level of care (Schubert et al. in press). In the present study, mothers spent approximately 57% of their time caring for young (similar to the findings of Schradin & Pillay 2003), while young helpers spent 38% of their time with the young. This suggests that mothers do not perceive their young daughters as helpers as they did not reduce their own level of care. There is a need to study the care provided by older daughters to determine if mothers will reduce their care when older daughters assist, and whether this will influence the development of paternal care behaviour shown by sons.

Young desert striped mouse helpers may impose costs on their mothers, such as increased competition for food (König 1997) or increased risk of infection with parasites or diseases (Hoogland 1979). However, young philopatric striped mouse helpers provide other benefits to mothers and young, which may explain why mothers tolerate these young helpers in the nest. Helpers participate in territorial defence and nest building (Schradin & Pillay 2004), but may also serve as babysitters when mothers leave the nest to forage, as is seen in banded mongooses *Mungos mungo* (Cant 2003), although this remains to be verified.

This study highlights that, while young sibling helpers do not directly influence the expression of paternal care behaviour in their younger brothers, their presence in the nest can lead to exaggerated maternal care, resulting in their younger brothers showing higher levels of paternal care. This study again provides support for the

finding that increased maternal care is an important non-genetic factor for the development of paternal care behaviour in male desert striped mice.

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## CHAPTER SIX

# Social transmission of information about novel food in two populations of the African striped mouse, *Rhabdomys pumilio*

TASMIN RYMER\*, CARSTEN SCHRADIN†\* & NEVILLE PILLAY\*

\*School of Animal, Plant and Environmental Sciences, University of the Witwatersrand

†Behavioural Biology, Zoological Institute, University of Zurich

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Social learning involves the transmission of information from demonstrators to conspecifics. The mother is expected to be the main demonstrator in solitary species, whereas several individuals can be demonstrators in group-living species. We studied social learning about novel food in two populations of the African striped mouse, with different social systems: a desert population (group living with paternal care and natal philopatry) and a grassland population (solitary, paternal care in captivity only and natal dispersal). We predicted that both parents would be reliable demonstrators for desert striped mice but only the mother would be a demonstrator for grassland striped mice. Adults and unweaned young were assigned to one of five treatments in captivity: (1) father or (2) mother fed novel food away from young; (3) novel food fed to both adults with young present; and (4) father or (5) mother fed mouse cubes (control) away from young. Juveniles from all treatments individually received novel food after weaning. The responses of juveniles to novel food were greater (shorter latency, more sniffs) when the mother was the demonstrator, regardless of population. Mothers may be more reliable demonstrators than fathers because information can be transmitted using multiple channels (olfaction, lactation). Our study also showed that fathers were more reliable demonstrators and responses to the novel food were greater in desert than grassland striped mice. These population differences reflect the different social organization of the populations and the unpredictable availability of highly nutritious food in the desert.

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**Keywords:** African striped mouse; demonstrator reliability; food novelty; information transfer; paternal care; *Rhabdomys pumilio*; social learning

Learning is a cognitive process (Duncan & Petherick 1991) enabling animals to acquire information about the state of their immediate environment (Katz & Lachlan 2003) and their own individual state (Duncan & Petherick 1991). An inherent part of learning concerns information about food, in particular determining whether food is palatable and nontoxic, and thus safe to consume (Galef & Clark 1971), and the location of this food in time and space (Ostfeld 1985).

*Correspondence:* T. Rymer, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa (email: [tasmin@gecko.wits.ac.za](mailto:tasmin@gecko.wits.ac.za)). C. Schradin is at the Zoological Institute, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland.

An individual may learn about novel foods individually through, for example, 'trial and error' learning (Noble & Franks 2002), but such learning creates the risk of ingesting noxious or unpalatable food. Alternatively, group living may promote social learning, which involves learning about the environment through the observation of (Heyes 1993) and interaction with (Katz & Lachlan 2003) conspecifics, or the products of their behaviours (Heyes 1994). This may reduce the costs often associated with individual learning (Zentall 2006). Individuals may be drawn to an area by the activity and behaviour of others (i.e. local enhancement; Range & Huber 2007), which promotes opportunities for learning through imitation or observational learning. Imitation is a process that involves learning about (Heyes 1993) and accurately replicating (Zentall 2006) a new behaviour, or part thereof

(Whiten et al. 2004), through the direct observation of conspecifics. Observational learning also involves learning about new behaviours by observing conspecifics, but does not lead to a duplication of the behaviour (Hall 1963).

Demonstrators are individuals that facilitate the learning process in conspecifics (Sherwin et al. 2002). Solitary and social mammals differ in their access to the number and type of demonstrators available to them. Solitary mammals principally rely on their mothers during the preweaning phase of their lives. For example, juvenile eastern woodrats, *Neotoma floridana*, showed a flavour preference for food to which they were exposed when suckling (Post et al. 1998). Social species, such as dwarf hamsters, *Phodopus campbelli* (Lupfer et al. 2003) and chimpanzees, *Pan troglodytes schweinfurthii* (Lonsdorf 2006), may also rely principally on their mothers to facilitate learning. Moreover, in social species, young may have the opportunity to learn from other adults or from siblings, if they associate with them during the preweaning phase. In addition, learning in a social context can occur throughout an individual's life span in group-living species, since there may be many opportunities for the exchange of information between individuals (Visalberghi & Addessi 2001), including learning about novel food (Nicol 1995). Observing conspecifics feeding can reduce fear of these novel foods (neophobia) and increases the likelihood of their acceptance (Galloway et al. 2005).

The African striped mouse is a small ( $\pm 40$  g) diurnal murid rodent with a widespread distribution in southern Africa. It offers a unique opportunity to investigate the influence of demonstrators on the ability of offspring to learn about novel foods, as this species shows regional differences in sociality. In the arid succulent karoo of South Africa, striped mice live in groups of three or four females and one male (Schradin & Pillay 2004). In the moist eastern grassland regions, this species is solitary and males do not associate with females or pups after parturition (Schradin & Pillay 2005a). In the natural environment, offspring of desert striped mice typically remain philopatric for a number of months, whereas grassland offspring stay with the mother for only a few weeks before dispersing soon after weaning (Schradin & Pillay 2005a). Differences in social organization and mating strategy between desert and grassland striped mice may be responses to a particular set of environmental conditions (Schradin 2005; Schradin & Pillay 2005b). In the desert, female striped mice form small groups together with their overwintering philopatric young because of a limited availability of suitable nesting sites, high population density and the need for huddling in groups; a male associates with a group and has access to mates. Conversely, in grasslands, females have large intrasexually nonoverlapping territories because food is patchily distributed. Young disperse after weaning since nesting sites are not limited and there is little need for huddling in the dense vegetation. Males adopt a roaming mating strategy by visiting several receptive females.

In captivity, males of both populations show extensive amounts of direct paternal care, with all the behaviours shown by females (e.g. huddling and retrieving) apart from lactation (Schradin & Pillay 2003). Paternal care has been demonstrated through direct observations and

experimental manipulations only in free-living desert striped mice (Schradin & Pillay 2003). Since males do not associate with females and pups in the grassland populations, the opportunities for paternal care may not exist, suggesting that the behaviour is plesiomorphic in grassland populations.

Apart from providing direct care, paternal behaviour may provide an opportunity for offspring to learn about novel foods from the father. Blissett et al. (2006) indicated that human fathers are more likely to control the feeding practices of their sons. We are not aware of any studies that have investigated the role of the father in the development of socially acquired food choice in a mammal, and only one study has investigated the role of the father as a demonstrator (Hatch & Lefebvre 1997).

Using an experimental protocol in which either one or both parents were demonstrators, we compared the responses of juvenile desert and grassland striped mice to a novel food to investigate evidence of social learning via olfactory, gustatory and visual cues. We predicted population differences in social learning, since desert striped mice (in the natural environment) have access to a greater number of demonstrators for a longer period of time than grassland striped mice (Schradin & Pillay 2005a). Specifically, we predicted that, because of population-specific differences in the occurrence of paternal care in nature and presumably selection for fathers to be demonstrators in desert striped mice, both parents would be reliable demonstrators for young striped mice from this population, but only mothers would be demonstrators for grassland young. This prediction assumes that offspring are genetically predisposed to learn from their fathers in the desert but not the grassland striped mice. However, we were mindful that males from both populations show paternal care in captivity, so we asked whether learning from the fathers may occur in both populations because of the postpartum association between fathers and offspring in the laboratory. If so, learning in both populations could be the result of social/environmental influences. We also predicted that desert striped mice would respond faster to novel food than grassland striped mice, because of the unpredictability of food availability in the desert and the low likelihood of encountering food of high nutritional value (Schradin 2007).

## METHODS

Striped mice used in this study were F1–F4 generation individuals derived from Goegap Nature Reserve, Northern Cape Province, South Africa (29.40 S, 17.53 E, designated desert striped mice) and Cullinan, Gauteng Province, South Africa (25.40 S, 28.31 E, designated grassland striped mice). They were housed in the Milner Park Animal Unit at the University of the Witwatersrand, under partially controlled environmental conditions (14:10 h light: dark regime, lights on at 0500 hours; 20–24 °C; 30–60% relative humidity).

Twenty breeding pairs, 10 from each population, were established. Breeding pairs were housed in glass tanks (46 × 30 cm and 32 cm high). The floor of the cages was

covered with a layer of wood shavings for bedding. A plastic nestbox (27 × 20 cm and 17 cm high) was provided. Nesting material comprised a handful of dry grass weekly and approximately 5 g of paper towel twice weekly. One cardboard toilet roll/paper cup and twigs were provided weekly for behavioural enrichment. Subjects had access to water and Epol (Epol, Pretoria West, South Africa) mouse cubes *ad libitum*. The diet was supplemented with fresh fruit or vegetables daily and approximately 5 g of seed at least twice a week.

Our intention in this study was to obtain five consecutive litters per breeding pair, and randomly assign each litter to one of five different treatments (see below). Fifteen pairs produced the required five litters, whereas three grassland and two desert pairs each produced three litters only. We used data from an additional five pairs (two litters per pair) to achieve the required sample size.

Experiments involved exposing demonstrators (parents) to novel or standard laboratory food (mouse) cubes on one occasion per litter when pups were either 10 or 12 days old (i.e. when striped mice start eating solid food; Pillay 2000). Litters were separated from their parents at 21 days of age, a few days before the birth of the next litter (interlitter interval 23–25 days). The five treatments were as follows. (1) Father removed + novel food (FRN): the father was removed from the breeding tank and housed in a holding cage (36 × 16 cm and 20 cm high) in a different room for 5 min. During this time, he had access to approximately 30 g of boiled egg as a novel food. After 5 min he was returned to the home tank. Chopped boiled egg was used as the novel food because the striped mice used in this study had never been exposed to egg previously, it has high nutritional value, and striped mice have a high preference for egg in the laboratory (N. Pillay, personal observation). (2) Mother removed + novel food (MRN): as in FRN, but the mother was removed. (3) Mother and father in home tank + novel food (MFN): approximately 30 g of boiled egg was fed to the breeding pair while their unweaned offspring were present in the breeding tank. (4) Father removed + standard food (FRS): the father was removed from the breeding tank, fed approximately 30 g of mouse cubes in a holding cage for 5 min, and then returned to the home tank. (5) Mother removed + standard food (MRS): as in FRS, but the mother was removed. We used 40 juveniles (20 desert and 20 grassland) for each treatment. The FRS and MRS treatments served as controls. Apart from food, holding cages used in the FRN, MRN, FRS and MRS treatments contained wood shavings, and the animals had access to water and shelter. All demonstrators consumed the egg or mouse cubes. The amount of egg consumed ranged from 10 g (FRN, MRN) to 22 g (MFN).

Juveniles were housed individually in holding cages under the conditions described above once they were weaned from their parents at 21 days of age. Two juveniles, one of each sex from each litter, were chosen randomly and housed individually overnight in rectangular, holding cages (45 × 30 cm and 30 cm high). Juveniles were tested individually since striped mice forage alone in nature (Schradin & Pillay 2004). The floor was covered with wood shavings and a handful of dry grass, 5 g of

paper towel and a cardboard toilet roll were provided for cover. Water, approximately 30 g of mouse cubes and a small piece of apple were provided. Tests were conducted between 0730 and 1100 hours on the following day. All cover, excess wood shavings and all mouse cubes were removed from the holding cages to facilitate video recording and scoring of the behavioural responses of test subjects; in pilot studies, cage furnishings and the mouse cubes obscured our view of test subjects. Approximately 30 g of chopped boiled egg was placed into a petri dish, approximately 4 cm from the front of the holding cage and approximately 6 cm from the side. The position of the petri dish containing the boiled egg was alternated along the long axis of the cage between treatments to account for positional biases. The behaviour of test subjects was video recorded for 30 min following the introduction of the egg. No observers were present in the room during taping sessions. Using continuous sampling, we scored the behaviour of test subjects for the 30 min taping session, and recorded the latency to make first contact with the egg, the number of sniffs of the egg in the first 5 min after making contact and the latency to start consuming the egg.

## Ethical Note

We provided animals with environmental enrichment (as described above). The experimental procedures used here had no obvious negative effects on the welfare of the striped mice. After tests, juveniles were returned to the captive striped mouse colony and used in other breeding experiments when they were fully grown. This study was approved by the Animal Ethics Screening Committee of the University of Witwatersrand.

## Statistical Analysis

For all analyses we used Statistica 7.1 (Statsoft Inc, [www.statsoft.com](http://www.statsoft.com)). The data set met the assumptions of normality (Shapiro–Wilk's test) and homogeneity of variances (Levene's test) after the behavioural variables were square-root (number of sniffs) or log (latency to approach and consume) transformed. Each dependent variable was analysed with mixed models, using the general linear model (GLM) module. In all analyses, population, sex of test subjects, treatment and litter order (i.e. the first to fifth litter produced by a pair, to account for their previous breeding experience) were entered as fixed categorical predictors. Random effects included breeding pair identity as well as litter identity nested in treatment and in breeding pair identity, so as to account for the similar genetic and/or environmental histories of test subjects (i.e. different litters per breeding pair were used in different treatments and two littermates, one male and one female, were used in each treatment). In addition, not all pairs produced five litters and we used two litters each from some other breeding pairs to achieve the required sample size. Litter size was included as a continuous predictor (covariate) in the analyses. Tukey honest significant difference (HSD) post hoc tests were used to identify specific

differences. The model-level significance was determined at  $\alpha = 0.05$ . However, because the measurements for the three dependent variables are interrelated, we adjusted alpha levels using a Bonferroni sequential adjustment ( $\alpha' = 0.017$ ) prior to conducting post hoc tests. All tests were two tailed.

## RESULTS

### Latency to Make First Contact

Offspring of desert striped mice made first contact with the novel food (boiled egg) significantly faster than their grassland counterparts (Table 1, Fig. 1). There was a significant treatment effect, with offspring from both populations making first contact with the novel food significantly faster in the MRN and MFN treatments (mother was the demonstrator or offspring had direct exposure to egg before weaning), followed by offspring in the MRS (mother fed standard food) and FRN (father fed novel food). The latency to make first contact was significantly longest in the FRS treatment (father fed mouse cubes; Table 1, Fig. 1). There was a significant population\*treatment interaction, which showed that offspring from the desert population responded faster to the novel food in the MRN, MFN, FRN treatments (i.e. direct or indirect prior exposure to egg) than those from the grassland population, and apart from the FRS treatment, desert striped

mice responded faster than grassland striped mice for all other treatments. In addition, the slowest responses were recorded in grassland individuals in the FRN and FRS treatments (i.e. when the fathers were demonstrators of novel and standard food; Table 1, Fig. 1).

The following variables were not significant predictors of the latency to make first contact with novel food: sex; litter order; population\*sex; population\*litter order; sex\*treatment; sex\*litter order; treatment\*litter order; breeding pair identity; litter identity (nested in treatment and in breeding pair identity); and litter size (Table 1).

### Number of Sniffs

Offspring of the desert striped mice sniffed the egg significantly more often than offspring of grassland striped mice (Table 1, Fig. 2). In addition, offspring from both populations sniffed the egg significantly more often in the MRN (mother fed egg) treatment than the MFN and FRN treatments, and least often in the MRS and FRS treatments (mother and father fed mouse cubes; Table 1, Fig. 2).

Sex, litter order, population\*sex, population\*treatment, population\*litter order, sex\*treatment, sex\*litter order, treatment\*litter order, breeding pair identity, litter identity (nested in treatment and in breeding pair identity) and litter size did not influence the number of sniffs of the novel food (Table 1).

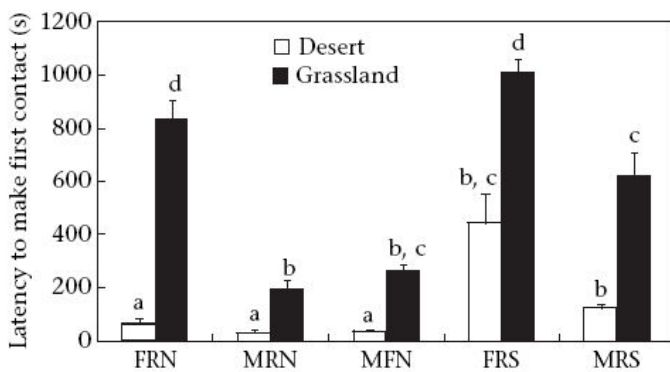
**Table 1.** Results of GLM analyses and Tukey HSD post hoc comparisons for the latency to make first contact, the number of sniffs and latency to start consuming novel food

Variables	Latency to make first contact	Number of sniffs	Latency to start consuming
Population	$F_{1,12.05} = 97.72, P < 0.001$	$F_{1,15.30} = 24.76, P < 0.001$	$F_{1,18.18} = 13.94, P = 0.002$
Sex	$F_{1,89.00} = 0.13, P = 0.721$	$F_{1,89.00} = 0.26, P = 0.608$	$F_{1,89.00} = 0.05, P = 0.816$
Treatment	$F_{4,44.63} = 30.33, P < 0.001$	$F_{4,46.92} = 28.89, P < 0.001$	$F_{4,43.14} = 31.33, P < 0.001$
Litter order	$F_{4,48.23} = 1.57, P = 0.198$	$F_{4,50.77} = 0.21, P = 0.931$	$F_{4,44.95} = 1.52, P = 0.213$
Population*sex	$F_{1,89.09} = 0.28, P = 0.597$	$F_{1,89.12} = 0.05, P = 0.833$	$F_{1,89.13} = 1.46, P = 0.231$
Population*treatment	$F_{4,44.89} = 5.08, P = 0.002$	$F_{4,46.94} = 2.06, P = 0.101$	$F_{4,43.16} = 9.24, P < 0.001$
Population*litter order	$F_{4,47.99} = 2.38, P = 0.065$	$F_{4,50.89} = 0.64, P = 0.636$	$F_{4,44.75} = 0.56, P = 0.694$
Sex*treatment	$F_{4,89.09} = 0.62, P = 0.650$	$F_{4,89.12} = 0.05, P = 0.995$	$F_{4,89.13} = 0.94, P = 0.445$
Sex*litter order	$F_{4,90.05} = 0.53, P = 0.718$	$F_{4,90.60} = 0.97, P = 0.426$	$F_{4,90.17} = 0.24, P = 0.917$
Treatment*litter order	$F_{16,60.57} = 1.43, P = 0.160$	$F_{16,52.70} = 0.86, P = 0.617$	$F_{16,60.31} = 1.24, P = 0.267$
Pair identity	$F_{22,41.79} = 1.33, P = 0.208$	$F_{22,42.29} = 1.13, P = 0.353$	$F_{22,42.51} = 0.39, P = 0.990$
Litter identity (Treatment)	$F_{44,89.00} = 0.78, P = 0.823$	$F_{44,89.00} = 0.83, P = 0.745$	$F_{44,89.00} = 0.90, P = 0.645$
Litter identity (Pair identity)	$F_{44,89.00} = 0.54, P = 0.986$	$F_{44,89.00} = 0.70, P = 0.902$	$F_{44,89.00} = 0.81, P = 0.778$
Litter size	$F_{1,42.95} = 3.17, P = 0.082$	$F_{1,42.33} = 2.13, P = 0.152$	$F_{1,42.56} = 1.79, P = 0.188$
Post hoc comparisons†			
Population	Desert < Grassland	Desert > Grassland	Desert < Grassland
Treatment	(MRN, MFN) < (MRS, FRN) < FRS	MRN > (MFN, FRN) > (MRS, FRS)	(MRN, MFN) < MRS < (FRN, FRS)
Population*treatment‡	(MRN <sub>D</sub> , MFN <sub>D</sub> , FRN <sub>D</sub> ), (MRS <sub>D</sub> , MRN <sub>G</sub> , FRS <sub>D</sub> , MFN <sub>G</sub> ), (FRS <sub>D</sub> , MFN <sub>G</sub> , MRS <sub>G</sub> ), (FRN <sub>G</sub> , FRS <sub>G</sub> )		(MFN <sub>D</sub> , MRN <sub>D</sub> ), MRS <sub>D</sub> , (MFN <sub>G</sub> , MRN <sub>G</sub> ), (FRS <sub>D</sub> , MRS <sub>G</sub> , FRN <sub>D</sub> , FRN <sub>G</sub> ), FRS <sub>G</sub>

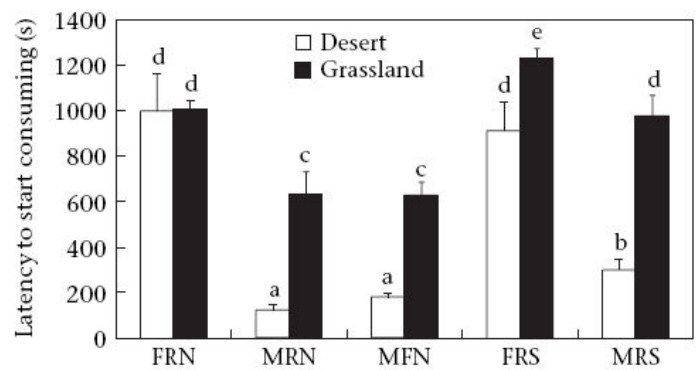
Four fixed factors (population, sex, treatment, litter order), three random factors (breeding pair identity, litter identity nested in treatment and in breeding pair identity) and one covariate (litter size) were included in the model. Post hoc comparisons are provided for significant variables (indicated in bold) only.

†Homogeneous (nonsignificant) subsets are given in parentheses; treatment codes: FRN (father removed and fed novel food); MRN (mother removed and fed novel food); MFN (both parents in home cage with novel food); FRS (father removed and fed standard food); and MRS (mother removed and fed standard food).

‡Subsets are arranged from shortest to longest latencies; subscripts D and G = desert and grassland, respectively.



**Figure 1.** Mean + SE time taken for juvenile desert and grassland striped mice to make first contact with the novel food in five treatments: FRN (father removed and fed novel food); MRN (mother removed and fed novel food); MFN (both parents in home cage with novel food); FRS (father removed and fed standard food); and MRS (mother removed and fed standard food). Bars with the same letters are not significantly different (population\*treatment effect, post hoc comparisons).



**Figure 3.** Mean + SE time taken for juvenile desert and grassland striped mice to start consuming the novel food in five treatments: FRN (father removed and fed novel food); MRN (mother removed and fed novel food); MFN (both parents in home cage with novel food); FRS (father removed and fed standard food); and MRS (mother removed and fed standard food). Bars with the same letters are not significantly different (population\*treatment effect, post hoc comparisons).

### Latency to Start Consuming Food

The latency to start consuming the egg was shorter for offspring of desert striped mice than those of grassland striped mice (Table 1, Fig. 3). However, offspring from both populations took significantly less time to start consuming food in the MRN and MFN (mother and offspring exposed to novel food) treatments than the MRS treatment, and took longest to start consuming food in the FRN and FRS treatments (i.e. when the father was fed away from offspring; post hoc tests; Fig. 3). There was a significant population\*treatment interaction, which showed that desert striped mice in the MFN, MRN and MRS treatments responded the quickest, and grassland striped mice responded the slowest (Table 1, Fig. 3). Offspring from the desert population did not take less time to start consuming novel food than those from the grassland in the FRN treatment (i.e. father fed novel food;

Fig. 3). All test subjects consumed the egg during experiments.

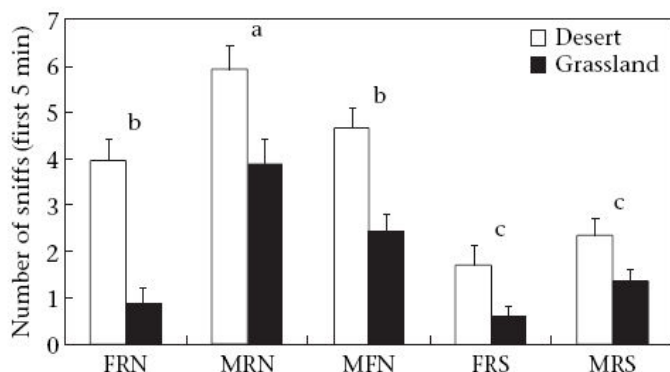
The latency to start consuming food was not influenced by the sex, litter order, population\*sex, population\*litter order, sex\*treatment, sex\*litter order, treatment\*litter order, breeding pair identity, litter identity (nested in treatment and in breeding pair identity) and litter size (Table 1).

### DISCUSSION

Our results indicate that social learning influences the responses of young striped mice to novel food in both desert and grassland populations. Even though the response of young striped mice to novel food was not an 'all or nothing' reaction, since they reacted to novel food even when they did not have prior experience with it (FRS and MRS treatments), their responses were greater (faster or more numerous) in the treatments in which they had direct (MFN) or indirect (FRN, MRN) prior exposure to the novel food.

Treatment was also an important predictor of social learning, since young striped mice showed shorter latencies to make first contact and to start consuming novel food and more investigatory behaviour when mothers were demonstrators, regardless of population. This indicates that offspring rely mainly on their mothers for learning about novel food. The importance of the mother for information transfer to offspring regarding novel food has been shown in a number of species, such as house mice, *Mus domesticus* (Valsecchi et al. 1989) and domestic chickens, *Gallus gallus* (Nicol 2006).

Mammals use olfactory cues to assimilate information from social interactions (Laland & Plotkin 1991; Galef & Allen 1995). In particular, offspring may be exposed to olfactory cues from food on the breath of conspecifics returning from foraging bouts, as occurs in dogs, *Canis familiaris* (Lupfer-Johnson & Ross 2007). Olfactory cues are important for social interactions in striped mice (Pillay



**Figure 2.** Mean + SE number of sniffs of novel food in the first 5 min after contact by juvenile desert and grassland striped mice in five treatments: FRN (father removed and fed novel food); MRN (mother removed and fed novel food); MFN (both parents in home cage with novel food); FRS (father removed and fed standard food); and MRS (mother removed and fed standard food). Bars with the same letters are not significantly different (treatment effect, post hoc comparisons).

et al. 2006), and our study shows that olfaction is also important for acquiring information about novel food from conspecifics (i.e. MRN, FRN, MFN treatments). None the less, other cues, such as auditory signals (e.g. Elowson et al. 1991), visual cues (e.g. Valsecchi et al. 1989) and molecular (taste) cues transmitted in the mother's milk (e.g. Wells & Hepper 2006), when used in conjunction with olfactory cues, may provide a stronger channel for the transfer of information (Taylor et al. 2007). Other studies have also shown that prenatal exposure to chemical stimuli in the mother's diet can influence postnatal food preferences (e.g. dogs, Wells & Hepper 2006).

Therefore, we suggest that striped mice mothers may be more reliable demonstrators of novel food than fathers because of the multiple channels of information transfer. Offspring responded just as fast to novel food when it was placed directly into their home cage (MFN treatment) as when the mother was the demonstrator (MRN), further supporting the hypothesis that multiple cues may be required for learning about novel food. The parents used in the present study were exposed to novel food when their offspring were 10–12 days old, the transition age between suckling and eating solid food in striped mice (Pillay 2000). This suggests that at least two channels for the transfer of information would have been present for the young: through olfactory cues and gustatory cues in the mother's milk.

The ability to learn from another individual is context dependent, and influenced by both the demonstrator and the observer (Nicol 2006). Hence, young may not learn about novel food from the father if they spend more time with the mother. This is not the case for striped mice, however, since fathers spend similar amounts of time with young as mothers do, at least in captivity (Schradin & Pillay 2003). Instead, we propose that male striped mice are not as reliable as mothers as demonstrators of novel food because there are fewer channels for information transfer from fathers. Because our study relied primarily on the olfactory transmission of information from fathers, it is possible that olfactory cues, in isolation from other cues, from the father may not be sufficient for the reliable transmission of information to the offspring. In white-footed mice, *Peromyscus leucopus*, weaned offspring follow their fathers, but not mothers, on foraging bouts (Schug et al. 1992). In addition, Galef & Clark (1971) stated that visual cues may be important in guiding young to a food source. It is thus possible that young striped mice may also require visual cues from their fathers, in addition to olfactory cues, to ensure reliability of information transfer. Desert striped mice forage alone, but because groups occupy small territories, group members feed in close proximity (Schradin & Pillay 2004, 2005a), potentially facilitating learning from visual cues.

In treatments where fathers were demonstrators (FRN, FRS), desert striped mice responded quicker to the novel food than their grassland counterparts. In nature, population differences in paternal care are expected in striped mice because males associate with females and their pups in the desert but not in the grassland (Schradin & Pillay 2005b). Although grassland striped mice show paternal care in the laboratory (Schradin & Pillay 2003), offspring

may still be constrained from learning from their fathers, even though the opportunities for social learning in the experimental set-up in the laboratory were the same for both populations. In wild grassland striped mice, offspring presumably rely on their mothers as the only reliable source of information transfer, and there is no selection pressure to learn from the father as he does not associate with the mother after conception (Schradin & Pillay 2005a). Our results therefore support the prediction that learning from the father has a genetic basis that is present in desert but not grassland striped mice.

Although female striped mice are more reliable demonstrators of novel food, fathers still provide vital care for juveniles in the desert population. Fathers lick and huddle with pups to the same extent as mothers, and will retrieve displaced pups back into the nest (Schradin & Pillay 2004). Night-time temperatures in winter in the succulent karoo (from where our desert population originated) often fall below 0 °C and the presence of the father in the nest during these times is important for offspring growth (Schradin & Pillay 2005c). Indeed, Schradin & Pillay (2003) showed that pup development is better under biparental care than exclusive maternal care, indicating that paternal care may have important fitness-enhancing benefits.

In all treatments, desert striped mice responded faster and with more intensity to novel food than their grassland counterparts. This could be a result of ecological constraints imposed by the desert environment or of genetically determined personality differences of striped mice from these two populations (A. Hinze & N. Pillay, unpublished data). We observed that, compared to grassland striped mice, desert striped mice are bolder in captivity, spending more time outside their nestboxes and more time investigating novel objects placed in their cages. However, as striped mice from both populations still responded to novel food, we postulate that the faster responses by desert striped mice may be an adaptation for exploiting unpredictable palatable food in the variable desert environment (Schradin 2007), even though such areas do have a stable year-round food supply (Schradin & Pillay 2004). Perrin (1980) described the striped mouse as an opportunistic omnivore, taking advantage of transient but nutritious food resources. Goegap Nature Reserve (from where the desert striped mice originated) experiences erratic winter rainfall, with an average of 160 mm of rain per year (Schradin 2005) and thus there is marked seasonal variation in food abundance. Therefore, the probability of encountering a palatable, highly nutritious food decreases during the dry season (Schradin 2007). As a consequence, striped mice from the desert show high levels of exploration (A. Hinze & N. Pillay, unpublished data), which improves their encounter rate with food.

In conclusion, social learning occurs in both desert and grassland striped mice and mothers are more reliable demonstrators than fathers for offspring learning about novel food. This may be because offspring are dependent on their mothers for at least the first 10 days of their lives (Pillay 2000), when they can acquire information about palatable food from their mothers via multiple channels, such as olfactory cues and molecular cues transmitted in

the milk. Two other important findings in our study were that (1) fathers of desert striped mice were more reliable demonstrators of novel food than fathers of grassland striped mice, despite both being present and showing paternal care in captivity, and (2) desert striped mice responded faster to novel food than their grassland counterparts, even though individuals of both populations were adequately provisioned in captivity. These population differences in social learning and responses to novel food may be related to differences in the social organization of desert (social) and grassland (solitary) striped mice and the unpredictability of highly nutritious food in the desert. Ultimately, population-specific behavioural responses of striped mice may be genetically determined adaptations for life in the harsh desert or more stable grassland habitats.

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## CHAPTER SEVEN

### Female mate choice for paternal quality in African striped mice

#### *Rhabdomys pumilio*

#### ABSTRACT

By preferentially mating with males showing specific morphological or behavioural traits, females may increase their own reproduce success and may increase the prevalence of these favoured traits in subsequent generations of offspring. I investigated female mate choice for paternal quality in a desert population of African striped mice *Rhabdomys pumilio*, in which males display high levels of paternal care. Females were exposed to olfactory cues from males differing in levels of paternal care ability and paternal care experience, or visual cues from males showing either higher levels of paternal care behaviour or no care. I predicted that females would discriminate between males displaying higher and lower levels of paternal care, preferring males showing higher levels of paternal care. In addition, I predicted that females would prefer to mate with experienced over inexperienced males. Finally, I predicted that females would prefer males housed with pups rather than males artificially separated from pups. My results showed that females did not distinguish between males of differing paternal care ability, but experienced females showed a preference for experienced over inexperienced males. Females also did not show a preference between males housed with pups and those separated from pups. My results suggest that females prefer experienced males since they are likely to provide care and remain with the female. Paternal quality (i.e. amount of care provided by males) may be a less reliable cue since females may not observe paternal quality of males unless they are resident breeding males, with which they are already familiar.

*Keywords:* African striped mouse, female mate choice, olfactory cues, paternal care, paternal quality, *Rhabdomys pumilio*, visual cues

## INTRODUCTION

Female mate choice for males with specific morphological or behavioural traits (e.g. long tail streamers in North American barn swallows *Hirundo rustica*, Smith & Montgomerie 1991; fanning bout rate in fifteen-spined sticklebacks *Spinachia spinachia*, Östlund & Ahnesjö 1998) functions to increase a female's current reproductive fitness, through increased offspring viability (Drickamer et al. 2000), as well as the prevalence of these preferred traits in subsequent generations of offspring (Smith & Montgomerie 1991). Females may use olfactory (Doty 1972), visual (Brooks & Caithness 1995), auditory (Forsman & Hagman 2006) or chemical (Marco et al. 1998) cues to assess a male's suitability as a mating partner. Alternatively, or in addition, females may use a combination of cues (e.g. chemical and visual cues in the squinting bush brown butterfly *Bicyclus anynana*; Costanzo & Monteiro 2007) to determine mate suitability.

Rodents use olfactory cues extensively to gain social and reproductive information from their surrounding environment (Horth 2007). Female degus *Octodon degus* use olfactory cues to discriminate between their own offspring and those of co-nesting females (Jesseau et al. 2008), while laboratory mice *Mus musculus* discriminate kin using odour cues (Barnard & Fitzsimons 1988). Females also use olfactory cues in mate choice (e.g. deer mice *Peromyscus maniculatus bairdi*, Doty 1972). While the importance of other cues, such as visual and auditory cues, in mate choice have been extensively studied in fish (e.g. guppies *Poecilia reticulata*, Brooks & Caithness 1995), insects (crickets *Teleogryllus oceanicus*, Tregenza et al. 2006) and birds (e.g. eastern kingbirds *Tyrannus tyrannus*, Murphy et al. 2008), their importance for mate choice in rodents has largely been ignored.

Diurnal rodent species, such as ground squirrels *Spermophilus beecheyi* (Kryger et al. 1998), show structural differences in retinal morphology to nocturnal rodent species, such as rats *Rattus norvegicus* (Szel & Rohlich 1992). Nocturnal species, with higher rod concentrations, are more sensitive to light than diurnal species (Schumann et al. 2005), while diurnal species, with higher cone concentrations, are more responsive to colour signals (Jacobs 1993). Therefore, it is possible that diurnal rodents could use visual cues in mate choice, although this has not yet been investigated.

Although not known for rodents, paternal care behaviour is known to be associated with paternal quality in fish (e.g. fanning bout rate in fifteen-spined sticklebacks) and females choose males actively engaging in these behaviours (Östlund & Ahnesjö 1998). Similarly, if diurnal female rodents do use visual cues in mate choice, they could use behavioural cues associated with paternal care behaviour shown by males (e.g. huddling and retrieving pups) to assess whether a male will be a good father for her offspring.

The African striped mouse *Rhabdomys pumilio* is a small ( $\pm 40$  g) diurnal murid rodent with a widespread distribution in southern Africa (de Graaff 1981). Striped mice from the succulent karoo (hereafter termed “desert” striped mice”) offer a unique opportunity for investigating female mate choice for paternal care behaviour because males exhibit extensive amounts of paternal care in both the field and captivity (Schradin & Pillay 2003), showing all the behaviours demonstrated by females (e.g. huddling and grooming pups) apart from lactation.

I ran three separate experiments to determine if female desert striped mice, using either visual or olfactory cues, distinguish between males of differing paternal quality and experience. In the first experiment, I investigated female choice using olfactory cues. In a previous study, I found that maternal care in desert striped mouse females has a patrilineal genetic component (Chapter 4). Therefore, I predicted that females would show a preference for males showing higher levels of paternal care, as this could increase the reproductive success of their daughters. Paternal care behaviour was recorded in males in a previous experiment and the amount of time spent in paternal care was summed over six days (Chapter 2). The amount of paternal care behaviour was used as an indicator of paternal quality. As female desert striped mice are already known to use olfactory cues in mate choice (Pillay 2000a), this prediction assumes that females can assess male quality from odour cues.

The second experiment was derived from the first and investigated female mate choice for paternal experience using olfactory cues. Schradin & Pillay (2004a) have shown that experienced desert striped mouse males have consistently higher prolactin levels than inexperienced males (Schradin & Pillay 2004a) and since prolactin is known to be associated with paternal care in male rodents (Gubernick & Nelson 1989), including the striped mouse (Schradin & Pillay 2003), I predicted that females would prefer experienced males. I also asked if female experience influences mate choice, as it has been suggested that older, more experienced, females are choosier

than younger, less experienced, females (e.g. reed buntings *Emberiza schoeniclus*, Bouwman & Komdeur 2005; smooth newts *Triturus vulgaris vulgaris*, Gabor & Halliday 1997).

In the third experiment, I investigated female choice for paternal quality using visual cues, as striped mice show retinal adaptations to a diurnal lifestyle, containing approximately 40% cone photoreceptors (Schumann et al. 2006). I experimentally manipulated paternal care behaviour by allowing females to visually choose between males that had access to pups and males that did not have access to pups. I predicted that females would prefer a male she observes physically caring for offspring as this may be an honest signal of his ability to care for young.

## METHODS

### General Maintenance and Husbandry

Striped mice used in this study were F1–F4 generation individuals derived from Goegap Nature Reserve in the succulent karoo (Northern Cape Province, South Africa; 29.40 S, 17.53 E). They were housed in the Milner Park Animal Unit at the University of the Witwatersrand, under partially controlled environmental conditions (14:10 h light: dark regime, lights on at 0500 hours; 20–24 °C; 30–60% relative humidity). Details of animal maintenance and husbandry are provided in Chapter 6 (Rymer et al. 2008).

### Experiment 1. Female choice for males displaying different levels of paternal care

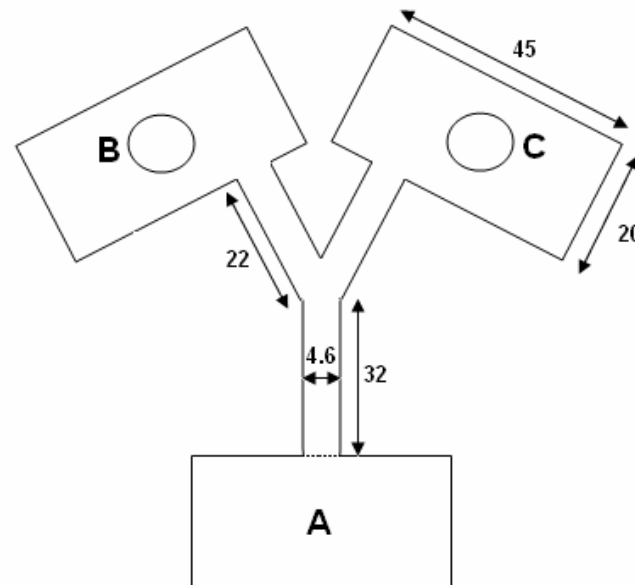
In this experiment, females were given a choice between the odour cues of males with different levels of paternal care. Twelve females and 15 donor males were used. Some donor males were used more than once, but they were not used more than three times and were never used in the same combination with the same males in choice tests. Females were only used once and all animals were unrelated to each other. As the level of paternal care may vary considerably between males, BETTER fathers were males which showed at least a 1.5 times greater level of paternal care than the male to which they compared (LOWER) in choice tests. Paternal care was assessed by means of behavioural observations (Chapter 2). Briefly, males raised a litter together with the female until the young were weaned at 21 days of age. Every second day from DAY 1

(DAY 0 = day of birth) until DAY 11, video recordings of males were made for 15 min between 0700 and 1100 hours. Paternal care was scored using the following behaviours (after Schradin & Pillay 2003): huddling and licking pups and time spent in close proximity (< 2 cm of pups). Time spent in paternal care was then summed for the six days of taping.

Two-way choice tests were conducted using a Perspex Y-maze apparatus attached to three equal-sized chambers (Fig. 1). Before each test, the apparatus was thoroughly cleaned with warm soapy water and alcohol and air dried. One week prior to testing, 30 g of week-old wood shavings (soiled with faeces, urine and other bodily secretions) were collected from the cages of donor males; samples were collected using latex gloves and were frozen in sealable freezer bags at -15 °C. 15 min prior to testing (one week later), the wood shavings were thawed at room temperature. Freezing does not have a significant effect on odour hedonicity in humans (Lenchova et al. 2008) or striped mice when kept at -20 °C (Pillay et al. 2006). Tests were conducted between 0700 and 1100, the peak period of striped mouse activity. A test female in oestrous (as determined using vaginal smears) was randomly chosen and placed into the start chamber (A, Fig. 1) and allowed full access to the maze for 5 minutes. After this period, the female was confined to the start chamber and the odour samples (placed in Perspex petri dishes) were introduced into the centre of the choice chambers (B and C, Fig. 1). The position of the odour cues from stimulus males was alternated at each test to avoid bias. The female was then allowed free access to the maze for 10 min. The apparatus was video recorded from above and no observers were present in the room during taping sessions. Using continuous sampling, I scored the duration (seconds) and frequency of sniffing bouts of each odour sample for the 10 min period.

## **Experiment 2. Female choice for males with and without paternal care experience**

In this experiment, maternally experienced and inexperienced females were given a choice between the odour cues of paternally experienced and inexperienced males. Thirty five females (18 experienced, 17 inexperienced) and 42 donor males (20 experienced, 22 inexperienced) were used. All animals were housed singly and were unrelated to each other. Some donor males were used more than once, but they were not used more than three times and were never used in the same combination with the



**Figure 1.** Y-maze apparatus used for female mate choice for males of differing paternal quality (BETTER or LOWER - Experiment 1) and for males of differing experience (EXPERIENCED or INEXPERIENCED - Experiment 2). Measurements are in cm. Petri dishes with odour samples from males were placed into the centre of each of choice chamber (B and C). The start chamber (A) and main branch were considered neutral areas. The start chamber could be closed off from the rest of the maze with a metal barrier.

same males in choice tests. Females were used once only. Both experienced males and females had produced at least one litter previously, whereas inexperienced males and females were all naïve. There was no difference in age between experienced and inexperienced females (mean ( $\pm$  SE) – experienced = 16 (1.23) months; inexperienced = 14 (2.11) months) or between experienced and inexperienced males (experienced = 18 (1.11) months; inexperienced = 17 (3.13) months), thus controlling for the possible confounding effects of age and experience. The test apparatus and procedure were identical to those described in Experiment 1 (see above).

### **Experiment 3. Female choice for males displaying or not displaying paternal care**

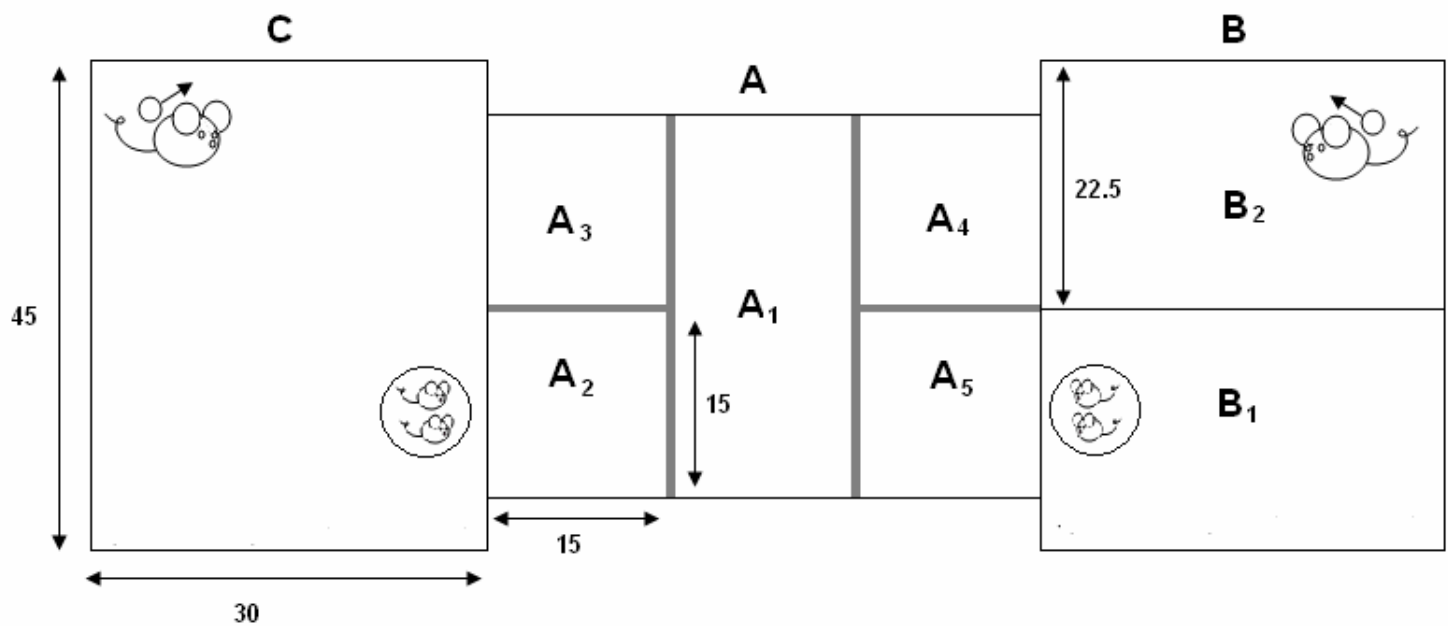
In this experiment, females were given a choice between males they could see caring for young and males not caring for young. Nineteen females and 30 males were used. Some males were used more than once, but they were not used more than twice and were never used in the same combination with the same males in choice tests.



Females were only used once. All individuals were unrelated to each other. Stimulus subjects consisted of one male and his four-day-old pups (ACCESS) and one male that had prior breeding experience, but was separated from pups (SEPARATED). Males may have been used in both ACCESS and SEPARATED trials as all males were involved in other breeding experiments. SEPARATED males were not fathers during testing. All pups used for both ACCESS and SEPARATED stimuli were sired by ACCESS stimulus males. SEPARATED males were unrelated to the offspring used, however striped mice are unable to discriminate between their own and alien pups until the young are at least 10 days old (Pillay 2000b). Stimulus males were matched for body size (Mean ( $\pm$  SE) – ACCESS = 74.49 (3.40) g; SEPARATED = 70.40g (2.53) g; Paired t test:  $t_{18} = 0.96$ ,  $P=0.352$ ).

Two-way choice tests were conducted in an apparatus consisting of three equal sized glass tanks arranged in an H-shape (Fig. 2). The centre tank (A, Fig. 2) was divided into three equal sections (left, middle, right) using masking tape and the central area ( $A_1$ , Fig. 2) was considered a neutral area. Each side section was subdivided into two equal areas (front left  $A_2$ , back left  $A_3$ , back right  $A_4$ , front right  $A_5$ , Fig. 2). This was done to determine if females respond to the male's interaction with pups or to pups only. One stimulus chamber (B, Fig. 2) was divided into two equal sections (front  $B_1$ , back  $B_2$ , Fig. 2) with a clear Perspex partition while the second stimulus chamber (C, Fig. 2) was unaltered. The positions of the stimulus chambers (left or right) were alternated between tests to avoid bias. The centre tank was not completely airtight (i.e. the tank lid had six 0.5 mm holes drilled in it) to allow air flow. There were no holes in the side walls between the centre tank and the two stimulus tanks. Before each test, the apparatus was thoroughly cleaned with warm soapy water and alcohol and left to air dry.

Four pups (2 males, 2 females) were removed from the breeding tank of the ACCESS male just prior to testing and two (1 male, 1 female each) were placed on a pad of cotton wool in each stimulus chamber, either in the front ( $A_2$  or  $A_5$ , Fig. 2) or back ( $A_3$  or  $A_4$ , Fig. 2). Placement (back or front) was alternated between tests to avoid bias. Both males were then introduced simultaneously into their respective chambers. ACCESS males were able to make contact with their pups (tank C, Fig 2) while SEPARATED males were placed on the other side of the Perspex partition ( $B_2$ , Fig. 2) in the stimulus tank and could not access pups.





**Figure 2.** Apparatus used for female mate choice for males displaying and not displaying paternal care (Experiment 3). Measurements are in cm. The centre tank (A) was divided into 3 main sections (left, central ( $A_1$ ), right) with the left and right sections being divided into 2 further sections ( $A_2$ ,  $A_3$ ,  $A_4$ ,  $A_5$ ). One stimulus chamber (B) was divided into 2 sections ( $B_1$ ,  $B_2$ ).  represents pups and  represents males and their position at the onset of the experiment.

An inexperienced test female was randomly chosen and placed into the central area ( $A_1$ ) of the test chamber. I used an inexperienced female as this represents the natural situation where naïve females are initially looking for mates. The apparatus was video recorded from above for 5 min and no observers were present in the room during taping sessions. The duration of tests were restricted to 5 min for ethical reasons, since small rodent pups require exogenous heat for thermoregulation (Wang & Novak 1994) and could therefore suffer from thermoregulatory stress. Using continuous sampling, I scored the duration (seconds) and frequency of visits by test females to the positions represented by  $A_2$ ,  $A_3$ ,  $A_4$ , and  $A_5$ .

### Statistical analysis

The datasets did not meet the assumptions of normality (Shapiro–Wilk’s test) and homogeneity of variances (Levene’s test), even after transformation, and therefore all data were analysed using nonparametric statistics. For both duration and frequency

data, I used Wilcoxon matched pairs test (Experiment 1 and 2) or Friedman ANOVA (Experiment 3). Dunn's post hoc test was used to identify specific differences for Friedman ANOVA testes. The model-level significance was determined at a  $\alpha = 0.05$ . All tests were two-tailed.

## RESULTS

### **Experiment 1. Female choice for males displaying different levels of paternal care**

Females did not show a preference for the odour cues of males showing higher levels of care (BETTER vs. (LOWER) (Table 1).

### **Experiment 2. Female choice for males with and without paternal care experience**

Experienced females showed a preference for experienced males, spending significantly more time sniffing the odour cues from experienced males (Table 1, Fig. 3), although the frequency of sniffs did not differ between odour samples (Table 1). In contrast, inexperienced females showed no preference for either experienced or inexperienced males (Table 1, Fig. 3).

### **Experiment 3. Female choice for males displaying or not displaying paternal care**

Females did not show a preference for males she observes physically caring for offspring over males she observes ignoring young (Table 1).

## DISCUSSION

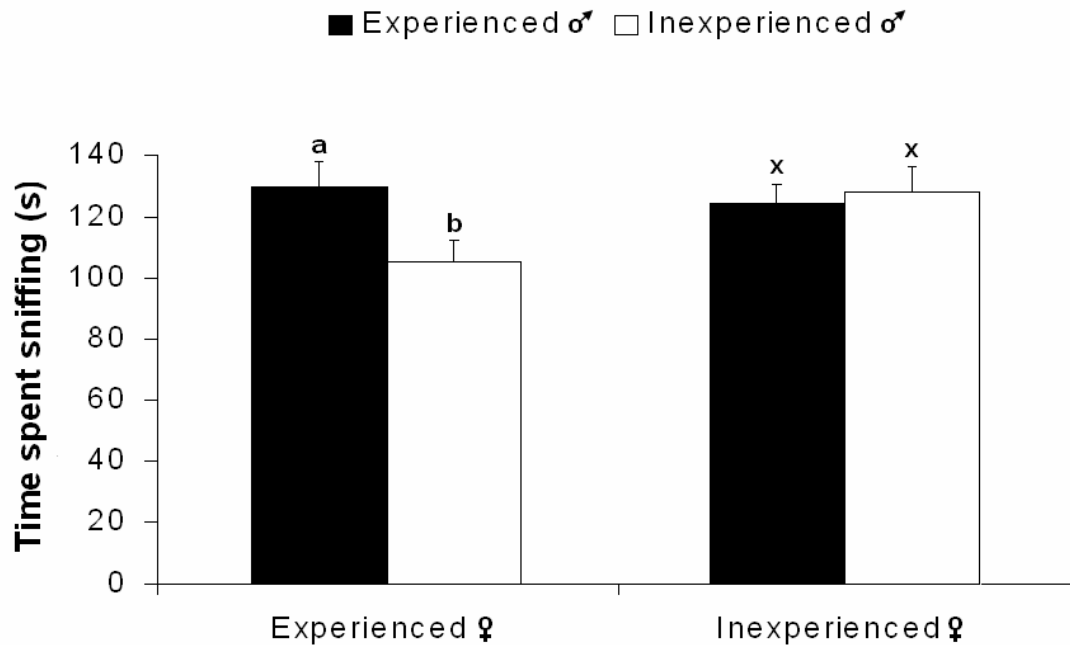
Overall, my results do not support the prediction that females prefer males that show higher levels of paternal care naturally (Experiment 1) or through experimental manipulation (Experiment 3). However, experienced females did prefer experienced males to inexperienced males (Experiment 2).

Female desert striped mice did not show a preference for the odour of males showing higher levels of paternal care (BETTER) over the odour of males showing lower levels of care (LOWER). This lack of preference could mean an inability by females to discriminate between males with different levels of paternal care or an

**Table 1.** Duration and frequency of female mate choice for males with different paternal care abilities (Experiment 1), experienced and inexperienced males (Experiment 2) and males that could and could not make contact with pups (Experiment 3). Statistics: Wilcoxon-matched pairs and Friedman ANOVA tests. Significant tests indicated in bold.

	Duration (s)		Frequency	
	Mean ( $\pm$ SE)	Statistics	Mean ( $\pm$ SE)	Statistics
<b>Experiment 1</b>				
BETTER	74.58 (6.67)	$Z=0.78$ , $n=12$ ;	9.58 (1.15)	$Z=0.00$ , $n=12$ ;
LOWER	85.21 (11.71)	$P=0.433$	9.50 (0.94)	$P=1.000$
<b>Experiment 2</b>				
<i>Experienced</i> ♀				
EXPERIENCED ♂	121.03 (7.76)	<b><math>Z=2.16</math></b> , $n=18$ ;	9.22 (0.77)	$Z=0.43$ , $n=18$ ;
INEXPERIENCED ♂	98.15 (6.47)	<b><math>P=0.031</math></b>	8.78 (0.96)	$P=0.670$
<i>Inexperienced</i> ♀				
EXPERIENCED ♂	116.09 (5.75)	$Z=0.73$ , $n=17$ ;	11.18 (1.21)	$Z=0.49$ , $n=17$ ;
INEXPERIENCED ♂	119.56 (8.13)	$P=0.463$	11.35 (1.17)	$P=0.623$
<b>Experiment 3</b>				
ACCESS	110.01 (8.63)	$F_{r3}=1.04$ , $n=19$ ;	13.16 (1.88)	$F_{r3}=2.15$ , $n=19$ ;
SEPARATED	118.66 (11.29)	$P=0.791$	12.05 (1.64)	$P=0.542$

indifference of females. If females were unable to assess paternal care abilities in the males, it is possible that the soiled bedding did not contain the appropriate chemical cues indicative of paternal care behaviour. Rodent odour cues contain both volatile and non-volatile compounds (Hurst et al. 1998) that provide a variety of information, such as an individual's reproductive state (Ferkin et al. 2004) and identity (Johnston & Jernigan 1994). Prolactin is known to be associated with paternal care in desert striped mice (Schradin & Pillay 2003, Schradin 2008) and breeding males have significantly higher levels of prolactin than non-breeding roamer and philopatric males (Schradin 2008). Prolactin levels in male desert striped mice increase following



**Figure 3.** The responses of experienced and inexperienced female desert striped mice in two-way choice tests to odour cues of experienced and inexperienced males. Mean  $\pm$  SE time spent sniffing (seconds) the soiled bedding of stimulus males. Bars with the same letter indicate non-significant differences.

the first experience of parenting and then remain at high levels throughout the lifespan of males (Schradin & Pillay 2004a). Female desert striped mice were able to distinguish between experienced and inexperienced males, suggesting that females can possibly detect the presence of prolactin in the urine of experienced males, although this remains to be verified as there is currently no information on whether prolactin has an odour plume. However, as prolactin secretion is an “all or none” response (Schradin & Pillay 2004a) and all males used in Experiment 1 had prior breeding experience, this suggests that prolactin levels may not vary with different levels of paternal care. Females would thus be unable to distinguish between breeding males of different parental care ability through detection of prolactin levels in urine.

Experienced female desert striped mice showed a preference for experienced males. Experienced male desert striped mice have higher prolactin (Schradin & Pillay 2004a) and lower testosterone (Schradin et al. in press) levels than inexperienced males, suggesting a trade off between dominant/aggressive behaviours and

sociopositive behaviours (Schradin et al. in press). These males are thus likely to be paternal group-living males (i.e. stay-at-home fathers) that will remain with the female and display paternal care (Schradin 2008). In addition, experienced males are likely to be territorial dominant breeders, which show socio-positive behaviours to gain access to females (Schradin et al. in press). Female preference for experienced males would thus result in increased care for her offspring. However, males may have differed in their body odours, not because they were paternally inexperienced, but because they were sexually inexperienced. Future studies should investigate the role of sexual experience in female mate choice in desert striped mice.

Females did not show a preference for males with and without pup contact. There are three possible explanations for this finding. Firstly, females may not use visual cues when assessing paternal quality, as assumed here. While desert striped mice live in small family groups, they forage alone (Schradin & Pillay 2004b) and females may not have the opportunity to observe potential mates interacting with pups prior to group formation. Secondly, females in this study may not have shown a preference because pups were present in both stimulus tanks. Pups are a potent stimulus for desert striped mouse females (N. Pillay, pers. comm.). All females used in this study were sexually mature, but naïve, and were therefore unrelated to the pups used. Females showed equal attraction to all pups, therefore their apparent lack of preference for males could have merely been an innate response to the presence of alien pups. Future studies should investigate this aspect. Thirdly, it is possible that female desert striped mice are able to distinguish between males, but choose not to. In general, multiple stimuli are more effective than a single stimulus in eliciting a response by females (Rowe 1999). In the present study, as each experiment focused on only channel of information transfer (either olfactory or visual cues), it is possible that females chose not to assess males because too few stimuli were available to allow for a reliable assessment.

While this study provides little support that female desert striped mice distinguish between males on the basis of their paternal care abilities, females do appear to prefer experienced males, which have prior breeding experience and are likely to remain in the nest and provide care to young. Females may require multiple stimuli to accurately assess male parental quality, but may be less choosy of parental quality than parental experience because offspring development can be facilitated by the presence of helpers other than the male.

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## CHAPTER EIGHT

### Discussion

This study had two broad aims. The first aim was to investigate how genetic and non-genetic factors influence the development and transmission of paternal care behaviour in African striped mice *Rhabdomys pumilio* from the succulent karoo (hereafter termed “desert striped mice”). At least one study of rodents (i.e. California mice *Peromyscus californicus*, Bester-Meredith & Marler 2003a) has shown that the development of paternal care behaviour is influenced by the early experience of receiving paternal care from their fathers. In contrast, the transmission of paternal care behaviour in desert striped mice does not appear to be non-genetically influenced by the father (Chapter 2). In addition, unlike some studies in birds suggesting that paternal investment can be genetically inherited from fathers (e.g. savannah sparrows *Passerculus sandwichensis*, Freeman-Gallant & Rothstein 1999; long-tailed tits *Aegithalos caudatus*, MacColl & Hatchwell 2003), the level of paternal care behaviour in desert striped mice does not appear to be genetically influenced (Chapter 4). An unanticipated finding of my study was that mothers overcompensate their level of investment when raising young alone, which results in their sons expressing greater levels of paternal care behaviour (Chapter 2). This pattern did not extend to daughters, which always showed high levels of maternal care behaviour, regardless of rearing condition (Chapter 3). This contrasts with other rodent studies showing a non-genetic maternal influence on the development of maternal care behaviour (e.g. rats *Rattus norvegicus*, Francis et al. 1999; laboratory mice *Mus musculus*, Kikusui et al. 2005). Instead, maternal care behaviour in desert striped mice appears to be under partial patrilineal genetic control, suggesting that daughters inherit care-giving behaviour from their fathers (Chapter 4). I also found that male desert striped mice (sons) raised by the mother and a second care-giver (helper) showed similarly high levels of paternal care behaviour as males raised by the mother alone (i.e. in the absence of the father); again mothers overcompensated investment when a helper was present (Chapter 5).

The second aim of this study was to investigate the significance of paternal care in: a) respect of its influence on offspring physical behavioural development; and b)

female mate choice. Despite the fact that paternal care has previously been shown to be important for offspring growth in desert striped mice kept under semi-natural conditions (Schradin & Pillay 2005a), I did not find the same influence of fathers in the laboratory, possibly because optimal conditions in the laboratory limit the energetic burden of the parents (Brown 1993). However, I found that fathers are important demonstrators about novel food for young desert striped mice, although mothers are still more reliable than fathers (Chapter 6). Finally, while females choose males on the basis of their paternal care quality in some species of fish (e.g. sand gobies *Pomatoschistus minutes*, Forsgren 1997; fifteen-spined sticklebacks *Spinachia spinachia*, Östlund & Ahnesjö 1997), female desert striped mice did not show a preference between males differing in their level of paternal care-giving ability, both inherently and experimentally manipulated (Chapter 7). Females, however, did show a preference for experienced males (Chapter 7).

### **The development of paternal care behaviour**

Behaviour is influenced by both genes and the environment in which an individual is raised (McFarland 1999; Goodenough et al. 2001). It has, however, been postulated that it is primarily the dynamic interaction between genes and the environment that influences the overall expression of the behaviour (Bjorklund 2006), although the relative influence of genetic or environmental effects can vary (Shutler et al. 2005). Environmental effects, in turn, can either directly or indirectly influence the development of behaviour. For example, young chimpanzees *Pan troglodytes schweinfurthii* learn termite-fishing behaviour through direct observation of their mothers (Lonsdorf 2006), while increased levels of gestational stress in guinea pigs *Cavia porcellus* causes androgen receptors of the hypothalamus to be upregulated in female offspring, resulting in females showing male-typical play and courtship behaviours (Kaiser et al. 2003).

The development of paternal care behaviour in desert striped mice does not appear to be either genetically or non-genetically transmitted from fathers to sons (i.e. the presence of the father does not influence the development of paternal care behaviour in sons and good fathers do not necessarily produce sons that will be better fathers), even though paternal care (through huddling) influences offspring growth and survival (by minimising heat loss in pups, Schradin & Pillay 2005a; Scantlebury et al.

2006; Schradin et al. 2007). Although desert striped mouse groups typically consist of 4-5 adult individuals (Schradin & Pillay 2004a), which is suggested to be the optimal group size for huddling in small rodents (Canals et al. 1989; 1998), females may raise young alone when the population density decreases, since reproductive competition may favour solitary living when the opportunity arises (Schradin et al. in preparation). Equally, males adopt a roaming strategy, mating with several females and showing no paternal care (Schradin 2008). Females would, therefore, not have the benefit of paternal care during these times and offspring survival would potentially be compromised if mothers did not adjust their level of investment appropriately. On the other hand, during periods of high population density, female striped mice are forced to aggregate due to the limited availability of nesting sites (Schradin 2005a; Schradin et al. in preparation) and dominant males will associate with a group of females and will show paternal care (Schradin 2008). In a communal nest, young can gain thermoregulatory benefits from huddling with individuals other than the father, such as aunts or philopatric adults (Schradin 2005a; Scantlebury et al. 2006). Therefore, as females are capable of raising young alone, the provisioning of paternal care (or care provided by aunts and philopatric older siblings) would be merely additive to the care provided by the mother, and the level of paternal care would not necessarily be important, as any care would be beneficial. This may also explain why females do not select males based on paternal quality (as discussed below).

It appears that the level of paternal care shown by male desert striped mice is strongly influenced by the early mother-young relationship. This relationship is known to be important for neural development of female offspring (Macrí et al. 2004), through its influence on the development of the hypothalamic-pituitary-adrenocortical (HPA) system (e.g. rats, Liu et al. 1997; Pryce & Feldon 2003), which affects later responsiveness to offspring (Macrí et al. 2004). For example, female rats that receive high levels of maternal care (licking and arched-back nursing) during the preweaning period show decreased levels of plasma adrenocorticotrophic hormone and corticosterone (Liu et al. 1997) and an associated increase in maternal investment in their own daughters (Francis et al. 1999). While no other studies have investigated the influence of mothers on the development of paternal care behaviour in their sons, the early mother-son relationship could also be postulated to have important influences on desert striped mouse male offspring neural development (through development of the

HPA system) as both male and female pups are dependent on their mothers for their early nutritional requirements.

Alternatively, or in addition, parental care influences the development of the mesocorticolimbic dopamine system (Meaney et al. 2002) and secretion of prolactin, a pituitary peptide hormone (Nedvídková et al. 2000) known to promote both maternal (Wynne-Edwards & Timonin 2007) and paternal care behaviour (Gubernick & Nelson 1989) in rodents, including the desert striped mouse (Schradin & Pillay 2004b; Schradin 2008), is under tonic inhibitory control by dopaminergic neurons in the medial basal hypothalamus (Romero & Phelps 1993). Prolactin regulates its own secretion via a negative feedback mechanism (Romero & Phelps 1993). It stimulates the tuberoinfundibular dopamine neurons to increase dopamine secretion into the circulatory system, which in turn inhibits further prolactin secretion (Grattan et al. 2008). During early development, suckling by young stimulates the mother's hypothalamus to increase prolactin production (Lupoli et al. 2001). Prolactin is then transferred to her milk and is subsequently ingested by the offspring (Pahwa & Pandey 1984; Ellis et al. 1996). Prolactin then passes through the pup's gut and enters the systemic circulation (Shyr et al. 1986). This circulating prolactin can then act together with locally synthesized prolactin (released in the brain) to modulate neuroendocrine responses (Roselli et al. 2008). I propose that it is this interaction between suckling behaviour of young and maternal prolactin secretion that primes the development of paternal care behaviour in male desert striped mice. I suggest the following model: 1) Mothers raising young alone return to the nest more often than mothers raising young together with the mate. 2) As a result, young raised by the mother alone have more opportunities to suckle. 3) Prolactin secretion by the maternal hypothalamus reaches a threshold level (where prolactin cannot be secreted at a faster rate) and thus increased suckling by young raised alone causes prolactin levels in the milk to decrease. 4) This then results in the suppression of dopamine in the young and a corresponding elevation of circulating plasma prolactin concentration after weaning, as seen in rats (Shyr et al. 1986). 5) High levels of prolactin then stimulate males to show higher levels of paternal care behaviour. This model remains to be investigated.

Other hormones, such as vasopressin, may be equally important in the expression of paternal care behaviour, particularly as vasopressin has been suggestively linked with paternal retrieval behaviour in California mice (Bester-Meredith & Marler 2003a). Males that retrieved young more often showed higher levels of arginine

vasopressin-immunoreactive (AVP-ir) staining in the bed nucleus of the stria terminalis (BNST) and young that were retrieved more often showed similarly high levels of paternal retrieval behaviour when adult (Bester-Meredith & Marler 2003a). The study in California mice suggests that the experience (non-genetic influence) of early paternal care influences secretion of vasopressin in the BNST, and high levels of circulating vasopressin then influence the expression of paternal care behaviour. However, vasopressin shows diversity in the genetic regulation of its receptors, which also influences the natural variation in social behaviour between and within species (Donaldson & Young 2008). Although paternal care in montane voles (*Microtus montanus*) has been associated with increased vasopressin gene expression (Wang et al. 2000), a direct link between vasopressin secretion and the experience of paternal care behaviour remains to be verified (Bester-Meredith & Marler 2003a). The influence of vasopressin on paternal care behaviour in striped mice is currently being investigated.

### **The function of paternal care behaviour**

The most commonly proposed function of paternal care is that it ensures offspring survival (Bester-Meredith & Marler 2003b) through provision of exogenous heat by huddling (e.g. Djungarian hamsters *Phodopus campbelli*, Wynne-Edwards 1995; California mice, Gubernick & Teferi 2000); however, a number of other functions have also been suggested. By showing paternal care, fathers may: 1) cause modifications in offspring social behaviour (e.g. aggression in California mice, Bester-Meredith & Marler 2003b); 2) protect young against predators (e.g. fat-tailed Dwarf lemurs *Cheirogaleus medius*, Fietz & Dausmann 2003); 3) promote learning opportunities for young (e.g. white-footed mice *Peromyscus leucopus*, Schug et al. 1992); and/or 4) supply young with additional food (e.g. blue tits *Cyanistes caeruleus*, Dickens et al. 2008). Alternatively, or in addition, provision of paternal care may be considered a mating strategy, where the function of providing care is to develop or maintain bonds with females in order to secure future reproductive opportunities (Fernandez-Duque et al. 2008). In my study, I investigated whether male desert striped mice promote learning, in particular about novel foods, in their offspring.

### ***Social transmission of information about novel food***

Some foods may be patchily distributed in space and time (Ostfeld 1985) or may be toxic and unpalatable (Galef & Clark 1971). Therefore, young group-living animals may rely on conspecifics to facilitate learning (i.e. demonstrators, Sherwin et al. 2002) and to gain information about the immediate environment (Galef & Laland 2005). My study suggests that paternal care in desert striped mice functions to facilitate learning about novel foods in young. Despite the fact that overall food abundance in the succulent karoo is high throughout the year, desert striped mice lose body condition during the hot summer months and require protein-rich foods (that are patchily distributed in both space and time, Schradin 2005a), to ensure survival during this period (Schradin & Pillay 2005a). Since natural selection will favour the evolution of information-acquiring systems when individual survival and fitness is positively influenced (Galef & Laland 2005), I suggest that young desert striped mice learn from their fathers because fathers may provide young with information about unpredictable highly palatable, protein-rich foods (plant material and insects) when these start appearing early in spring (Schradin 2005a). Furthermore, male striped mice from a grassland population do not show paternal care under natural conditions and are not reliable demonstrators of novel food for their young, supporting the premise that paternal care in desert striped mice must have some adaptive value. I also found that a hierarchical order of demonstrator reliability exists for desert striped mice. Mothers are the primary demonstrators because young are completely dependent on their mothers initially and mothers can provide information for young through multiple channels (e.g. olfactory and gustatory cues, Rymer et al. 2008). Fathers can be considered secondary demonstrators for two reasons. Firstly, they have fewer channels for information transfer, and secondly, males may not always be present to provide learning opportunities for young; for example, during periods of low population density when males adopt a roaming mating strategy and show no paternal care (Schradin 2008).

### **The importance of paternal care in desert striped mice**

Gestation and lactation are energetically demanding for female mammals (Millar 1978). Males may reduce the workload of females (McGuire 1997) by providing paternal care, allowing females to meet these costs through a reduction in maternal

investment and an associated increase in time spent in other activities, such as foraging. For example, in European ground squirrels *Spermophilus citellus*, females with paternal help spend more time foraging than females raising young alone, as males reduce the maternal workload by digging burrows for females and young (Huber et al. 2002). Similarly, I propose that paternal care in desert striped mice is important for reducing the maternal workload of the female, as female desert striped mice show lower levels of care when raising young together with a male. Females nesting with their mates spend more time foraging when away from the nest, and they are able to do this because males return to the nest at a similar rate to females (i.e. they spend equal amounts of time in the nest, Schradin 2006). In contrast, females nesting alone would need to return to the nest more often to minimize thermoregulatory and nutritional stress of her offspring and would show a corresponding decrease in foraging and other activities, as indicated in this study (Chapter 2).

Although this study suggests that paternal quality is not as important as the occurrence of paternal care, it is possible that female desert striped mice do not show a preference for males with different paternal care-giving abilities because the opportunity to exercise choice for paternal quality may not exist in the succulent karoo. Desert striped mice favour *Zygophyllum retrofractum* shrubs as nesting sites (Schradin & Pillay 2004a) but these are generally patchily distributed and there is strong interspecific competition with bush karoo rats *Otomys unisulcatus* for these sites (Schradin 2005b). As a result, females form small aggregations in one shrub, which is then defended by a dominant territorial male (female-defence polygyny, Ostfeld 1987; Seki et al. in press). Therefore, females may live and breed communally with the dominant male, whose status has been determined by previous encounters with other males (Schradin 2004) and his age (Schradin 2008), and not by his paternal care-giving abilities. It is possible that dominance may be linked with paternal care-giving ability as dominant territorial breeders show higher levels of prolactin than roaming or philopatric males (Schradin 2008). This, however, still requires investigation in desert striped mice. One study in sand gobies has shown that dominant males do not have better care-giving abilities and females do not choose males based on dominance status (Forsgren 1997), but I am unaware of studies investigating the relationship between dominance and paternal care-giving abilities in male rodents. It is also possible that female desert striped mice may exercise choice



for males, but may base their decisions on traits other than paternal care-giving ability, such as level of aggressiveness (e.g. meadow voles *Microtus pennsylvanicus*, Spritzer et al. 2005), nutritional state (e.g. swordtail fish *Xiphophorus birchmanni*, Fisher & Rosenthal 2006) or age (e.g. fruit flies *Drosophila pseudoobscura*, Avent et al. 2008).

### **The evolution of paternal care in desert striped mice**

Two general hypotheses (not necessarily mutually exclusive) have been proposed to explain the evolution of paternal care. The “male care hypothesis” suggests that males will provide care: 1) when their certainty of paternity is high; 2) to secure future mating opportunities; and 3) when offspring development, growth and/or survival is enhanced (Smuts & Gubernick 1992). On the other hand, the “mating constraints hypothesis” suggests that males will provide care when they are ecologically and/or socially constrained from securing additional mating opportunities (Orians 1969; Queller 1997). In accordance with previous studies in striped mice (Schradin 2005a; Schradin & Pillay 2005b; Schradin & Pillay 2005c), my study provides evidence that paternal care in the desert striped mouse has evolved because males are socially (high population density resulting in habitat saturation) and ecologically (limited number of nesting sites in *Zygophyllum retrofractum* bushes) constrained from securing additional mating opportunities. Secondary effects of providing paternal care were the benefits accrued through increased offspring survival and development (Schradin & Pillay 2005a; Scantlebury et al. 2006; Schradin et al. 2007) and the promotion of learning opportunities for young (Rymer et al. 2008).

### **Future studies**

The influence of fathers and older helpers on the maternal workload of females under natural conditions needs to be addressed. Studies could investigate time investment (as studied in Eurasian beavers *Castor fiber*, Sharpe & Rosell 2003) between mothers and additional helpers (i.e. fathers, aunts, philopatric young). Current studies suggest that older helpers provide similar amounts of care to young as fathers (Schubert et al. in press). Therefore, I would predict that female desert striped mice increase the time

spent foraging and decrease the level of care when males or older helpers are present, as suggested for European ground squirrels (Huber et al. 2002).

The influence of experience on paternal care behaviour should also be investigated. Schradin & Pillay (2004b) showed that experienced males have higher prolactin levels than inexperienced males; however, my study showed that inexperienced males raised by mothers alone showed higher levels of paternal care. This suggests that prolactin has the ability to prime paternal care behaviour in males. Males raised by mothers alone show a heightened initial paternal response to offspring due to higher initial prolactin levels, while males raised by both parents show a delayed response to young. This response in males raised by both parents, however, improves with time and experience. In my study, I investigated the paternal care behaviour of males (sons from different treatments) for one litter. Future studies should consider paternal care behaviour in subsequent litters. I would predict that as males become more experienced fathers, they will show a corresponding increase in prolactin levels and a corresponding increase in paternal care to their young (Schradin & Pillay 2004b).

Finally, the proximate mechanisms of information transfer about parental care from mothers to sons needs to be addressed. It would be worthwhile investigating the influence of the mother on the development of the HPA system in both male and female desert striped mice (as studied in rats, Pryce & Feldon 2003). I would predict that, if mothers influence the development of the HPA system, young desert striped mice should show decreased fearfulness in response to novelty, as suggested for rats (Caldji et al. 1998). The role of ingested prolactin in the mother's milk and its influence on elevating circulating plasma prolactin in young could also be investigated. I would predict that ingestion of milk would result in increased circulating plasma prolactin levels (measured through blood collection; see Schradin 2008) in young males as prolactin can be transferred to milk (Pahwa & Pandey 1984; Ellis et al. 1996).

### **Conclusion**

Paternal care is an unusual behaviour in mammals because males are unable to provide direct care during the prenatal period and can thus desert females during this time (Maynard Smith 1977). However, paternal care can evolve a) if the benefits

accrued from providing care (e.g. through increased offspring survival) outweigh the costs associated with lost mating opportunities; and/or b) because of social and ecological constraints (e.g. low population density). My study has shown that fathers are reliable demonstrators about novel foods in striped mice from the succulent karoo, adding to the positive influences that fathers provide for their young (i.e. growth and survival). However, the expression of paternal care behaviour does not appear to show a paternal genetic or non-genetic pattern (i.e. good fathers do not produce sons that will be better fathers). This, together with the inability of females to distinguish between males based on paternal quality (i.e. better or poor quality fathers), suggests that paternal quality is not as important as the occurrence of paternal care, and any care provided by the male is therefore better than no care at all.

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