Sociality and reproductive biology of the bushveld gerbil *Gerbilliscus leucogaster*

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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.

Tracy Kim Lötter

13th day of August 2010

ABSTRACT

I studied sociality and reproduction in mainly captive, but also free-living, bushveld gerbils *Gerbilliscus leucogaster* from a grassland region in South Africa. Little is known about these aspects in bushveld gerbils, and this study aimed to investigate these further and to propose a model of sociality for the species.

The investigation of the reproduction and postnatal development revealed that some aspects of reproduction, such as litter size and breeding season, seem to vary with geographic location, but that the slow postnatal development appears to be phylogenetically constrained. Staged dyad encounters were employed to investigate social interactions in different temporal and spatial contexts, focussing on male–female interactions but with a secondary investigation of same-sex interactions. Tolerance between strangers was generally low for all sex combinations. However, while male–female interactions revealed overall low tolerance levels throughout the week-long study, same-sex, particularly female, interactions showed an increase in tolerance over time. Females appeared to be cautious of males initially, but later became aggressive towards them. Females were also aggressive towards males during pregnancy and lactation, which may function to reduce potential infanticide risk. Observations of mothers with weaned juveniles indicated that maternal tolerance remained high in the absence of a subsequent litter, and consequently that philopatry is possible. Although few mothers had another litter, it appears that maternal aggression may trigger dispersal of the previous litter in this situation. Dyad encounters between weaned juveniles and unfamiliar adults over three nights were highly variable, but adults generally tolerated juveniles, particularly after the first night, and I suggest that adults may often tolerate juveniles in nature. The above social encounters indicated a high level of behavioural variation among individuals. In the field, breeding and space use patterns were investigated by employing mainly capture–mark–recapture techniques. Low population density at my field site may have been due to poor rainfall and perhaps to suboptimal habitat. Despite often small sample sizes and related limitations, some interesting trends were evident: breeding was associated with the summer rainfall season, and space use data suggested a lack of male territoriality, while females appeared to occupy exclusive areas with respect to one another. Both field and laboratory data supported a promiscuous mating system.

There were some discrepancies between my laboratory data, the field data and the literature, and I conclude that these are best explained by a flexible social system whereby

individuals live alone at times, such as at low population density, but are able to tolerate one another in close proximity, for example when density is high. Since prolonged male–female affiliations are unlikely, at least during the breeding season, any group formation is probably due to female or sibling associations, or to natal philopatry. This study has demonstrated that bushveld gerbils display plasticity in various aspects of sociality and reproduction, a characteristic that would allow them to adjust to changing environmental conditions, including fluctuating population densities.

I dedicate this work to my long-suffering family, especially:
my parents, Lawrie & Kathy Aenmey, and my husband, Mervyn Lötter
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CHAPTER ONE

GENERAL INTRODUCTION

LITERATURE REVIEW

Social and mating systems

Forms

The terms "solitary" and "social" should not be viewed as discrete forms of sociality, but rather as endpoints along a continuum (reviewed in Lacey & Sherman 2007). On one extreme are solitary species such as the brown desert mouse *Pseudomys desertor*, which apparently lives in isolation apart from associations between a male and female for mating, and between a mother and her dependent offspring (Happold 1976). On the other extreme is the eusocial naked mole-rat *Heterocephalus glaber*, where colonies display reproductive skew (such that only one female breeds), worker castes and co-operative brood care (Jarvis 1981). There are many forms of sociality between these extremes (Lacey & Sherman 2007), such as that of the degu *Octodon degus*, where female kin form social groups and nest communally (Ebensperger et al. 2004) or the ice rat *Otomys sloggetti robertsi*, which is territorial above-ground but huddles in groups below-ground as a consequence of the cold conditions in which it lives (Hinze 2005).

The mating system of a population or species is closely related to its social system (Lott 1991). Waterman (2007) reviewed the three primary mating systems described for rodents, namely monogamy, polygyny and promiscuity. Monogamy occurs when both sexes access only one mate. In rodents it is inferred through traits such as home range overlap of male–female pairs, pair-bonding, parental care or a lack of sexual dimorphism. Polygyny occurs when a male is able to monopolise access to more than one female. There are two main categories: defence polygyny, where males defend territories and/or access to females, and non-defence polygyny, where no defence takes place and access to females is determined by dominance hierarchies or competitive searching. Promiscuity occurs when both sexes mate with more than one partner, and is common among rodents. Although polygyny was thought to be the predominant mating system among rodents, paternity studies have revealed numerous instances of multi-male mating by females in species previously considered polygynous (Waterman 2007).

Mechanisms

Spacing patterns, in terms of home range size and distribution, form an important component of mammalian social and mating systems, and can be used to infer social and mating systems in rodents (Ribble & Stanley 1998). A number of spacing systems are employed by mammals, such as territoriality, undefended home ranges, dominance and coloniality (Lott 1991). From a spatial perspective, individuals living in a group are expected to show substantial overlap and may share a nest (Lacey & Sherman 2007), whereas individuals living alone should maintain a relatively large inter-individual distance (Lott 1991). Animals will be territorial if important resources are distributed such that the defence of them increases reproductive success (Ims 1987). Hypotheses explaining territoriality in small mammals suggest that females defend territories to protect food resources and/or to protect their young from infanticide, whereas males are territorial to defend mating opportunities (reviewed in Ostfeld 1990; Wolff 1993). California voles *Microtus californicus* exhibit male territoriality, while female home ranges frequently overlap (Ostfeld 1986). This likely reflects a polygynous mating system with one male defending a number of females (Ostfeld 1986). Male brush mice *Peromyscus boylii* and pinyon mice *P. truei* have undefended home ranges, such that male home ranges overlap with a number of females and other males, and the suggested mating system is promiscuous (Ribble & Stanley 1998). In the multimammate mouse *Mastomys natalensis* from Tanzania, both sexes have undefended home ranges (Leirs et al. 1996).

The social behaviour of conspecifics towards one another also reveals much about the social organisation and mating system. Salo et al. (1993) note that the social and mating systems of different species are a product of collections of traits, including behavioural tendencies, expressed by individual animals. For example, they found that the duration of huddling in four species of *Microtus* was a reliable indicator of the different social and mating systems of these species, with the more social species showing prolonged huddling behaviour. From a behavioural perspective, interactions within groups are likely to be affiliative, co-operative and nepotistic (Lacey & Sherman 2007), whereas solitary individuals either react impartially towards or are repelled by conspecifics, attacking, ignoring or avoiding them apart from mates and offspring (Lott 1991). The Olympic marmot *Marmota olympus* lives in distinct colonies and interactions between conspecifics are exceptionally tolerant and playful, reflecting the high degree of sociality in this species, whereas aggressive interactions characterise conspecific exchanges in solitary woodchucks *Marmota monax* (reviewed in Barash 1974). Lacey & Sherman

(2007) point out that, although spatial and behavioural criteria for sociality do not conclusively reveal social structure, information on these two aspects together can be used to get a fair indication of which taxa are group-living.

Social systems are not fixed within a species, and intraspecific variation is determined by aspects such as ecology, demography, kinship and social behaviour (Lott 1991). For example, female meadow voles *Microtus pennsylvanicus* are solitary in summer but are more social at other times of the year (reviewed in Madison & McShea 1987), a behaviour pattern that seems to be influenced by day length (Beery et al. 2008). As with social systems, mating systems may also vary within a species and are influenced by ecological and demographic factors as well as intraspecific conflict, such as the spatial and temporal distribution of receptive females, male–male competition, habitat structure and female reproductive strategies (Emlen & Oring 1977; Lott 1991; Waterman 2007). For example, Randall et al. (2002) found that the giant kangaroo rat *Dipodomys ingens* displayed a monogamous or polygynous/promiscuous mating system depending on density and oestrous synchrony. Furthermore, female reproductive strategies, such as multi-male mating, can lead to subtle forms of competition among males, such as sperm competition (Waterman 2007).

Finally, since rodent societies are formed primarily as a result of natal philopatry (Lacey & Sherman 2007; but note debate on this subject in Ebensperger & Hayes 2008), philopatry and dispersal are important mechanisms influencing both social and mating patterns. For philopatry to occur, there must be post-weaning tolerance by the parent(s) and any other group members towards the juveniles. Indeed, Nunes (2007) notes that co-operation and philopatry are closely related. In the absence of philopatry, juveniles will disperse and attempt to establish their own territory/home range, thus increasing the probability of encountering strange conspecifics. These conspecifics can exert a strong influence on the dispersal process, depending on their levels of tolerance towards the dispersers (Solomon 2003). For example, Boonstra (1984) found that lactating female meadow voles were aggressive towards strange young, which was consistent with previous field studies suggesting that female density on the one hand, and juvenile survival and recruitment on the other, were inversely correlated.

Reproductive biology

Although my study focuses on sociality, including mating systems, it is also of interest to investigate reproductive biology, since reproductive traits may be associated

with social and mating systems. For example, multi-male mating may affect female reproductive success, for instance through an increase or decrease in the likelihood of conception, and even through increased pup survival (reviewed in Solomon & Keane 2007). In the giant kangaroo rat, data by Randall et al. (2002) suggested that females mating exclusively with a single male weaned more offspring than those experiencing male competition. On the other hand, female yellow-toothed cavies *Galea musteloides* have been shown to wean more offspring when paired with four males compared with one male (Sachser et al. 1999).

The formation of groups such as extended families can enhance investment in offspring, leading to increased reproductive success through, for instance, increased quantity or quality of offspring (Solomon & Keane 2007). For example, prairie vole *Microtus ochrogaster* pups reared with older siblings opened their eyes sooner and weighed more at weaning than those without older siblings (Solomon 1991). In addition, females that were larger at weaning had shorter interlitter intervals and their pups had a higher pre-weaning growth rate than those of small females, demonstrating a reproductive advantage of higher weaning mass and thus of the presence of older siblings (Solomon 1994). It therefore appears that the formation of family groups can provide a reproductive advantage in some species.

General biology of the bushveld gerbil *Gerbilliscus leucogaster*

Some aspects of the biology of bushveld gerbils, as cited in the literature, are reviewed in detail in the various chapters of this thesis. To avoid excessive repetition, I do not give an in-depth review of the literature on these subjects here, but rather a broad overview.

Phylogeny

Gerbils belong to the murid subfamily Gerbillinae, consisting of 16 genera and 103 described species (Musser & Carleton 2005). The taxon *Gerbilliscus* was formerly considered a subgenus of *Tatera*, but has recently been recognised as a genus separate from the Asian *Tatera indica* and consisting of all the former African *Tatera* species (Musser & Carleton 2005). Three genera and nine species of gerbils occur in southern Africa, including four *Gerbilliscus* species: the little-known Gorongosa gerbil *G. inclusus*, which is found in Tanzania, Mozambique and marginally in Zimbabwe; the Cape gerbil *G. afra*, which is restricted mainly to the Western Cape, South Africa; the highveld gerbil *G.*

brantsii, which is widespread in southern Africa, occurring from Namibia, Botswana and marginally in Zimbabwe down to the Eastern Cape in South Africa; and the bushveld gerbil *G. leucogaster*, which is widespread in Africa, occurring from Angola, the Democratic Republic of Congo and Tanzania down to South Africa (Skinner & Chimimba 2005). *Gerbilliscus leucogaster* and *G. inclusus* are sympatric in some parts of their range, as are *G. leucogaster* and *G. brantsii*, while *G. afra* is allopatric to all its congeners (Skinner & Chimimba 2005). *Gerbilliscus afra* and *G. brantsii* are more closely related to one another than to *G. leucogaster* and share the same karyotype (2n = 44), whereas *G. leucogaster* has a karyotype of 2n = 40 (Qumsiyeh 1986; Colangelo et al. 2007). Comparisons of *G. leucogaster* with closely related species should include species of the genus *Gerbillurus*: the study by Colangelo et al. (2007) resolved three distinct *Gerbilliscus* clades (eastern, southern and western) and suggests that the southern clade (comprising *G. afra*, *G. brantsii* and *G. leucogaster*; *G. inclusus* was not included in the study) may be more closely related to the genus *Gerbillurus* than to the eastern *Gerbilliscus* clade.

General description

Gerbilline rodents are characterised by tawny-coloured upper parts, white under parts, large eyes, and well-developed ear bullae and hind legs; they are adapted to desert or semi-desert habitats (Skinner & Chimimba 2005). The bushveld gerbil is a common, nocturnal, burrowing rodent of medium size (± 48–98 g; De Graaff 1981), and exhibits no sexual dimorphism (Smithers 1983). In the southern African subregion, it occurs in large parts of Namibia, Botswana, Zimbabwe, Mozambique and Swaziland, and in South Africa can be found in north-eastern KwaZulu Natal, Limpopo Province, the North West Province, and parts of Gauteng, Mpumalanga, the Free State and the Northern Cape, north of the Orange River (Skinner & Chimimba 2005). Bushveld gerbils are associated mainly with sandy soils and occur in a wide range of habitats, including open grassland, open woodland, thornveld and bushveld; they do not appear to be associated with any specific vegetation-type (De Graaff 1981; Smithers 1983). Their diet consists predominantly of seeds and insects, but they also feed on vegetation (Perrin & Swanepoel 1987; Neal 1991; Odhiambo et al. 2008; Kinahan & Pillay 2008).

Reproduction

A number of studies report that breeding in *G. leucogaster* is seasonal and associated with rainfall, and some report that the duration of the breeding season is variable

(Chidumayo 1980; Perrin & Swanepoel 1987; Neal 1991; Odhiambo et al. 2008). However, Smithers (1971) reports that in Botswana, gravid females were trapped in every month except September, indicating that young are born throughout the year. There is often substantial recruitment at the end of the rains and during the dry season, following breeding in the preceding rainy season (Chidumayo 1980; Perrin & Swanepoel 1987; Neal 1991); some young may begin breeding in the season of their birth (Chidumayo 1980; Neal 1991). Many studies provide variable litter sizes, but most give a mean litter size of between four and five, while minimum and maximum litter size reported is one and nine respectively (e.g. Wilson 1975; Chidumayo 1980; Rautenbach 1982; Smithers 1983; Perrin & Swanepoel 1987).

Social organisation and mating system

Little is known about the social organisation and mating system of bushveld gerbils. De Graaff (1981) reports that they are communal, and Skinner & Chimimba (2005) state that burrows are occupied by a pair, but that warrens can be found with many entrances and that these are possibly connected underground. Smithers (1971) also notes that bushveld gerbils are communal and live in warrens, although solitary burrows are sometimes found. According to a study by Choate (1972), burrows of *G. leucogaster* were occupied by families or several adults. Behaviour patterns in staged male–female encounters suggest that *G. leucogaster* is more tolerant of conspecifics than the solitary Cape short-tailed gerbil *Desmodillus auricularis* (Dempster et al. 1993). The above literature suggests that bushveld gerbils are tolerant of conspecifics and exhibit some form of sociality. Neal (1991) speculated that the mating system is promiscuous based on the large relative testes size (see Harcourt et al. 1981; Kenagy & Trombulak 1986).

MOTIVATION AND AIMS OF THE STUDY

Making up 44% of all mammals, rodents are an incredibly diverse order and often easily maintained in captivity, which has led to their use as model systems for studies of a wide range of subjects (Wolff & Sherman 2007). A small percentage of rodents are pests, damaging agricultural crops, raiding grain stores and houses, and spreading disease (Lidicker 2007). Rodents are most likely the chief natural reservoirs for human disease-causing pathogens, and social behaviour, specifically fighting, is one factor that has been associated with the prevalence of pathogen infection in rodents (Ostfeld & Mills 2007). However, rodents are also invaluable in biomedical research, are essential components of

healthy ecosystems, provide countless opportunities for biological research and even provide food supplements for humans (Lidicker 2007). Due to their importance, rodents deserve to be of conservation concern and a number have already become extinct due to anthropogenic activities, while many more are threatened (reviewed in Lidicker 2007). An understanding of social behaviour and life-history variables is necessary for effective conservation (Lidicker 2007).

Despite their overwhelming importance in both negative and positive contexts, rodents are not well known in most parts of the world (Lidicker 2007). In particular, compared with well-studied North American and Eurasian temperate rodent species, very little is known about the social systems of rodents from the developing world (Tang-Martínez 2003). Tang-Martínez (2003) stresses the importance of not only collecting information on rodent sociality from understudied areas, but also integrating such information into our thinking, to give us a more comprehensive understanding of rodent social evolution.

Gerbilliscus leucogaster represents an African rodent species for which we have relatively little information, in spite of its widespread occurrence. Although some aspects of the biology such as breeding season, litter size and diet have been well-studied, detailed studies of other aspects such as social biology and postnatal development are lacking. Furthermore, the genus *Gerbilliscus* has been implicated in the transmission of diseases such as plague (Davis 1964; Smithers 1975; De Graaff 1981). *Gerbilliscus leucogaster* is also apparently subject to significant explosions in population numbers (Choate 1972; Smithers 1975), which adds to the risk of plague outbreaks if populations are infested (Smithers 1975). For all of the above reasons, further knowledge of the biology of this species is of great value.

My study therefore aimed to add to our baseline knowledge of *G. leucogaster*, focussing on the poorly known aspects of postnatal development and social organisation, including the mating system. My primary aim was to investigate the social organisation in greater detail, and thus to propose a model of sociality for the species: while much of the literature suggests that *G. leucogaster* is social (see above), most of my field research did not reveal this. Although my study began as a field-based investigation, the population density was very low at that time. I thus used mainly laboratory techniques, but also incorporated earlier field studies, to develop a greater understanding of the social structure. A secondary aim was to investigate aspects of the reproductive biology. Chapter 2 provides detailed information about the reproduction and postnatal development, and compares

these life-history aspects in *G. leucogaster* with those of other closely and distantly related murid rodents to assess differences in terms of ecological versus phylogenetic influences. Chapter 3 investigates the social behaviour of adults as influenced by both time and space. Male–female interactions form the primary focus of the chapter, but a secondary investigation of intrasexual interactions is also included. Chapter 4 examines male–female interactions further by assessing them in the context of pregnancy and lactation, specifically investigating how social behaviour changes with the changing reproductive condition of the female. Chapter 5 investigates two aspects of the dispersal process. Firstly, interactions and space use of the mother and her weaned offspring are assessed to ascertain if there are any behavioural changes that might influence juvenile dispersal. Secondly, the interactions between weaned juveniles and strange adults are investigated to evaluate the social environment that a juvenile might experience after leaving the natal nest. Wolff (2003) points out the importance of validating the results of laboratory studies with field investigations. Unfortunately, low sample sizes obtained during fieldwork limit the interpretation of the patterns emerging from the research; however, some interesting and important trends are evident, and the results are thus included in the final experimental chapter (Chapter 6). Here I examine aspects of the reproductive patterns of *G. leucogaster* (using demographic data) from the highveld grassland region where the laboratory animals originated, to place animals from this region in the context of other studies of free-living bushveld gerbils. I also conduct a preliminary investigation of space use patterns with the aim of complementing the laboratory findings on the social and mating system.

GENERAL ARRANGEMENT OF THE THESIS

This thesis is comprised of seven chapters: the present introductory chapter, five experimental chapters (Chapters 2–6) and a general discussion chapter (Chapter 7). Chapter 2 was published in Mammalian Biology in 2008 (73: 430–437), co-authored with Prof. Neville Pillay. Consequently, all other experimental chapters follow the format of a manuscript for publication, including an abstract, keywords, an introductory section and a separate reference list, although no other chapters have been submitted for publication as yet. There is thus some repetition of material between chapters. Chapter 6, although written in the format of a manuscript for publication for consistency with the other experimental chapters, was primarily intended to provide support for Chapters 2–5, rather than for publication purposes, owing to the poor trapping success. Scientific names of mammals have recently undergone several changes. Apart from the genus *Gerbilliscus*, for which I

use only the new names, I use scientific names in accordance with the reference being cited, but include a glossary at the end of the thesis (Appendix A) to give any relevant changes as per Wilson & Reeder (2005). Tables and figures are numbered in sequence for each chapter, and pages are numbered sequentially for the entire thesis. Each chapter has its own reference list.

REFERENCE LIST

Barash, D.P. (1974). The evolution of marmot societies: a general theory. *Science* **185**: 415–420.

Beery, A.K., Loo, T.J. & Zucker, I. (2008). Day length and estradiol affect same-sex affiliative behavior in the female meadow vole. *Hormones and Behavior* **54**: 153–159.

Boonstra, R. (1984). Aggressive behavior of adult meadow voles (*Microtus pennsylvanicus*) towards young. *Oecologia* **62**: 126–131.

Chidumayo, E.N. (1980). Population ecology of *Tatera leucogaster* (Rodentia) in southern Zambia. *Journal of Zoology, London* **190**: 325–335.

Choate, T.S. (1972). Behavioural studies on some Rhodesian rodents. *Zoologica Africana* **7**: 103–118.

Colangelo, P., Granjon, L., Taylor, P.J. & Corti, M. (2007). Evolutionary systematics in African gerbilline rodents of the genus *Gerbilliscus*: inference from mitochondrial genes. *Molecular Phylogenetics and Evolution* **42**: 797–806.

Davis, D.H.S. (1964). Ecology of wild rodent plague. In: Davis, D.H.S. (ed.). *Ecological Studies in Southern Africa*. Dr W. Junk: The Hague.

De Graaff, G. (1981). *The Rodents of Southern Africa*. Butterworths: Durban.

Dempster, E.R., Dempster, R. & Perrin, M.R. (1993). Behavioural divergence in allopatric and sympatric gerbil species (Rodentia: Gerbillinae). *Ethology* **93**: 300–314.

Ebensperger, L.A. & Hayes, L.D. (2008). On the dynamics of rodent social groups. *Behavioural Processes* **79**: 85–92.

Ebensperger, L.A., Hurtado, M.J., Soto-Gamboa, M., Lacey, E.A. & Chang, A.T. (2004). Communal nesting and kinship in degus (*Octodon degus*). *Naturwissenschaften* **91**: 391–395.

Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215–223.

Happold, M. (1976). Social behavior of the conilurine rodents (Muridae) of Australia. *Zeitschrift für Tierpsychologie* **40**: 113–182.

Harcourt, A.H., Harvey, P.H., Larson, S.G. & Short, R.V. (1981). Testis weight, body weight and breeding system in primates. *Nature* **293**: 55–57.

Hinze, A. (2005). Social behaviour and activity patterns of the African ice rat *Otomys sloggetti robertsi*. PhD thesis. University of the Witwatersrand: Johannesburg.

Ims, R.A. (1987). Male spacing systems in microtine rodents. *The American Naturalist* **130**: 475–484.

Jarvis, J.U.M. (1981). Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science* **212**: 571–573.

Kenagy, G.J. & Trombulak, S.C. (1986). Size and function of mammalian testes in relation to body size. *Journal of Mammalogy* **67**: 1–22.

Kinahan, A.A. & Pillay, N. (2008). Does differential exploitation of folivory promote coexistence in an African savanna granivorous rodent community? *Journal of Mammalogy* **89**: 132–137.

Lacey, E.A. & Sherman, P.W. (2007). The ecology of sociality in rodents. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

Leirs, H., Verheyen, W. & Verhagen, R. (1996). Spatial patterns in *Mastomys natalensis* in Tanzania (Rodentia, Muridae). *Mammalia* **60**: 545–555.

Lidicker, W.Z. Jr (2007). Issues in rodent conservation. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University

of Chicago Press: Chicago.

Lott, D.F. (1991). *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge University Press: Cambridge.

Madison, D.M. & McShea, W.J. (1987). Seasonal changes in reproductive tolerance, spacing, and social organization in meadow voles: a microtine model. *American Zoologist* **27**: 899–908.

Musser, G.G. & Carleton, M.D. (2005). Superfamily Muroidea. In: Wilson, D.E. & Reeder, D.M. (eds). *Mammal Species of the World: A Taxonomic and Geographic Reference*. Johns Hopkins University Press: Baltimore.

Neal, B.R. (1991). Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae: Rodentia), in Zimbabwe. *Zeitschrift für Säugetierkunde* **56**: 101–111.

Nunes, S. (2007). Dispersal and philopatry. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

Odhiambo, R.O., Makundi, R.H., Leirs, H. & Verhagen, R. (2008). Demography, reproductive biology and diet of the bushveld gerbil *Tatera leucogaster* (Rodentia: Gerbillinae) in the Lake Rukwa valley, south-western Tanzania. *Integrative Zoology* **3**: 31–37.

Ostfeld, R.S. (1986). Territoriality and mating system of California voles. *Journal of Animal Ecology* **55**: 691–706.

Ostfeld, R.S. (1990). The ecology of territoriality in small mammals. *Trends in Ecology and Evolution* **5**: 411–415.

Ostfeld, R.S. & Mills, J.N. (2007). Social behavior, demography, and rodent-borne pathogens. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

Perrin, M.R. & Swanepoel, P. (1987). Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life history theory. *South African Journal*

of Zoology **22**: 218–227.

Qumsiyeh, M.B. (1986). Phylogenetic studies of the rodent family Gerbillidae: I. Chromosomal evolution in the southern African complex. *Journal of Mammalogy* **67**: 680–692.

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

Rautenbach, I.L. (1982). Mammals of the Transvaal. *Ecoplan Monograph* **1**: 1–211.

Ribble, D.O. & Stanley, S. (1998). Home ranges and social organization of syntopic *Peromyscus boylii* and *P. truei*. *Journal of Mammalogy* **79**: 932–941.

Sachser, N., Schwarz-Weig, E., Keil, A. & Epplen, J.T. (1999). Behavioural strategies, testis size, and reproductive success in two Caviomorph rodents with different mating systems. *Behaviour* **136**: 1203–1217.

Salo, A.L., Shapiro, L.E. & Dewsbury, D.A. (1993). Affiliative behavior in different species of voles (*Microtus*). *Psychological Reports* **72**: 316–318.

Skinner, J.D. & Chimimba, C.T. (2005). *The Mammals of the Southern African Subregion*. (3rd ed.). Cambridge University Press: Cape Town.

Smithers, R.H.N. (1971). The mammals of Botswana. *Memoirs of the National Museums of Rhodesia* **4**: 1–340.

Smithers, R.H.N. (1975). *Guide to the Rats and Mice of Rhodesia*. Trustees of the National Museums and Monuments of Rhodesia: Salisbury.

Smithers, R.H.N. (1983). *The Mammals of the Southern African Subregion*. University of Pretoria: Pretoria.

Solomon, N.G. (1991). Current indirect fitness benefits associated with philopatry in juvenile prairie voles. *Behavioral Ecology and Sociobiology* **29**: 277–282.

Solomon, N.G. (1994). Effect of the pre-weaning environment on subsequent reproduction in prairie voles, *Microtus ochrogaster*. *Animal Behaviour* **48**: 331–341.

Solomon, N.G. (2003). A reexamination of factors influencing philopatry in rodents. *Journal of Mammalogy* **84**: 1182–1197.

Solomon, N.G. & Keane, B. (2007). Reproductive strategies in female rodents. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

Tang-Martínez, Z. (2003). Emerging themes and future challenges: forgotten rodents, neglected questions. *Journal of Mammalogy* **84**: 1212–1227.

Waterman, J. (2007). Male mating strategies in rodents. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

Wilson, D.E. & Reeder, D.M. (eds). (2005). *Mammal Species of the World: A Taxonomic and Geographic Reference*. (3rd ed.). Johns Hopkins University Press: Baltimore.

Wilson, V.J. (1975). Mammals of the Wankie National Park, Rhodesia. *Museum Memoir of the National Museums and Monuments of Rhodesia* **5**: 1–147.

Wolff, J.O. (1993). Why are female small mammals territorial? *Oikos* **68**: 364–370.

Wolff, J.O. (2003). Laboratory studies with rodents: facts or artifacts? *Bioscience* **53**: 421–427.

Wolff, J.O. & Sherman, P.W. (2007). Rodent societies as model systems. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

CHAPTER TWO

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ORIGINAL INVESTIGATION

Reproduction and postnatal development of the bushveld gerbil *Gerbilliscus* (formerly *Tatera*) *leucogaster*

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Abstract

The reproduction and postnatal development of the bushveld gerbil *Gerbilliscus* (formerly *Tatera*) *leucogaster* was studied in the laboratory. Nineteen pairs produced 23 litters. Mean litter size was 3.5 and gestation was 21–22 days. Neonates weighed 3.7 g on average and were altricial. Development was slow, with eyes usually opening 16–18 days after birth, and weaning occurring by about 24 days of age. The earliest age of sexual maturity was 6.6 weeks in females and 9.9 weeks in males. A comparison with other studies of *G. leucogaster*, and with closely and distantly related similar-sized murid rodents, indicates that reproduction generally varies with geographic location, and that the slow postnatal development of *G. leucogaster* appears to be phylogenetically constrained.

Keywords: *Gerbilliscus leucogaster*; Life history; Ontogeny; Behaviour; Phylogeny

Introduction

The life-history traits of a population or species often reflect the twin forces of phylogenetic constraints and adaptive variation (Boyce 1988; Stearns 1992). Variation in environmental factors such as geographic location, climate and food (and the interplay between them) can lead to variation in life-history traits (Stearns 1992). For example, Cameron and McClure (1988) showed that areas exhibiting strong climatic seasonality may also show strong seasonality in the quality and availability of food, which directly influences litter size in the hispid cotton rat *Sigmodon hispidus*. Braithwaite (1979) showed that, although mean litter size appeared similar between populations of *Rattus lutreolus* inhabiting three different habitats, the mean number of litters and the proportion of young breeding in the season of their birth was greater in the habitats with a longer breeding season. He suggested that the length of the breeding season may be determined by the productivity and availability of food plants.

Untangling the various determinants of life histories will aid in the understanding of the adaptive significance of a particular life-history trait, as well as the role of constraints. For this, there is a need for careful estimates of reproductive parameters such as litter size, age at weaning, size at weaning and growth rates, as well as an investigation of the variation and interrelationships (particularly the trade-offs) among the parameters within species (Millar 1977). One approach to understand the diversity of life-history traits is to compare them across taxa (Harvey and Read 1988), and a number of studies have used a comparative approach to investigate life-history (e.g. Case 1978; Creighton and Strauss 1986; Neal 1990; Pillay 2001). Comparing the life-history traits of a species to other closely related species, as well as to species which inhabit a similar

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environment, would facilitate understanding of the roles that both ecological adaptations and phylogenetic constraints have played in shaping the life-history traits (Pillay 2003).

In this study, we describe the life-history traits of the bushveld gerbil *Gerbilliscus* (formerly *Tatera*) *leucogaster* (Musser and Carleton 2005), a member of the family Muridae and subfamily Gerbillinae (Skinner and Chimimba 2005). *Gerbilliscus leucogaster* is a medium-sized rodent (mean adult mass = 78.1 g for wild-caught animals trapped for this study) and is not sexually dimorphic (Smithers 1983). The bushveld gerbil has a widespread distribution in Africa, occurring from Tanzania and the Democratic Republic of Congo down to South Africa (Skinner and Chimimba 2005). In southern Africa, it inhabits a number of different biomes, including open grassland, open woodland, thornveld and bushveld (De Graaff 1981; Skinner and Chimimba 2005). Bushveld gerbils are nocturnal and burrow in sandy soils, usually under vegetation, but also in the open (De Graaff 1981; Skinner and Chimimba 2005). They are classified as granivorous insectivores, feeding on herbage in the absence of preferred foods (Perrin and Swanepoel 1987).

Information from a number of field studies provides a collective, yet incomplete, impression of the reproductive biology of *G. leucogaster*. Whereas breeding is reported as being seasonal (although the length of the breeding season may vary) and often associated with rainfall in certain parts of its distribution range (Zambia: Chidumayo 1980; South Africa: Rautenbach 1982; Perrin and Swanepoel 1987; Zimbabwe: Neal 1991), such seasonality is not seen in other parts of its distribution range. In a different area in Zimbabwe, gravid females were caught in both summer and winter (Wilson 1975), while in neighbouring Botswana, gravid females were reported in every month except September (Smithers 1983). Griffin (1990) found reproductively active individuals in all seasons in the central Namib Desert, but breeding was opportunistic and associated with favourable environmental conditions. The range of the mean litter size reported in the literature is 3.2–5.6 (Wilson 1975; Scott 1979; Smithers and Wilson 1979; Chidumayo 1980; Rautenbach 1982; Smithers 1983; Perrin and Swanepoel 1987; Neal 1990, 1991). Only two studies have investigated more detailed aspects of postnatal development: Neal (1990) studied two litters from gravid wild-caught females in Zimbabwe, approximately 850 km from the location of our study population, and Scott (1979) conducted a M.Sc study on 18 laboratory-bred litters born to five females collected from KwaZulu-Natal, South Africa, approximately 370 km away from our study population. We compared our findings with those of Neal (1990) and Scott (1979) to assess geographic variation in postnatal development and reproduction. These localities comprised different habitats: the populations in Zimbabwe (Neal 1990) were apparently collected in a deciduous woodland, the KwaZulu-Natal population inhabited a tree savanna with low grass cover (Scott 1979), and our study was conducted on a population that inhabited a wooded grassland (see below).

The first objective of this study was therefore to conduct a detailed investigation of various aspects of the reproduction and postnatal development of *G. leucogaster*. The second objective was to compare the breeding and postnatal data for *G. leucogaster* with congeners occurring in South Africa, namely *G. brantsii* and *G. afra*, as well as with the more distantly related *Aethomys chrysophilus* (subfamily Murinae, Skinner and Chimimba 2005). *Gerbilliscus brantsii* is sympatric with *G. leucogaster* in parts of its range, including the locality from which the *G. leucogaster* used in this study were obtained. *Gerbilliscus afra* is endemic to the southern parts of the Northern and Western Cape and inhabits the fynbos and succulent karoo biomes, where *G. leucogaster* is absent (Skinner and Chimimba 2005). *Gerbilliscus afra* eats grass, bulbs, roots and seeds, and *G. brantsii* eats leaves, seeds and insects (Skinner and Chimimba 2005). *Aethomys chrysophilus* occurs in grasslands consisting of scrub cover and in savanna woodland, and its distribution thus overlaps with that of *G. leucogaster* (Skinner and Chimimba 2005). It has a similar diet to *G. leucogaster*, consisting of seeds, foliage and insects (Skinner and Chimimba 2005). We surmised that if reproduction and development of *G. leucogaster* resembles those of its congeners, phylogeny is a likely constraint on the life-history traits of the species, although the close relationship and syntopy between *G. leucogaster* and *G. brantsii* is a confounding factor, which is one reason for including data from *G. afra* for comparison. If the life-history traits of *G. leucogaster* are more similar to those of *A. chrysophilus*, ecological adaptations to similar habitats may be more important.

Material and methods

Study animals were either wild-caught individuals trapped at Ezemvelo Nature Reserve (25°42.451′S; 29°00.999′E) near Bronkhorstspruit, South Africa, or were F1 or F2 descendents of these animals. The habitat where bushveld gerbils were trapped consisted mainly of grassland, with a few scattered trees. Laboratory studies were conducted in the Milner Park Animal Unit of the University of the Witwatersrand. Animals were maintained under partially controlled environmental conditions (light regime of 14L:10D, lights on at 5 am; 20–24 °C; 30–60% rh). Non-breeding animals were housed in lab-o-tec cages (410 × 245 × 230 mm), and provided with coarse wood shavings and hay for litter and nesting material, respectively. Wild-caught individuals were housed singly, and captive-born individuals were housed in same-sex sibling groups to prevent inbreeding, with a maximum of three

animals per cage. All animals were provided with Epol® mouse cubes and water ad libitum. In addition, the diet was usually supplemented on a weekly basis with a small quantity of sunflower seeds, peanuts and apple.

Reproduction

Breeding pairs were typically either housed in two smaller tanks (465 × 310 × 350 mm each), connected with an opaque PVC pipe, or in one large tank (855 × 305 × 350 mm). A small tank was often attached to the large tank to allow the males a chance to avoid aggressive behaviour by the female. Many females displayed aggression, which seemed to increase after parturition. Males were separated from the females if aggression became too high. Tanks were constructed of galvanised steel on three sides, with a clear perspex front to allow for observation, and a wire mesh lid. Each breeding individual was provided with its own galvanised steel nest box (150 × 150 × 150 mm), water bottle and food dish. In addition to the diet described above, breeding animals were provided with extra sunflower seeds and peanuts, as well as mealworms once a week, to increase protein intake for reproduction.

Because aggression was often high at first, pairs were initially prevented access to one another for at least 2 days by means of an opaque barrier to allow them to become familiar with one another. The opaque barriers had gaps which permitted mainly olfactory but probably also partial visual communication. After removal of the barrier, pairs were usually checked daily to assess their well-being and to check for litters close to parturition; the date of birth is referred to as day 0. Males were either separated from the female after birth, or were allowed to remain with her for behavioural experiments in other studies and/or to allow for a second litter.

The following parameters were recorded for each breeding pair: interval between pairing and birth of the first litter, interlitter interval, litter size and sex ratio of young. Sex of neonates was determined by measuring the distance between the urogenital papilla and the anus (approximately 4 mm in males and 2 mm in females). The reproductive effort of females was calculated as: $R_e = NW_w^{0.75}(m^{0.75})^{-1}$ (Millar 1977), where R_e = reproductive effort, N = litter size, W_w = mass of offspring at weaning and m = adult female mass.

Postnatal development

Several developmental milestones were monitored (typically every second day from day 0 or 2), including: fur growth, locomotory proficiency, opening of the eyes, incisor eruption, hearing (assessed by the response of the young to a high-pitched sound) and smell (assessed by moving food in front of the nose or exhaling gently in the proximity of the face, as described by Pillay 2001). The age of onset to completion of weaning was determined by observation of independent feeding behaviour (either nibbling at bedding or eating/handling food), and changes in faeces colour from a light tan to dark brown when solids are eaten and remnants of solid food are visible. The development of the following behaviours (similar to Brooks 1972) was also monitored: grasp reflex, righting ability, cliff-drop aversion and negative geotaxis. In addition, the development of exploratory behaviour, self-grooming, the ability of littermates to locate one another or the nest when experimentally separated, aggression and meeting behaviour (sniffing one another upon meeting) was recorded. The age at sexual maturity was determined for males by observing when the testes were of mean adult size (mean, range: 44 mm, 32–51 mm), and for females by observing when the vaginal orifice became perforate.

Mass and linear measurements of litters were calculated every second day until 26 days of age (recorded as the pre-weaning phase; weaning age given as 25 days by Scott 1979), and approximately weekly thereafter to 124 days of age (recorded as the post-weaning phase). Young were weighed to the nearest 0.1 g. The mass of the mother was also recorded at regular intervals during the pre-weaning phase. The following linear measurements were taken: head-body length, tail length, hind foot length and ear length. The increase in body mass was fitted with the Gompertz equation (Zullinger et al. 1984), modified as follows: $y = a \cdot \exp[-\exp(t_i - kt)]$, where y = predicted mass at time t; a = asymptotic mass; k = growth rate constant; t_i = inflection time. Asymptotic mass was taken as the mean body mass at 124 days. Using this model, a growth rate and inflection point were obtained. Growth rate from birth to weaning was also calculated as follows: $(M_w - M_b)/24$, where M_w = mass at weaning, M_b = birth mass and 24 = days from birth to weaning (see Results). Mean adult linear measurements were calculated from 13 animals used in this study, against which the growth of young gerbils was compared.

There was an opportunity to study a small number of *G. brantsii* animals trapped from a location near to where *G. leucogaster* was caught. Six pairs were established under similar laboratory conditions described above and some aspects of postnatal development were investigated using similar methodology.

Results

Reproduction

Sixteen pairs, plus an additional three females that were pregnant when captured, produced 23 litters (81 young). The mean interval between pairing and birth of the first litter was 24.4 days (n = 14; SE = 0.59). This does not include two outliers of 82 and 45 days. Apart from the outliers, all first litters were born 21–30 days after pairing. The interlitter interval of two pairs in our study and another 10 pairs in our colony was 25.8 days on average (range 24–32 days), suggesting a postpartum oestrus. Mating was only observed in two pairs, and the time from mating to parturition was 21 and 22 days which together with the minimum interval between pairing and birth of the first litter indicates that gestation is 21–22 days in *G. leucogaster*. Mean litter size was 3.52 (SE = 0.30), with a range of 1–6 young per litter. Sex ratio at birth was 34:47 (males:females). This did not differ significantly from parity ($\chi^2 = 2.09$, $P = 0.15$).

The reproductive effort of *G. leucogaster* was 1.44, calculated from 14 litters, a mean postpartum female mass of 100.39 g (SE = 3.73), a mean mass of young at weaning (taken as day 24) of 27.71 g (SE = 0.74) and a mean litter size of 3.79 (SE = 0.38).

Postnatal development

The following description of the postnatal development of *G. leucogaster* is applicable to the majority of the individuals assessed. Young were altricial at birth and development was slow. Apart from vibrissae on the snout, young were born naked and pink, with claws of about 0.5 mm in length. The ear pinnae were folded from birth until about day 4–6. Skin colour changed from pink to progressively darker grey on the dorsal surface. A very fine layer of fur appeared on the dorsal and ventral surface by day 6–8. By day 12–16, the dorsal surface was all brown, except for the tail, and most of the ventral surface was covered in white fur. The tail and the inguinal area took the longest to become fully furred, but young appeared to be fully furred by day 24–26. Pups demonstrated cliff-drop avoidance within the first week of life (day 0–4), as well as a righting response (day 2–8) and negative geotaxis (onset day 2–4, well developed by day 10–12). Many of the other milestones were achieved at the end of week one and in the second week, including incisor eruption (day 6–10), grasping ability (day 6–12), and the onset of smelling (day 8–10). The eyes opened later (day 16–18), coinciding with the attainment of hearing (day 14–16) and co-ordinated locomotion (onset day 14, completion day 18–20). Independent feeding behaviour was first observed from about day 20, and weaning appeared complete by day 24–26.

Litters usually displayed social interactions in the third week after birth (day 14–22). Aggression was not often noted during the pre-weaning phase, but was occasionally seen by day 24 (e.g. boxing), which coincided with weaning. Exploratory behaviour was displayed by about day 12–14, even though the eyes were still closed. Grooming behaviour was recorded as early as day 12, but was usually evident by day 14–16.

The earliest age of female sexual maturity was day 46–55 (56–74 g). The earliest age that a female gave birth in the colony was 70 days. Assuming a gestation of 21 days, she would have mated at 49 days, which is consistent with the earliest age that females became perforate. The earliest age that males reached sexual maturity was day 69–83 (96–120 g). The youngest male to breed in the colony was paired at 73 days, supporting the above findings.

Twenty litters from 16 pairs were used to investigate the growth of *G. leucogaster*. We obtained data for the pre-weaning phase from 16 litters, and for the post-weaning phase from 14 litters. For the pre-weaning phase, six litters were measured from day 0, and most of the remaining litters were measured from day 2. Figs. 1 and 2 illustrate the growth of *G. leucogaster* from birth to 124 days of age. Body mass continued to increase throughout the period of measurement, but slowed down after about day 110 (Fig. 1). Variation in individual body mass was very low initially, but increased substantially from day 75 to day 124, when the range in body mass was 84.8–152.2 g. A Gompertz curve equation was fitted to nine litters and generated an r value of 0.999, a growth rate of 0.038 and an inflection of 1.155 days. Head-body and tail length reached an asymptote at 61 days, while hind foot and ear length reached an asymptote much sooner, at about 24 days (Fig. 2). Hind foot reached 95% of adult size at 41 days, followed by ear, tail and head-body lengths (Fig. 2).

The six pairs of *G. brantsii* each produced one litter (i.e. six litters in total). The data are given in the Discussion section for comparison with *G. leucogaster*.

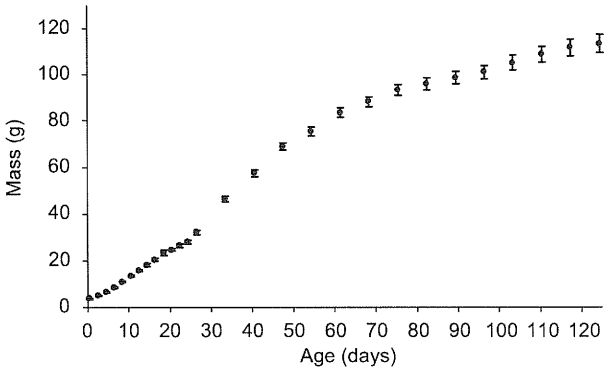

Fig. 1. Mean (±SE) mass of *Gerbilliscus leucogaster* from birth to 124 days of age.

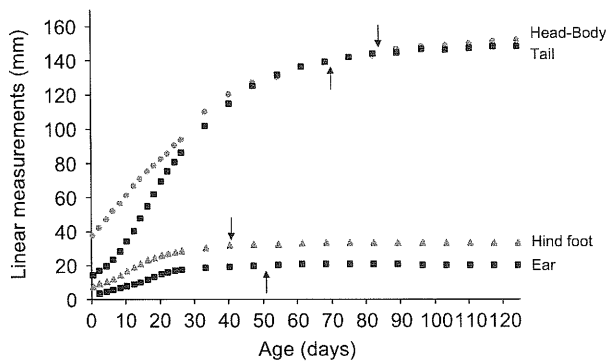

Fig. 2. Increase in linear measurements of *Gerbilliscus leucogaster* from birth to 124 days of age. Arrows indicate 95% of adult size.

Discussion

Gestation, litter size, birth mass as a percentage of adult body mass and reproductive effort in *Gerbilliscus leucogaster* are very similar to other altricial rodents (Neal 1986, 1990). *Gerbilliscus leucogaster* in this study had a shorter gestation compared to *G. leucogaster* in other studies (21–22 days compared to 25 and 28 days; Scott 1979; Chidumayo 1980). Mean litter size (3.5) in our study is similar to the other laboratory studies-3.2 (Scott 1979) and 3.5 (Neal 1990), but is smaller than in other studies (mean number of offspring = 4.0–5.6; Wilson 1975; Smithers and Wilson 1979; Chidumayo 1980; Rautenbach 1982; Smithers 1983; Perrin and Swanepoel 1987; Neal 1990, 1991). However, these estimates are usually based on embryo counts, which perhaps do not reflect the number of young at birth. Even among the studies using embryo counts, mean number of embryos per female still varies substantially, with a range of 4 (Wilson 1975) to 5.6 (Neal 1991).

Reproductive studies of *G. leucogaster* have been conducted on populations from a large geographic area – e.g. from ±17°45′S in Zambia (Chidumayo 1980) to ±27°45′S in South Africa (Scott 1979). These populations occur in a variety of habitats, such as wooded grassland (our study), Miombo and mixed woodland (Neal 1991) and bushveld (Perrin and Swanepoel 1987). Thus, the differences in litter size may reflect local adaptation of different populations. For example, Neal (1991) found differences in reproductive traits among two populations of *G. leucogaster* in Zimbabwe occurring in different habitats, which were probably related to differences in food abundance and quality. The population with apparently lower food abundance/quality delayed the onset of breeding by 3 months and had both a lower mean number of offspring (4.8 versus 5.6) and a lower reproductive capacity (12 versus 28 young per adult female) than the population with higher food abundance/quality. Given that number of offspring is a key adaptive variable of reproduction (Millar 1977), changes in number of young in relation to geographic location, climate and diet are to be expected. The differences in the timing and duration of breeding in *G. leucogaster* (discussed earlier) are also probably related to these factors. For example, Perrin and Swanepoel (1987) suggest that seasonal rainfall influences diet composition and quality, resulting in seasonal breeding in *G. leucogaster* from a region in northern South Africa.

Table 1 gives a comparison of various life-history parameters from our study with two other studies (Scott 1979; Neal 1990) on *G. leucogaster*. The parameters are very similar in all three studies, although neonates were smaller and the eyes of pups opened later in the study by Neal (1990). These differences perhaps indicate: (1) differences in condition of females, since Neal (1990) collected data from gravid wild-caught females, which presumably experienced less favourable conditions than the captive females in the other two studies; and (2) the small sample size ($n = 2$) in the study by Neal (1990); comparable data were not available from the gravid wild-caught females in our study. Females in our study reached sexual maturity in half the time than in the study by Scott (1979), which may reflect differences in the sampling procedure, since we used the external appearance in the genitalia (perforate vagina; testes size) rather than the timing of parturition (Scott 1979). Even so, the earliest mating by females in our colony was 7 weeks compared to 12.9 weeks, and since both studies were conducted in captivity, perhaps it is possible that the differences are due to geographic variation between populations, which could reflect differences in food quality and/or abundance, as discussed elsewhere.

Table 1 also compares some reproductive and ontogenetic traits for *G. leucogaster*, *G. brantsii*, *G. afra* and *Aethomys chrysophilus*. Gestation of *G. leucogaster* is very similar to that of *G. brantsii*, but longer in *A. chrysophilus*. Mean litter size is similar in all species, but sometimes smaller in *A. chrysophilus* and *G. brantsii*. Small litter size is often associated with precociality (Meester and Hallett 1970; Neal 1986) and/or nipple-clinging (Brooks 1982; Dempster and Perrin 1989; Neal 1990), which is the case in *A. chrysophilus* (Brooks 1972). It is unclear why *G. brantsii* has a smaller litter size than *G. leucogaster* or *G. afra*. Although the litter size was similar in *G. leucogaster* (3.5) and *G. brantsii* (3.2) in our study, perhaps because of their close proximity to one another, this is not universally the case. Perrin and Swanepoel (1987) suggest that the smaller litter size of *G. brantsii* compared to *G. leucogaster* is a result of a less nutritious diet and insufficient protein, even when the species are sympatric, as confirmed by studies of gut morphology (Kinahan and Pillay 2008).

Many of the key postnatal developmental milestones (e.g. eyes opening, hearing and incisor eruption) are similar in all three *Gerbilliscus* species in Table 1, but slower than *A. chrysophilus*, which attains these milestones considerably faster. Although weaning is similar in all four species, the *Gerbilliscus* species display independent feeding behaviour later than *A. chrysophilus* (Table 1), which concurs with their slower development. The early eruption of incisors is probably to facilitate nipple-clinging in *A. chrysophilus* (Neal 1990). Other factors must be responsible for the remaining developmental differences between *A. chrysophilus* and the *Gerbilliscus* species, and it is possible that development is phylogenetically constrained. From these comparisons it appears that, in spite of occupying a

Table 1. Comparison of adult body mass and various aspects of the reproduction and postnatal development of *Gerbilliscus leucogaster* (two previous studies and the present study), *G. brantsii*, *G. afra* and *Aethomys chrysophilus*

Parameters	*G. leucogaster*[a]	*G. leucogaster*[b]	*G. leucogaster*[c]	*G. brantsii*[c,d,e]	*G. afra*[e,f,g,h]	*A. chrysophilus*[d,i]
Mean (range) adult body mass (g)	103.4 (–)	72 (–)	78.1 (63–93)	115 (98–132)	97.1 (78–113)	117 (–)
Gestation (days)	25	–	21–22	22–24	–	26
Mean (range) litter size	3.2 (1–5)	3.5 (3–4)	3.5 (1–6)	2.6–3.3 (1–5)	4 (2–6)	2.7–4.1 (1–6)
Mean (range) birth mass (g)	3.7 (3.2–4.5)	2.8 (2.6–3.0)	3.7 (3.3–4.0)	4.7 (4.2–6.2)	4.1 (–)	4.1 (3.5–4.5)
Birth mass (% adult mass)	3.6	3.9	4.7	4.1	4.2	3.5
Eyes open (days)	15–18	19–21	16–18	15–22	18–21	11–14
Hearing (days)	13–16	–	14–16	14–17	–	8
Incisor eruption (days)	7–11	5–6	6–10	5–8	10	0
Co-ordinated locomotion (days)	10	16	14–20	13–19	24	12–20
Independent feeding behaviour (days)	17	25	20	16	22–23	12
Age at weaning (days)	25	18–28	24–26	25–26	–	26
Mass at weaning (g)	24	16–22	28 (21.1–35.3)	25 (18.0–29.1)	–	26
Earliest sexual maturity (weeks)						
Male	–	–	9.9	7.7–9.6	6–7	7
Female	12.9	–	6.6	8.7–9.5	12	8
Pre-weaning growth rates (g/day)	0.8	0.8	1.0	0.9	–	0.8

Superscripts indicate the source of information. A dash (–) indicates that no data were available.
[a]Scott (1979).
[b]Neal (1990).
[c]Present study.
[d]Skinner and Chimimba (2005).
[e]Measroch (1954).
[f]De Graaff (1981).
[g]Dempster et al. (1992).
[h]Allanson (1958).
[i]Brooks (1972).

different habitat, *G. afra* is similar to *G. leucogaster* and *G. brantsii*.

The development rate of the three *Gerbilliscus* species is also slow when compared to other altricial rodents of similar body size (see Neal 1990). The genus *Gerbilliscus* apparently has high energy requirements during lactation (Neal 1982), and perhaps this contributes to the slow development rate in the above three species. One way of coping with energy limits during reproduction is to reduce the daily energy requirements for offspring growth by increasing the time to weaning (Millar 1977). In addition, the three *Gerbilliscus* species have a relatively small litter size, and prolonged time to independence could be beneficial by increasing the survival of their litters. Since size at weaning/independence is indicative of a mammal's ability to cope with its adult niche (Millar 1977), a longer development time may increase the survival rate of juveniles. The well-developed hind feet of the *Gerbilliscus* species represent another potential factor influencing development rate, as a number of studies on other slow-developing rodent species have related their development rates to their well-developed hind limbs and resulting mode of locomotion (Dempster and Perrin 1989).

Ascaray and McLachlan (1991) suggest that the slow development of *Gerbillurus* species may be attributed to the protection of underground nests. As described above, there are a number of potential benefits to the slow development of the *Gerbilliscus* species compared in the current study, and the use of underground nests by all three species (Skinner and Chimimba 2005) may allow for this slower development. Case (1978) notes that increasing energetic demands of young would cause parents to be away from the nest for longer periods, leaving the young exposed to predation and the elements. Thus, a burrow not only affords greater protection to both mother and offspring, it also allows the mother to leave the nest unprotected for a longer period of time in order to forage, thereby increasing her ability to meet her energy requirements.

In conclusion, the life-history traits of *G. leucogaster* seem to reflect the twin forces of adaptive variation and

phylogenetic constraints. Reproductive traits, such as litter size and breeding season, vary with geographic location and associated environmental factors, but postnatal development appears to be phylogenetically constrained. This may be associated with a number of factors, such as high energy requirements for lactation, which result in slower development, as well as with the consistent use of protected burrows. We studied one population and compared our findings with those of other populations reported in previous studies, which used different methodologies. In addition to providing data of the reproductive biology of a highveld population of *G. leucogaster*, our findings will be of value in laboratory and field studies, but we suggest that future studies should compare more populations, using similar methodologies.

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References

Allanson, M., 1958. Growth and reproduction in the males of two species of gerbil, *Tatera brantsii* (A Smith) and *Tatera afra* (Gray). Proc. Zool. Soc. London 130, 373–396.

Ascaray, C.M., McLachlan, A., 1991. Postnatal growth and development of the hairy-footed gerbil, *Gerbillurus paeba exilis*. S. Afr. J. Zool. 26, 70–77.

Boyce, M.S., 1988. Evolution of life histories: theory and patterns from mammals. In: Boyce, M.S. (Ed.), Evolution of Life Histories of Mammals: Theory and Pattern. Yale University Press, New Haven, pp. 3–30.

Braithwaite, R.W., 1979. The ecology of Rattus lutreolus II. Reproductive tactics. Aust. Wildl. Res. 7, 53–62.

Brooks, P.M., 1972. Post-natal development of the African bush rat, *Aethomys chrysophilus*. Zool. Afr. 7, 85–102.

Brooks, P.M., 1982. Aspects of the reproduction, growth and development of the four-striped field mouse, *Rhabdomys pumilio* (Sparrman, 1784). Mammalia 46, 53–63.

Cameron, G.N., McClure, P.A., 1988. Geographic variation in life-history traits of the hispid cotton rat (*Sigmodon hispidus*). In: Boyce, M.S. (Ed.), Evolution of Life Histories of Mammals: Theory and Pattern. Yale University Press, New Haven, pp. 33–64.

Case, T.J., 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Q. Rev. Biol. 53, 243–282.

Chidumayo, E.N., 1980. Population ecology of *Tatera leucogaster* (Rodentia) in southern Zambia. J. Zool. (London) 190, 325–335.

Creighton, G.K., Strauss, R.E., 1986. Comparative patterns of growth and development in cricetine rodents and the evolution of ontogeny. Evolution 40, 94–106.

De Graaff, G., 1981. The Rodents of Southern Africa. Butterworths, Durban.

Dempster, E.R., Perrin, M.R., 1989. Maternal behaviour and neonatal development in three species of Namib Desert rodents. J. Zool. (London) 218, 407–419.

Dempster, E.R., Perrin, M.R., Nuttall, R.J., 1992. Postnatal development of three sympatric small mammal species of southern Africa. Z. Säugetierk. 57, 103–111.

Griffin, M., 1990. A review of taxonomy and ecology of gerbilline rodents of the Central Namib Desert, with keys to the species (Rodentia: Muridae). In: Seely, M.K. (Ed.), Namib Ecology: 25 Years of Namib Research. Transvaal Museum, Pretoria, pp. 83–98.

Harvey, P.H., Read, A.F., 1988. How and why do mammalian life histories vary? In: Boyce, M.S. (Ed.), Evolution of Life Histories of Mammals: Theory and Pattern. Yale University Press, New Haven, pp. 213–232.

Kinahan, A.A., Pillay, N., 2008. Does differential exploitation of folivory promote coexistence in an African savanna granivorous rodent community? J. Mammal. 89, 132–137.

Measroch, V., 1954. Growth and reproduction in the females of two species of gerbil, *Tatera brantsi* (A Smith) and *Tatera afra* (Gray). Proc. Zool. Soc. London 124, 631–658.

Meester, J., Hallett, A.F., 1970. Notes on early postnatal development in certain southern African Muridae and Cricetidae. J. Mammal. 51, 703–711.

Millar, J.S., 1977. Adaptive features of mammalian reproduction. Evolution 31, 370–386.

Musser, G.G., Carleton, M.D., 2005. Superfamily muroidea. In: Wilson, D.E., Reeder, D.M. (Eds.), Mammal Species of the World: A Taxonomic and Geographic Reference, third ed. Johns Hopkins University Press, Baltimore, pp. 894–1531.

Neal, B.R., 1982. Reproductive biology of three species of Gerbils (Genus *Tatera*) in East Africa. Z. Säugetierk. 47, 287–296.

Neal, B.R., 1986. Reproductive characteristics of African small mammals. Cimbebasia Ser. A 8, 113–127.

Neal, B.R., 1990. Observations on the early post-natal growth and development of *Tatera leucogaster*, *Aethomys chrysophilus* and *A. namaquensis* from Zimbabwe, with a review of the pre- and post-natal growth and development of African Muroid rodents. Mammalia 54, 245–270.

Neal, B.R., 1991. Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae: Rodentia), in Zimbabwe. Z. Säugetierk. 56, 101–111.

Perrin, M.R., Swanepoel, P., 1987. Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life-history theory. S. Afr. J. Zool. 22, 218–227.

Pillay, N., 2001. Reproduction and postnatal development in the bush Karoo rat *Otomys unisulcatus* (Muridae, Otomyinae). J. Zool. (London) 254, 515–520.

Pillay, N., 2003. Reproductive biology of a rare African rodent, the water rat, *Dasymys incomtus*. J. Mammal. 84, 505–512.

Rautenbach, I.L., 1982. Mammals of the Transvaal. Ecoplan Monogr. 1, 1–211.

Scott, E.D., 1979. A comparison of postnatal development in South African myomorph rodents. University of Natal, Pietermaritzburg M.Sc. Thesis.

Skinner, J.D., Chimimba, C.T., 2005. The Mammals of the Southern African Subregion, third ed. Cambridge University Press, Cape Town.

Smithers, R.H.N., 1983. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria.

Smithers, R.H.N., Wilson, V.J., 1979. Check list and atlas of the mammals of Zimbabwe Rhodesia. Mus. Mem. Nat. Mus. Monum. Rhod. 9, 1–147.

Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, New York.

Wilson, V.J., 1975. Mammals of the Wankie National Park, Rhodesia. Mus. Mem. Nat. Mus. Monum. Rhod. 5, 1–147.

Zullinger, E.M., Ricklefs, R.E., Redford, K.H., Mace, G.M., 1984. Fitting sigmoidal equations to mammalian growth curves. J. Mammal. 65, 607–636.

CHAPTER THREE

Adult social interactions in the bushveld gerbil *Gerbilliscus leucogaster*: temporal and spatial patterns

ABSTRACT

The social interactions of adult bushveld gerbils *Gerbilliscus leucogaster* were investigated by means of dyad encounters to gain a greater understanding of the social and mating system of the species. This study focussed on male–female interactions, but some aspects of same-sex interactions were also investigated. Interactions between strangers were recorded over a period of one week as they became familiar with one another. Individuals were each provided with their own 'home' tank connected to a 'neutral' tank to allow for an assessment of changes in behaviour in different spatial contexts, since the location of social interactions is known to affect the behaviour of many animals. Tolerance between strangers was generally low, but male–female interactions revealed overall low levels of tolerance throughout experiments, whereas same-sex, particularly female–female, interactions showed an increase in tolerance over time. In male–female dyads, females appeared to be cautious of males initially, but later became aggressive towards them. The location of interactions did not seem to have a considerable effect on behaviour. The data provide preliminary evidence for intrasexual overlap in home ranges and a lack of territoriality in the wild, but more studies are needed to confirm this. I also suggest that group formation is possible among same-sex individuals, especially females. Pair-bonding and a monogamous mating system are unlikely; promiscuity is the most probable mating system.

Keywords: *Gerbilliscus leucogaster*; social behaviour; sex differences; social system; promiscuity

INTRODUCTION

The study of social interactions can give us important insights into the social organisation and mating system of a species. While group-living individuals (particularly in an egalitarian society) engage in attracting behaviour that promotes close proximity to at least some conspecifics, solitary individuals react to conspecifics either by ignoring them

or by repelling them through aggressive or avoidance behaviour (Lott 1991). For example, whereas the northern hopping-mouse *Notomys alexis* engages in attracting behaviour between multiple individuals of both sexes, resulting in the formation of groups, the brown desert mouse *Pseudomys desertor* is solitary and all adults are strongly repelled by each other, apart from males and females during mating (Happold 1976).

While it is ideal to study behaviour under natural field conditions, this is often not possible with small, secretive animals such as rodents, especially if they are nocturnal (Nel 1975; Bondrup-Nielsen et al. 1993). Although laboratory studies have a number of limitations (Wolff 2003), the findings of such studies have been shown to reflect inferences resulting from field studies (e.g. Behrends et al. 1986; Schradin & Pillay 2003), thus supporting the value of laboratory studies. Furthermore, Wolff (2003) points out that the strengths of behavioural laboratory studies far outweigh the weaknesses, although one needs to bear the limitations in mind.

The use of staged encounters to study the behaviour of small mammals has been successfully employed in numerous species (Bondrup-Nielsen et al. 1993). Many of these involve observations of two individuals in a neutral arena for a very limited duration of, for example, 10 or 20 minutes (e.g. Colvin 1973; Cranford & Derting 1983; Gromov et al. 2001). However, animals in their natural environment probably seldom encounter conspecifics on neutral ground (Ostfeld 1985), and their social systems tend to involve complex interactions that differ when exposed to resident individuals compared to intruders (e.g. Ågren et al. 1989). Zuri & Rado (2000) have shown that the social behaviour of lesser white-toothed shrews *Crocidura suaveolens* is dependent on familiarity with conspecifics. Even in highly social species such as the naked mole-rat *Heterocephalus glaber* (Jarvis 1981), colony members respond aggressively towards foreign conspecifics (O'Riain & Jarvis 1997). The encounter site (e.g. own versus foreign territory) is also important in determining interactions between individuals (e.g. Porter 1976; Gleason et al. 1980). Hurst et al. (1996) note that agonistic interactions between individuals meeting in different sites can provide valuable information about their social organisation. It is thus important to study behaviour in a variety of social/spatial contexts. Indeed, Happold (1976) states that social behaviour, space (e.g. encounter site) and time (e.g. duration, since relationships change over time) are essential elements to consider in any investigation of social interactions.

The bushveld gerbil *Gerbilliscus leucogaster* is a medium-sized (± 48–98 g; De Graaff 1981), nocturnal, burrowing murid rodent inhabiting a number of different biomes

from Angola, the Democratic Republic of Congo and Tanzania down to South Africa (Skinner & Chimimba 2005). It has been classified as a predominantly granivorous insectivore, but also consumes vegetation (Perrin & Swanepoel 1987; Kinahan & Pillay 2008a). Very little is known about the social and mating system of this species. Skinner & Chimimba (2005) state that burrows are occupied by a pair, but that warrens can be found with many entrances and that these possibly connect underground. De Graaff (1981) describes bushveld gerbils as being communal, and Choate (1972) found that burrows were occupied by families or several adults. A study of male–female interactions by Dempster et al. (1993) suggested that *G. leucogaster* and the Cape gerbil *G. afra* were more tolerant of conspecifics than the solitary Cape short-tailed gerbil *Desmodillus auricularis*, which displayed more agonistic and less huddling behaviour. Neal (1991) predicted that the mating system of *G. leucogaster* is promiscuous based on the large relative testes size. This inference is based on the findings that mammals with promiscuous mating systems have larger testes relative to body weight than those with single-male mating systems (Harcourt et al. 1981; Kenagy & Trombulak 1986; but see Schradin et al. 2009).

The primary aim of my study was to investigate social interactions between adult male and female *G. leucogaster* to gain insight into the social and mating system of the species. Limited comparisons were also made with data from same-sex interactions. Although Dempster et al. (1993) investigated some aspects of the social behaviour of male and female bushveld gerbils, these were studied under very specific conditions: interactions took place in a single cage, after probable induction of oestrous behaviour and for a very limited period of time (20 minutes). Since relationships change both temporally (e.g. Happold 1976; Pillay et al. 1995) and spatially (e.g. Porter 1976), I specifically aimed to investigate changes in the behaviour of two strangers, exposed to a variety of spatial contexts (involving their own tank, a neutral tank and a stranger's tank) over a period of time, as they became familiar with one another. Based on the above literature on bushveld gerbils, I predicted that test subjects would ultimately be tolerant of one another and that males and females would form pair-bonds. In particular, I predicted that aggression would be high initially, due to unfamiliarity, but would decrease over time with a corresponding increase in amicable behaviour. Furthermore, based on the prediction of tolerance, I did not expect test subjects to be more aggressive in their own tank compared to their partner's tank (at least after the first meeting), or to show clear dominance patterns.

MATERIALS AND METHODS

The origin of study animals and the housing conditions are described elsewhere (Lötter & Pillay 2008, Chapter 2).

Dyad encounters

Eight male–female dyad encounters were staged. The experimental set-up consisted of three linearly arranged tanks (each 465 x 310 x 350 mm) connected with PVC pipes (± 300 mm long, 45 mm diameter). Tanks were constructed of galvanised steel on three sides, with a clear Perspex front to allow for video-recording, and a wire mesh lid. Each end tank served as a home tank for one individual, and contained wood shavings and hay. The middle tank, containing only a layer of wood shavings, served as a neutral area separating the two end tanks. Each end tank was also furnished with a water bottle, a food dish containing mouse cubes and a galvanised steel nest-box (150 x 150 x 150 mm) with a 50 mm entrance hole. This experimental set-up was similar to that used by Vassallo & Busch (1992), which is more natural than the neutral arena often used for dyad encounters (e.g. Bondrup-Nielsen et al. 1993; Volodin & Goltsman 2002), as it allows behaviour to be tested in different social/spatial contexts. Furthermore, since each individual was given a separate tank and nest-box, test subjects could potentially avoid/escape their opponent, which is also more natural (Ostfeld 1985) and ethical (Bondrup-Nielsen et al. 1993).

Members of a dyad had never previously been paired in the laboratory and were considered strangers. Both animals were weighed prior to experiments and fitted with either a black or white plastic cable-tie neckband (similar to that described in Schwaibold & Pillay 2006) to identify individuals on video tapes (see below). Individuals were placed in their experimental 'home' tanks at least two days prior to the start of taping to allow for a familiarisation period. To facilitate acceptance of the new tank as a 'home' tank, some bedding from the lab-o-tec cage, in which the test subject was housed prior to experiments, was placed in the home tank. Dyad partners were prevented from making physical contact by confining them to their home tanks with a removable steel barrier placed in the middle of each interconnecting PVC pipe. Individuals thus had no access to the middle (termed 'neutral') tank or their partner's (termed 'foreign') tank prior to the day of video-taping. The barriers were removed on the day that taping commenced. Test subjects received a large handful (± 6 g) of sunflower seeds scattered into the middle tank on the days of taping, excluding the first day. This was done to investigate the resource holding potential

of dyad members in the neutral tank, since sunflower seeds are a preferred food (Kinahan & Pillay, unpublished data).

Dyads were video-taped for eight hours on the first night, and every second night thereafter for four hours per night, beginning approximately 15 minutes prior to the dark phase of the light–dark regime in captivity (i.e. 14L:10D, lights on at 05h00; taping thus began at ± 18h45). Under natural light conditions, Choate (1972) found that a pair of *G. leucogaster* was typically most active between about 18h30 (the commencement of the dark phase in his study) and 01h30. Dyads in my study were taped over a period of seven nights, resulting in four nights of taping per dyad. Taping was conducted under red light (Dempster et al. 1992) using a video camera connected to a video recorder. In his investigation of activity patterns, Choate (1972) included studies conducted under red light to represent night, and he noted that the response of nocturnal species to red light was similar to their response to darkness.

Focal sampling and a one–zero recording method with one minute intervals (Martin & Bateson 2007) were used to score behaviours (Table 1) for each dyad member. Any behaviour was thus only scored once per individual per tank per minute. Obvious sexual behaviour was extremely rare and was not included (apparent mating was only observed in two dyads, and in only one of these was mating observed during scoring sessions). Scoring of behaviour on the video tapes commenced 30 minutes after the start of the taping session (to increase the likelihood that individuals would be active) and was conducted for the first 20 minutes of each hour thereafter. Where there were gaps in the data set owing to an individual not being visible for a full minute (e.g. hidden in an interconnecting pipe between tanks), I assumed the behaviour and, where necessary, the tank position (i.e. home, neutral, foreign) of the individual for that minute to complete the data set. This was done by taking the context into account: I noted the behaviour/position of the dyad partner while the individual was not visible, and I took into account the previous and subsequent behaviours/positions of both dyad partners. The number of minutes in which an individual was not visible for a full minute only amounted to approximately 1% of all minutes scored for males and females combined. To investigate tank occupancy and tank-sharing during the largely inactive diurnal period, the location of each individual was also recorded once daily during the light phase of the light–dark cycle for the seven days of the experiment, usually between about 10h00 and 12h00.

Vaginal smears were taken daily from all female subjects, beginning on the day that taping commenced and ending on the day following the final night of taping (i.e. 7th night).

Table 1. Behavioural categories scored during dyad encounters.

Category	Broad definition
Explore	Exploratory movement around tank, including standing up against objects
Overt agonistic	Chasing, attacking, boxing, lunging, fighting
Ritualised agonistic	Tail wagging, foot drumming (more difficult to see, only scored if clear)
Submissive	Any submissive behaviour in response to aggression, e.g. fleeing and jumping backwards
Avoidance	Avoidance (e.g. moving away) in response to the presence of the dyad partner, but with no visible aggression by the dyad partner
Amicable	Allogrooming, huddling/close proximity (i.e. tolerance within ± 5 cm of partner), sharing a nest-box/outside nest
Other	Anything not covered in the previous categories e.g. self-grooming, digging, eating, occupation of nest-box/outside nest, social investigation

This sampling strategy would likely have included at least one oestrous day per female, since the oestrous cycle appears to be approximately 4–6 days when a male is present with the female (N. Pillay, unpublished data). Based on the relative abundance of cornified cells, leucocytes and macrophages, females were scored as being in oestrus or anoestrus, and these results were used to investigate the effect of oestrous state on behaviour and tank-sharing in both sexes (see data analysis). Vaginal smears were usually taken in the morning, after recording the position of individuals, so as not to influence behaviour during taping at night. Males were also handled during these periods (by removing them briefly from the tank) to reduce potential handling bias.

The primary focus of this study was male–female interactions. However, to understand the social and mating system of bushveld gerbils more completely, a number of female–female and male–male encounters were also staged using similar methodology. These dyads were usually video-taped for eight hours every second night, but due to technical difficulties, some dyads were taped for a shorter period, and a few dyads were only taped for three nights instead of four. Sample sizes for each night were as follows: female–female dyads on night 1: n = 5, all other nights: n = 9; male–male dyads on nights 1 and 7: n = 8, nights 3 and 5: n = 10. The data from these intrasexual encounters were used for limited comparisons with the male–female data.

Testes size

Five males were euthanased and weighed to the nearest 1 g, their testes dissected and the weight of the paired testes (excluding the epididymides) measured to the nearest 0.001 g. I then calculated testes mass as a percentage of body mass.

Data analysis

Data were analysed using STATISTICA 6.0 (StatSoft, Inc. 2001). All tests were two-tailed, with model-level significance determined at $\alpha = 0.05$. Alpha levels for individual tests were adjusted when several component tests were conducted (see below), and in these cases the adjusted alpha is provided below as well as in the Results for clarity; otherwise all tests were conducted at $\alpha = 0.05$. Detailed descriptions of the analyses employed are given under the individual sections below. When General Linear Model (GLM) tests were used, a multivariate design was employed when dependent variables were not independent (unless otherwise specified), and Fisher LSD post hoc tests were used to determine specific differences when categorical predictors/repeated measures factors had a significant effect. GLM tests were used owing to the robust nature of the model and because it allows one to assess complex interrelationships among many variables (Grafen & Hails 2002). Where the input matrix for repeated measures tests contained missing data cells a mean substitution was performed on any missing values to complete the matrix and ensure that the full data set was incorporated by the test. This was only necessary for male–female (M–F) dyads when the analysis used all eight 20 minute scoring sessions of night 1, as two dyads were only taped for five hours on the first night, resulting in missing data for the last three scoring sessions. In female–female (F–F) and male–male (M–M) dyads, a mean substitution was performed where all dyads were not taped on each night (as indicated by above sample sizes i.e. F–F: four dyads required substitutions on night 1; M–M: two dyads required substitutions on night 1 and two dyads required substitutions on night 7). The percentage of data requiring mean substitutions ranged from 2.5–9.4% per test where this was necessary. All figures were generated without the mean substitutions to display the original data for comparison.

Apart from the test analysing night 1 on its own (see below), I summed the data for all the 20 minute scoring sessions for each night to give one value per behaviour per tank per night. M–F interactions were analysed using actual frequencies. When all four nights were used in an analysis, only the first four hours of night 1 were included (i.e. 80 minutes of scoring), to enable comparison between nights, since the other nights were only taped

for four hours. During comparisons between the three dyad-types (i.e. M–F, F–F, M–M), the data for individual dyad partners were pooled; data were converted to proportions and arcsine-transformed, since the number of recording hours and the number of diurnal location records were not always the same within and between the different dyad-types: the proportions standardised the data set for analyses.

Aggressive and amicable behaviour

I first wanted to obtain an overall impression of aggressive versus amicable behaviour in the dyads. To achieve this, I performed a number of modifications to the data set. Firstly, I combined the following forms of aggression into one behavioural category: overt agonistic, ritualised agonistic and submissive behaviour, as well as those instances where a nest-box was briefly co-occupied, but where this appeared aggressive rather than amicable. Secondly, neither the sex of the dyad partners nor the tank in which the behaviour occurred were taken into account. Therefore, aggressive and amicable behaviour were scored as occurring or not occurring during each minute (1/0 recording), regardless of the sex performing the behaviour and regardless of the tank in which the behaviour was performed. This gave me an overall impression of social behaviour in the dyads without the complicating factors of sex and tank, which are investigated below. Night 1 was first analysed on its own using a GLM to assess changes in aggressive and amicable behaviour, with scoring session (i.e. the eight 20 minute scoring sessions on night 1) as the repeated measures factor; there was no categorical predictor since there was no grouping variable. The design of the input matrix in STATISTICA did not generate the degrees of freedom for a combined analysis of behaviours, and thus each behaviour was analysed separately with the alpha levels adjusted using sequential Bonferroni adjustments (Rice 1989); $\alpha' = 0.025$ (α' refers to the first adjusted alpha in the sequence of the Bonferroni adjustment procedure). Aggression and amicability over all four nights were then assessed using a GLM (multivariate design) with night (i.e. 1, 3, 5, 7) as the repeated measures factor; again, there was no categorical predictor.

Sex differences and dominance patterns

I investigated sex differences in both the temporal (night) and spatial (tank) aspects of four socio-negative behaviours (overt agonistic, ritualised agonistic, submissive, avoidance) to assess the extent to which each sex performed these behaviours. A GLM with night and tank (i.e. home, neutral, foreign) as the first and second repeated measures

factors, and sex as the categorical predictor, was used to assess changes in these behaviours. Again, the design of the input matrix in STATISTICA did not generate the degrees of freedom for a multivariate design, and thus each behaviour was analysed separately with alpha levels adjusted using sequential Bonferroni adjustments ($\alpha' = 0.013$). The first night represented a very different set of conditions to the subsequent nights (i.e. the interactions between two strangers, as opposed to between individuals that were more familiar with one another). I therefore ran the above test twice, with night 1 excluded on the second run, so that the effects of night 1 could be more clearly discerned.

Dominance of one sex over the other was assessed using methods similar to Colvin (1973), Cranford & Derting (1983) and Kinahan & Pillay (2008b). Winners of each dyad had to display both more exploratory and more overt agonistic behaviour than their partner overall (i.e. all nights combined). Where there was no clear winner, the result was regarded as a tie. A chi-squared goodness-of-fit test was then used to determine whether the number of female winners, male winners and ties were evenly distributed among the dyads. This assessment was also conducted twice, with night 1 excluded the second time.

Tank occupancy during the day

A GLM with tank as the repeated measures factor and sex as the categorical predictor was used to analyse the total number of days that individuals were found occupying each tank, as recorded during the daily observations made during the light (i.e. diurnal) phase of the light–dark cycle. The percentage of days that dyads were found to be sharing a tank was also calculated.

Oestrus

Spearman rank correlations were used to test the effect of oestrus, in both sexes where applicable, for the following variables: behaviours during scoring sessions (i.e. explore, overt agonistic, ritualised agonistic, submissive, avoidance, amicable) and tank-sharing during the day. Spearman rank analyses were done since the oestrous data were dichotomous data (i.e. oestrus/anoestrus). For the analyses of behaviours during scoring sessions, one value per minute was used (1/0 scoring) regardless of the tank in which the behaviour occurred. In all analyses, I used the oestrous cycle data collected the day before a night's taping.

Comparison with intrasexual dyad encounters

The temporal and spatial aspects of overt agonistic and amicable behaviour were compared between M–F, F–F and M–M dyads. Sharing of a nest-box was not scored for same-sex dyads, and thus amicable behaviour excluded instances of sharing a nest-box for all dyad-types. A GLM with night and tank as the first and second repeated measures factors, and dyad-type as the categorical predictor, was used to assess changes in these behaviours. As mentioned above, the test was run twice, with night 1 excluded on the second run.

Dominance in intrasexual dyads, in terms of winners and ties, was assessed in the same way as for M–F dyads to determine if one individual tended to dominate the other. Those dyads that were not taped on night 1 (i.e. four F–F dyads and two M–M dyads) were excluded from the first test (i.e. all nights combined) to avoid biasing the results of the first test, and to allow for a comparison with the second test that excluded night 1.

Tank occupancy during the day was analysed for same-sex dyads using a GLM with tank as the repeated measures factor; each dyad-type was analysed separately. Again, the percentage of days that dyads were found to be sharing a tank was also calculated.

RESULTS

Intersexual dyad encounters

Aggressive and amicable behaviour

Variation in the levels of aggressive and amicable behaviour among dyads was very high (see Figures 1 & 2). Of the eight dyads established, three never displayed amicable behaviour and one showed levels of amicability that were more than five times greater than that of any other dyad. The investigation of changes in these behaviours over the eight scoring sessions of night 1 revealed that scoring session was a significant predictor of both aggressive ($F_{7,49} = 3.84$, $p = 0.002$) and amicable behaviour ($F_{7,49} = 3.92$, $p = 0.002$); $\alpha' = 0.025$. Aggression was higher in the first scoring session than all other sessions, while amicable behaviour, which first appeared in one dyad during the 6th scoring session, was highest in the 7th and 8th sessions (post hoc tests; Figure 1). Comparing the changes in these behaviours over all nights revealed that night was also a significant predictor of behaviour ($F_{6,2} = 31.38$, $p = 0.031$) due to higher aggression on night 1 than all other nights; amicable behaviour did not change significantly over the four nights of taping (post hoc tests; Figure 2). Interestingly, the levels of aggressive versus amicable behaviour on nights 3, 5 and 7 remained more or less equal to one another (Figure 2).

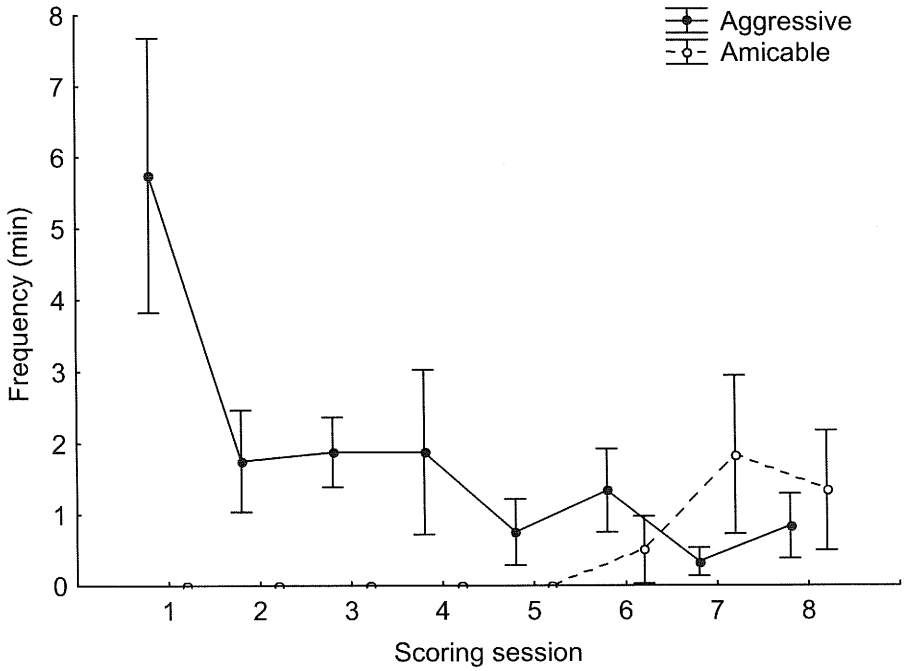


Figure 1. Changes in aggressive and amicable behaviour over the eight 20 minute scoring sessions of night 1, expressed as the mean (± SE) number of minutes in which these behaviours were displayed per session.

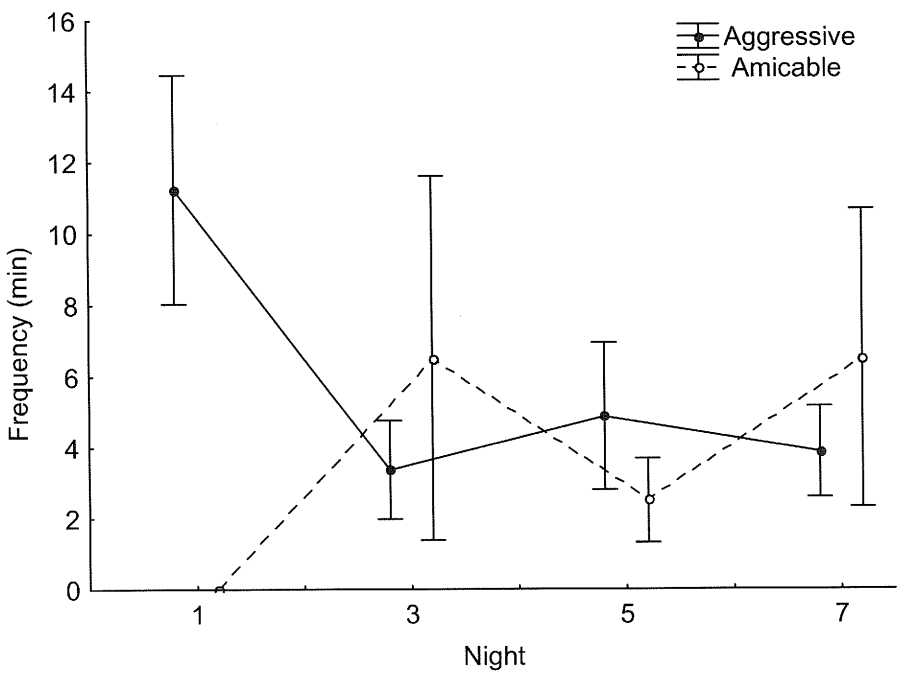


Figure 2. Changes in aggressive and amicable behaviour over all four nights of taping, expressed as the mean (± SE) number of minutes in which these behaviours were displayed per night. Maximum minutes = 80.

Sex differences and dominance patterns

The results of the GLM analyses are provided in Table 2 and the means (± SE) in Figure 3. Although sex showed a statistical trend towards influencing a number of behaviours (especially submissive behaviour), none were significant after sequential Bonferroni adjustments. Night significantly influenced ritualised agonistic behaviour and avoidance (night 1 > all other nights; post hoc tests). The interaction between night and sex was a significant predictor of three behaviours: ritualised agonistic—females performed more of this behaviour on night 1 than any other night/sex combination; submissive—males were more submissive on nights 5 and 7 compared to night 1, and were also more submissive on nights 5 and 7 compared to females on nights 3, 5 and 7; avoidance—females displayed more avoidance on night 1 than any other night/sex combination (post hoc tests). Although all females displayed more avoidance on night 1 than night 7, some displayed much higher levels than others, which accounts for the high variation on night 1. Tank x sex also significantly affected avoidance, most importantly due to: 1) females avoiding males more in the neutral tank than in their (the female's) home tank, and 2) males avoiding females more in their (the male's) home tank than in both other tanks (post hoc tests). Furthermore, there was a strong statistical trend towards females performing high levels of overt agonistic behaviour in the foreign tank, and males performing high levels of submission in their home tank (Table 2; Figure 3). Night x tank significantly influenced avoidance, most importantly due to higher levels in the neutral and foreign tanks compared to the home tank on night 1, whereas on night 7 (with a statistical trend on night 5) avoidance was higher in the home than the foreign tank (post hoc tests).

When the above test was re-run excluding night 1, the only variable to significantly affect behaviour (after sequential Bonferroni adjustments) was sex for overt agonistic ($F_{1,14} = 9.61$, $p = 0.008$) and submissive behaviour ($F_{1,14} = 13.58$, $p = 0.002$): females performed more overt agonistic and males more submissive behaviour (post hoc tests). There were also some strong statistical trends; the two most important are given here. Firstly, night x tank influenced overt agonistic behaviour ($\alpha' = 0.013$; $F_{4,56} = 3.49$, $p > 0.013$) due to high levels in the foreign tank on night 5 and especially night 7 (Figure 3, which also indicates that females were the aggressors). Secondly, tank x sex influenced submissive behaviour ($\alpha' = 0.013$; $F_{2,28} = 3.79$, $p = 0.035$) owing to males performing more submissive behaviour in their home tanks than any other tank x sex combination (Figure 3).

The dominance assessment is summarised in Table 4 under the comparison with intrasexual dyads to facilitate later comparison between the dyad-types. There was no

Table 2. Outcome of GLM analyses showing the effects of sex, night (1, 3, 5, 7), tank (home, neutral, foreign) and the interactions between these on each socio-negative behaviour. Significant effects are shown in bold ($\alpha' = 0.013$).

		Overt agonistic	Ritualised agonistic	Submissive	Avoidance
Sex	$F_{1,14}$	4.37	0.24	7.27	4.53
	p	0.055	0.631	0.017	0.052
Night	$F_{3,42}$	0.68	**4.60**	0.69	**4.66**
	p	0.572	**0.007**	0.565	**0.007**
Night x Sex	$F_{3,42}$	2.10	**3.93**	**3.97**	**7.08**
	p	0.114	**0.015**	**0.014**	**0.001**
Tank	$F_{2,28}$	1.77	1.32	4.06	0.40
	p	0.189	0.284	0.028	0.675
Tank x Sex	$F_{2,28}$	4.25	0.67	4.28	**7.11**
	p	0.024	0.518	0.024	**0.003**
Night x Tank	$F_{6,84}$	1.80	1.56	1.62	**5.24**
	p	0.108	0.169	0.153	**<0.001**
Night x Tank x Sex	$F_{6,84}$	1.02	0.96	1.44	1.47
	p	0.418	0.456	0.208	0.199

difference in the number of female winners, male winners and ties, whether night 1 was included or not. However, females won 63% of encounters when night 1 was excluded, and males never won an encounter, indicating a tendency for female dominance after the first night.

Tank occupancy during the day

Sex had no effect on ad hoc observations of tank occupancy during the diurnal phase of the light–dark cycle ($F_{1,14} = 2.99$, $p = 0.106$), and hence the data for the sexes were pooled. Tank significantly influenced position during the day ($F_{2,30} = 3.32$, $p = 0.050$): the home tank was occupied more often than the neutral tank, and there was also a strong statistical trend towards the home tank being occupied more often than the foreign tank (post hoc tests; see Figure 5 under intrasexual comparison). During day inspections, dyads were sharing a tank on only 10 of the 56 days (18%) and seven of these were attributable to the one exceptionally amicable dyad.

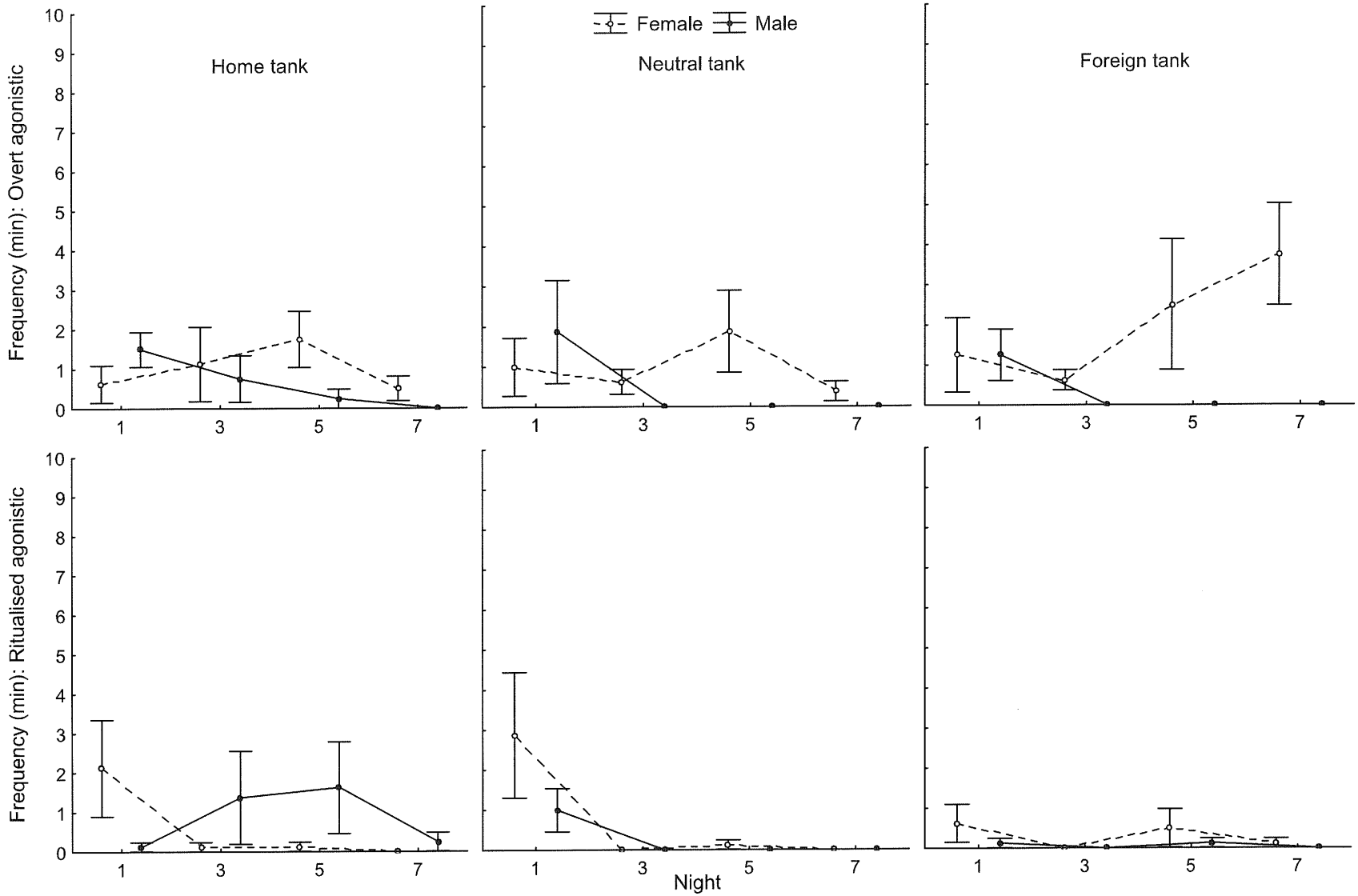
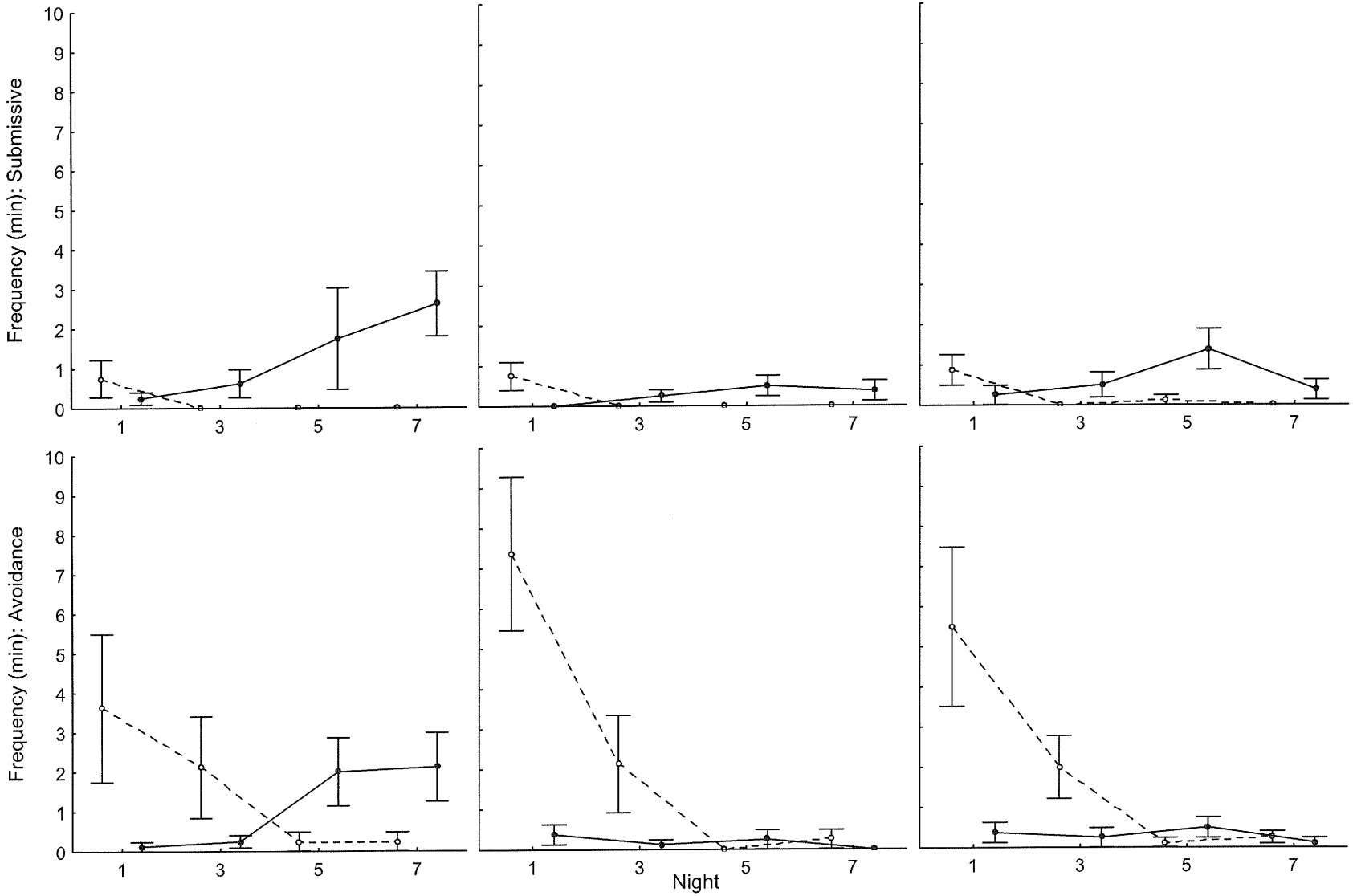


Figure 3. Changes in the four socio-negative behaviours over the four nights of taping, as displayed by each sex in the three tanks, expressed as the mean (± SE) number of minutes in which these behaviours were displayed per night. Maximum minutes = 80.

Figure 3 continued.



Oestrus

No relationship was detected between the oestrous stage of females and any behaviour for either sex (Spearman r range = 0.03 to –0.19, $p > 0.050$ in all cases). Oestrus did not either appear to affect tank-sharing during the day ($r = 0.09$, $p > 0.050$).

Comparison of inter- and intrasexual dyad encounters

Overt agonistic and amicable behaviour

The results of the GLM (multivariate design) are presented in Table 3. Owing to the high number of post hoc results, only those most relevant to the aims of the study are summarised here; Figure 4 gives the means ± SE. The large variation in amicable behaviour in F–F dyads is attributable to the fact that, while most dyads took some time to display amicable behaviour, by night 7 some dyads were highly amicable, while others (four of the nine dyads) showed almost no amicable behaviour. Overall, M–F dyads displayed more overt agonistic behaviour than both F–F and M–M dyads, while F–F dyads were more amicable than both other dyad-types. There was more overt agonistic behaviour on night 1 than on any other night, and amicable levels were progressively higher each night. Compared to night 1, M–F dyads showed less overt agonistic behaviour on night 3, while F–F dyads displayed lower levels on nights 5 and 7; M–M dyads showed similar levels on all nights, although post hoc results combined with Figure 4 suggest a tendency for more overt agonistic behaviour on night 1 than night 7. There were no significant differences in the levels of overt agonistic behaviour between nights 3, 5 and 7 for any dyad-type. Although Figure 4 suggests that M–F dyads showed more overt agonistic behaviour, particularly on nights 5 and 7, than same-sex dyads on equivalent nights, post hoc tests did not reveal significant differences between dyad-types on any one night. Amicable behaviour was displayed at lower levels on night 1 compared to: nights 3 and 7 in M–F dyads, all nights in F–F dyads, and nights 5 and 7 in M–M dyads. M–F dyads displayed similar levels of amicability on nights 3, 5 and 7, while levels for F–F dyads were higher on night 7 than nights 3 and 5, and M–M dyads were higher on nights 5 and 7 than night 3. Apart from night 7 when F–F dyads were more amicable than the other dyad-types, there were no differences in amicability between dyad-types on any one night. The relative levels of overt agonistic and amicable behaviour are of particular interest: Figure 4 suggests that amicable behaviour exceeded overt agonistic behaviour by night 3 in F–F dyads and by night 5 in M–M dyads, whereas the levels of amicable versus overt agonistic behaviour were similar on all nights in M–F dyads. The significant tank effect was owing

to more overt agonistic behaviour overall in the home and foreign tanks than the neutral tank. There were no relevant post hoc results for the interaction between night and tank. The most important result incorporating space use was the lack of interaction between tank and dyad-type, suggesting that none of the dyad-types distinguished between the three tanks in their behaviour, and thus that the home tanks were not defended against dyad partners.

Table 3. Outcome of GLM analysis showing the effects of dyad-type (male–female, female–female, male–male), night (1, 3, 5, 7), tank (home, neutral, foreign) and the interactions between these on overt agonistic and amicable behaviour. Significant effects are shown in bold.

	F	d.f.	p
Dyad-type	**2.98**	**4,100**	**0.023**
Night	**6.11**	**6,46**	**<0.001**
Night x Dyad-type	**2.75**	**12,92**	**0.003**
Tank	**8.91**	**4,48**	**<0.001**
Tank x Dyad-type	0.72	8,96	0.675
Night x Tank	**3.25**	**12,40**	**0.002**
Night x Tank x Dyad-type	1.55	24,80	0.076

When night 1 was excluded, the main results were similar to those in Table 3, except that night x tank no longer had a significant effect ($F_{8,44} = 1.98$, $p = 0.071$). In terms of relevant changes to post hoc results, M–F dyads displayed more overt agonistic behaviour overall than F–F dyads, but no longer M–M dyads. There was also a strong statistical trend for M–M dyads to display more overt agonistic behaviour on night 3 than night 7.

Dominance

A summary of the dominance patterns in inter- and intrasexual dyads is provided in Table 4. There were very few winners in F–F dyads or in M–M dyads when night 1 was excluded from the analysis. Fifty percent of M–M dyads showed dominance relationships when the analysis included night 1. The chi-squared tests showed no difference in the number of winners and ties in intrasexual dyads, whether night 1 was included or not, although there was a strong statistical trend towards more ties than winners in M–M dyads when night 1 was excluded.

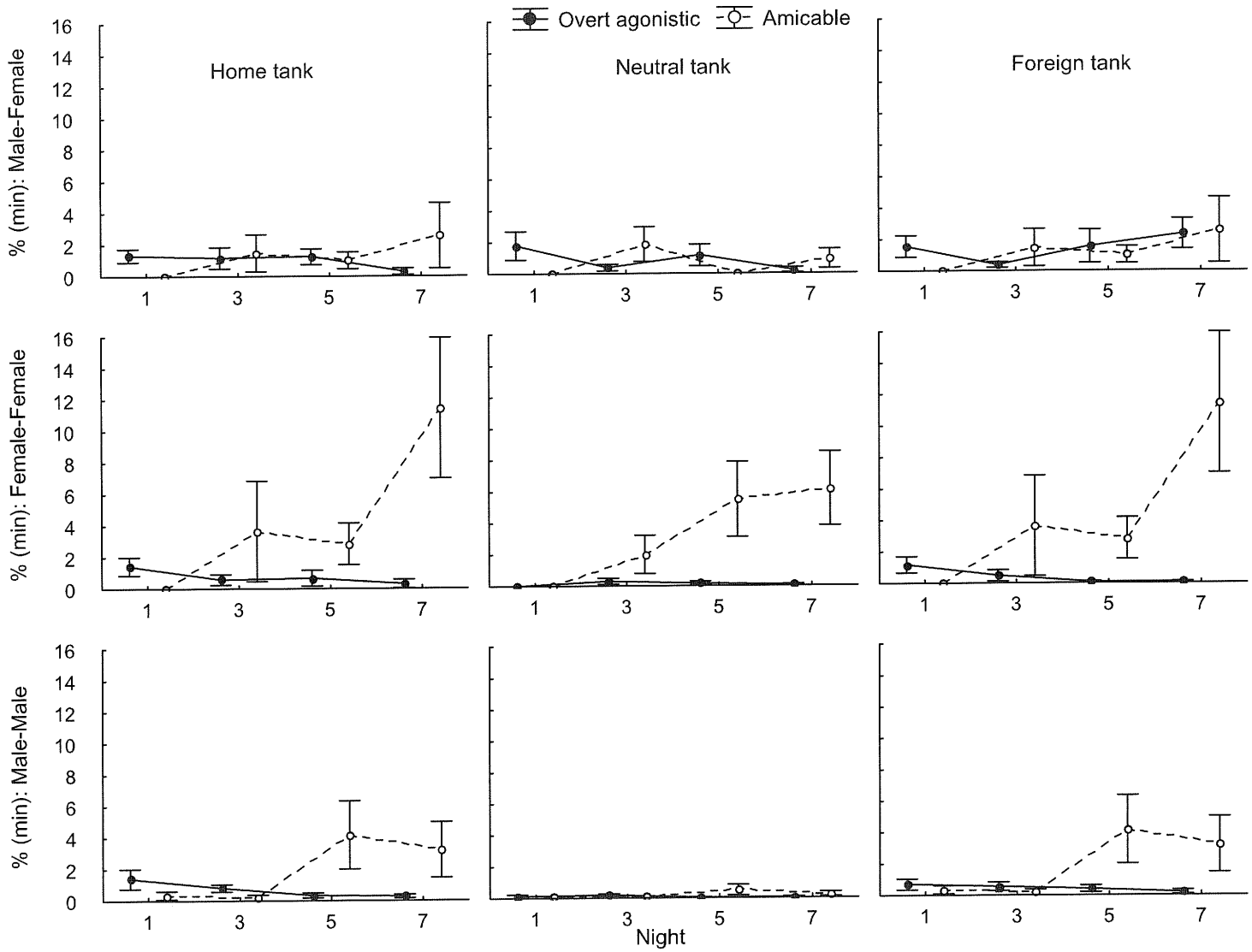


Figure 4. Changes in overt agonistic and amicable behaviour over the four nights of taping as displayed by each dyad-type in the three tanks, expressed as the mean (± SE) number of minutes in which these behaviours were displayed per night (given as a percentage of the total number of minutes scored).

Table 4. Number of dyads in which one individual won the encounter, or in which there was no clear winner (i.e. ties), using data for all nights (i.e. 1, 3, 5, 7) as well as excluding night 1 (i.e. 3, 5, 7). Results of the χ^2 tests are included.

	Male–Female dyads			Female–Female dyads		Male–Male dyads	
	Female winners	Male winners	Ties	Winners	Ties	Winners	Ties
All nights	3	0	5	1	4	4	4
χ^2; d.f.; p	4.75; 2; 0.093			1.80; 1; 0.180		0.00; 1; 1.000	
Excluding night 1	5	0	3	2	7	2	8
χ^2; d.f.; p	4.75; 2; 0.093			2.78; 1; 0.096		3.60; 1; 0.058	

Tank occupancy during the day

Figure 5 includes the data for M–F dyads to facilitate comparison between the dyad-types. Tank significantly affected position during the day in both same-sex dyads. In F–F dyads ($F_{2,34} = 4.91$, $p = 0.013$), the home tank was occupied more than both the neutral and foreign tanks during the day, while in M–M dyads ($F_{2,38} = 7.07$, $p = 0.002$) individuals occupied both the home and foreign tanks more than the neutral tank, but there was no difference between the home and foreign tanks (post hoc tests; Figure 5). Females were found to be sharing tanks on 39% of days and males on 33% of days; this is about twice that of the 18% sharing found in M–F dyads.

Testes size

The mean paired testes mass was 5.14 g (range: 4.79–5.54 g) and the mean body mass was 126.8 g (range: 118–137 g). This gave a mean testes size relative to body mass of 4.07% (range: 3.74–4.69%).

DISCUSSION

Temporal patterns

In male–female encounters, the frequencies of aggressive and amicable behaviours changed over time. As predicted, aggression was high on the first night (especially during the first scoring session) and some level of tolerance was reached over time. However, aggressive behaviour persisted, even after pairs had co-existed for a week, and amicable behaviour did not change significantly from the first to the last night. Contrary to predictions, even once amicable behaviour became apparent, the frequencies of amicable

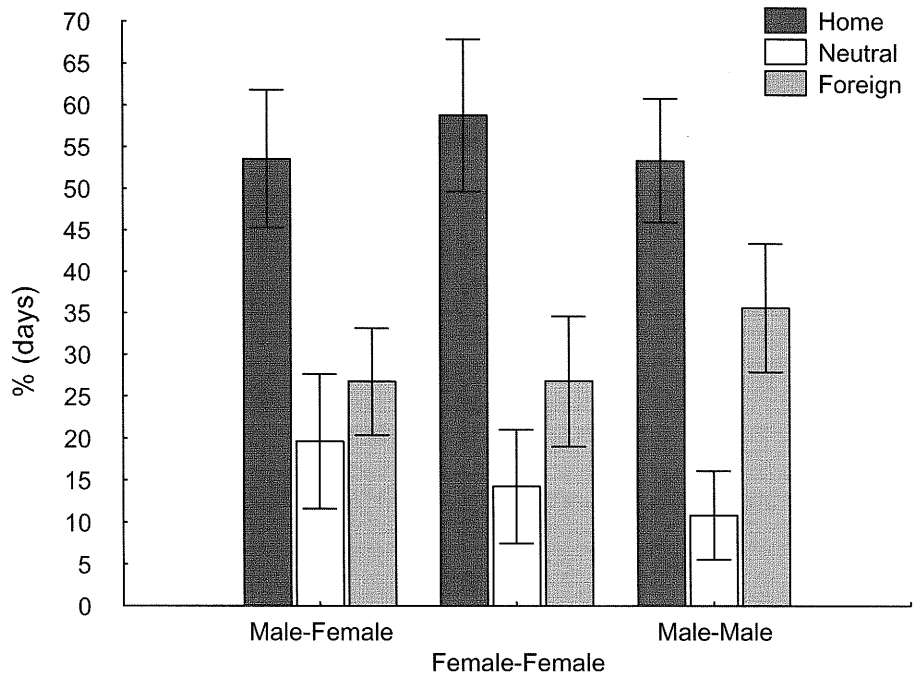


Figure 5. Mean (± SE) number of days that individuals from the three dyad-types were found occupying the home, neutral and foreign tanks during day inspections (given as a percentage of the total number of days of observations).

and aggressive behaviour were similar. Furthermore, very little tank-sharing was evident during observations made in the diurnal phase of the light–dark cycle.

My findings contrast somewhat with those of Dempster et al. (1993) who also conducted male–female dyad encounters in *G. leucogaster* and found relatively high frequencies of amicable compared to aggressive behaviour. They did, however, attempt to induce oestrous behaviour in their female subjects, which was probably successful as they recorded a number of sexual behaviours seldom observed in my study (e.g. mounting, lordosis). Although the number of dyads observed was higher (i.e. 15 versus 8) in the study by Dempster et al. (1993), the number of minutes scored per dyad was higher in my study (i.e. minimum of 340 minutes versus 20 minutes), such that sexual behaviour should still have been observed in my study if it was common. Perhaps the lower aggression and higher amicability in their study reflected specific behaviour during courtship/mating, rather than the general behaviour of the species. In support of this, Mongolian gerbils *Meriones unguiculatus* showed a slight decrease in aggression towards non-cagemates when in oestrus (Ågren & Meyerson 1977). Although I found no association between oestrous state and amicability or aggression, a larger sample size would have been preferable to detect an association. The behavioural differences may also reflect other

differences in the methods employed by me and by Dempster et al. (1993), who used single cages and scored interactions for shorter periods of time (20 minutes). It is possible that my methodology even underestimated direct aggression between individuals as the separate cages provided greater opportunity for avoidance of the dyad partner: Bronson (1964) found that, while overt agonistic behaviour in woodchucks *Marmota monax monax* was high in neutral arenas, it was low in nature where individuals could avoid one another.

There were strong temporal effects on sex differences in behaviour. Higher ritualised agonistic behaviour and avoidance by females on night 1, followed by overall higher levels of overt agonistic behaviour by females when night 1 was excluded from analyses, suggest that females are initially very cautious of males but later become aggressive towards them. Contrary to predictions, my data also support a tendency for female dominance over males after night 1. The increase in overt agonistic behaviour by females is reflected by the increase in male submission from night 1 to nights 5 and 7, and the overall greater levels of submission by males compared to females when the first night was excluded from analyses.

Although no sex differences in aggression were found in *G. leucogaster* in the study by Dempster et al. (1993), *G. afra* females were more aggressive than males, and Dempster et al. (1992) found that highveld gerbil *G. brantsii* females were also the more aggressive sex. It thus appears that *G. leucogaster* from my study showed similar sex differences in aggression to its two South African congeners, suggesting that phylogenetic constraints may play a role in the social behaviour of this genus. It should be noted, however, that methodological differences such as induction of oestrous behaviour and temporal/spatial differences between the three studies make comparison difficult. For example, females from my study only showed overall higher levels of overt agonistic behaviour after the first night was excluded from analyses.

Spatial patterns

In male–female encounters, spatial predictions (in terms of differences in behaviour between the three tanks) were supported in that overt agonistic behaviour was not higher in the home tank compared to the other tanks, suggesting that the home tank might not have been defended. The finding that avoidance on the first night was highest in the neutral and foreign tanks suggests that unfamiliarity with the area contributed to this behaviour. Male avoidance of females in the male's tank, as well as the trend for female overt agonistic behaviour and male submission to occur in the male's tank, was unexpected. This finding

is contrary to a study of spiny mice *Acomys cahirinus* in which females in their home cage were dominant over males, yet there were no differences in male and female aggression in the male's cage (Porter 1976). It also contrasts with reports of animals having a greater chance of victory when intraspecific conflict occurs on their own territory or in a familiar area (Porter 1976; Waage 1988; Stamps & Krishnan 1994).

Inter- versus intrasexual dyads

Like intersexual dyads, some time was needed for tolerance to develop in same-sex dyads. The comparison between dyad-types of overt agonistic behaviour, amicability and tank-sharing during day inspections suggests that female–female dyads were the most tolerant, followed by male–male dyads, with male–female dyads being the least tolerant. The differences in intra- (especially female–female) compared to intersexual encounters contrast with *Gerbillurus* species, where behaviour in 10 minute male–female encounters was very similar to that of same-sex encounters (Dempster & Perrin 1989a, b). However, in 10 minute encounters between two unfamiliar Mongolian gerbils, intrasexual pairs showed much lower levels of agonistic behaviour than intersexual pairs (Swanson 1974), providing some support for my findings. Again, comparisons should be made with caution given methodological differences between my study and the above studies. All dyad-types were similar in their lack of discrimination between their own and their partner's tank during behavioural observations at night. There was no clear evidence of dominance relationships in either intrasexual dyad-type, except perhaps for male–male dyads when night 1 was included in the analysis.

There was no evidence of higher overt agonistic behaviour in the neutral tank, which contained seeds on nights 3, 5 and 7, than the other tanks for any dyad-type, suggesting a lack of competition for this resource. However, if dominance played a role (e.g. in male–female interactions) then the subordinate individual may have avoided the resource or the neutral tank owing to the greater resource holding potential of the dominant individual (see Parker 1974). Furthermore, individuals sometimes began eating the seed before the start of video-taping, such that not all behaviour relating to the seeds would have been taped. There was a tendency for mild aggression over limited supplemental food (e.g. peanuts) in the non-experimental lab-o-tec cages containing same-sex siblings (personal observation), though these cages were smaller than the experimental tanks.

Social organisation and mating system

The social and mating system of a species is the product of several traits, including behaviour patterns, expressed by individuals of the species (Salo et al. 1993). Various elements of social behaviour either attract or repel conspecifics, and behavioural studies can be used to better understand the social organisation of a species (Happold 1976). In my study, the tendency for high levels of overt agonistic combined with low levels of amicable behaviour initially in all dyad-types suggests that *G. leucogaster* in the wild might be intolerant of unfamiliar conspecifics. Male–female behaviour suggests that (contrary to predictions), although some form of tolerance is reached over time, bushveld gerbils do not form pair-bonds or prolonged associations with the opposite sex, at least during the breeding season; the mating system is thus unlikely to be monogamous. In the blunt-nosed rat *Pseudomys shortridgei*, which forms pair-bonds, repelling behaviour was only apparent on day 1, and pairs spent much time together during the 10-day observation period (Happold 1976). In the Mongolian gerbil, which also forms pair-bonds (Ågren 1984), pairs showed much lower levels of aggression and more affiliative behaviour towards cagemates than towards non-cagemates (Ågren & Meyerson 1977; Razzoli & Valsecchi 2006). Thus, although the initial intolerance of bushveld gerbil male–female pairs is not surprising, the fact that only a low level of tolerance was reached over time is indicative of a lack of pair-bonding. It may be that *G. leucogaster* is similar to *G. brantsii*, where burrows are apparently occupied by single females, with males only co-occupying the burrow when the female is in oestrus (Nel 1975).

My data suggest that females became aggressive towards males over time, and that males were even cautious of females within their own home tank. Female aggression has been related to promiscuity (Pillay et al. 1995): females mating promiscuously would meet males fairly frequently, reducing selection for male attractiveness (Alder et al. 1981) and increasing aggression towards males, which may function as a mate choice mechanism (Ferkin 1987). Hence, female aggression in bushveld gerbils may be evidence of a promiscuous mating system. Another consideration is that at least six of the eight females in my study became pregnant, and were probably pregnant for approximately 3–6 days of the study, as calculated from subsequent litters born (Chapter 4) and a gestation period of 21–22 days (Lötter & Pillay 2008, Chapter 2). This may have affected the behaviour of females and suggests that females are aggressive towards males even after mating.

It would appear that my predictions of tolerance in *G. leucogaster* are more applicable to intrasexual, especially female–female, dyads. Also in support of predictions,

individuals did not seem to show more overt agonistic behaviour in their own compared to their partner's tank, tentatively suggesting intrasexual overlap of home ranges and a lack of territoriality in nature. However, further investigations are needed to assess this assumption. While the clear preference for the home tank during day inspections in female–female dyads conflicts with this suggestion, male–male dyads did not appear to distinguish between their own and the foreign tank during the day, supporting a lack of territoriality in males. The tendency towards relatively high amicable versus low overt agonistic behaviour over time in same-sex (particularly female–female) compared to opposite-sex dyads is further evidence that home ranges of residents may overlap intrasexually and that group formation, at least among females, is possible. Choate (1972) found that bushveld gerbils were 'somewhat communal' in the field, but in captivity large, mature adults of both sexes would mark, foot drum and threaten strangers/neighbours, treating cages as territories. This further indicates that more studies are needed to clarify territoriality in this species. Larger sample sizes would also aid in decreasing behavioural variation, and thus help to clarify some of the patterns observed in this study.

Testes mass relative to body mass of field-trapped *G. leucogaster* is reported as 6.0–6.2%, with that of congeners ranging from 0.4% in the black-tailed gerbil *G. nigricaudus* to 7.7% in *G. afra* (Neal 1991). Although my data indicate only 4.1% for *G. leucogaster*, this is probably due to the tendency of laboratory animals to weigh more than field-trapped animals (Neal 1990). The relative testes size of *G. leucogaster* falls towards the upper limits for mammals as a whole, since *G. afra* represents the largest known relative testes size for all mammals (Kenagy & Trombulak 1986). If relative testes size in *G. leucogaster* is related to the mating system as reported for other species of mammals (Harcourt et al. 1981; Kenagy & Trombulak 1986), then, as suggested by Neal (1991), the large relative testes size gives strong evidence for promiscuity. However, recent research by Schradin et al. (2009) suggests that large testes may also be an adaptation to the risk of sperm depletion in polygynous striped mice *Rhabdomys pumilio* mating with synchronously breeding females. Thus large relative testes size alone may not necessarily imply a promiscuous mating system. Boonstra et al. (1993) suggested that sexual dimorphism in body mass is related to mating system in microtines such that polygynous species should show the greatest sexual dimorphism, presumably due to male competition, followed by promiscuous species and finally species that display obligate monogamy; bushveld gerbils show no sexual dimorphism (Smithers 1983; Skinner & Chimimba 2005; Chapter 6). High intermale aggression has also been related to a polygynous mating system (Granjon &

Duplantier 1993; Sachser et al. 1999), and perhaps the relative tolerance shown by males in my study is suggestive of a lack of polygyny.

In conclusion, this study has shown that social behaviour, and thus social relationships, can change over time in bushveld gerbils. It would appear that *G. leucogaster* in nature may be intolerant of unfamiliar conspecifics, but that tolerance can increase with increasing familiarity, particularly in same-sex interactions. It is doubtful that males and females form pair-bonds or prolonged associations, at least during the breeding season. It is possible that home ranges overlap intrasexually and that group formation may take place, especially among females. Altogether, the large relative testes size, lack of sexual dimorphism and the possibility of intrasexual male tolerance make it unlikely that *G. leucogaster* is polygynous. This, together with the improbability that they form monogamous pairs, supports the claim that the species is promiscuous (see also Chapter 6). Further studies are necessary to increase our understanding of sociality, and particularly same-sex interactions, in bushveld gerbils. There are also several different contexts that one could provide when investigating social behaviour, apart from those used in the current study. For example, the compatibility of males in the presence of females is related to mating system in two caviomorph rodents: males from a polygynous species were highly incompatible whereas those from a promiscuous species showed much greater tolerance (Sachser et al. 1999). It would thus be of interest to test male–male interactions in the presence of an oestrous female, which would provide some indication of whether males compete for females or whether females mate with both males.

REFERENCE LIST

Ågren, G. (1984). Pair formation in the Mongolian gerbil. *Animal Behaviour* **32**: 528–535.

Ågren, G. & Meyerson, B.J. (1977). Influence of gonadal hormones and social housing conditions on agonistic, copulatory, and related socio-sexual behaviour in the Mongolian gerbil (*Meriones unguiculatus*). *Behavioural Processes* **2**: 265–282.

Ågren, G., Zhou, Q. & Zhong, W. (1989). Ecology and social behaviour of Mongolian gerbils, *Meriones unguiculatus*, at Xilinhot, Inner Mongolia, China. *Animal Behaviour* **37**: 11–27.

Alder, E.M., Godfrey, J., McGill, T.E. & Watt, K.R. (1981). The contributions of genotype and sex to variation in mating behaviour between geographical subspecies of the

bank vole (*Clethrionomys glareolus* Schreber). *Animal Behaviour* **29**: 942–952.

Behrends, P., Daly, M. & Wilson, M.I. (1986). Range use patterns and spatial relationships of Merriam's kangaroo rats (*Dipodomys merriami*). *Behaviour* **96**: 187–209.

Bondrup-Nielsen, S., Lambin, X. & Fredga, K. (1993). An overview of dyadic behaviour encounters with an example: behaviour of female wood lemmings (*Myopus schisticolor*). In: Stenseth, N.C. & Ims, R.A. (eds). *The Biology of Lemmings*. Academic Press, Harcourt Brace and Company: London.

Boonstra, R., Gilbert, B.S. & Krebs, C.J. (1993). Mating systems and sexual dimorphism in mass in microtines. *Journal of Mammalogy* **74**: 224–229.

Bronson, F.H. (1964). Agonistic behaviour in woodchucks. *Animal Behaviour* **12**: 470–478.

Choate, T.S. (1972). Behavioural studies on some Rhodesian rodents. *Zoologica Africana* **7**: 103–118.

Colvin, D.V. (1973). Agonistic behaviour in males of five species of voles *Microtus*. *Animal Behaviour* **21**: 471–480.

Cranford, J.A. & Derting, T.L. (1983). Intra and interspecific behavior of *Microtus pennsylvanicus* and *Microtus pinetorum*. *Behavioural Ecology and Sociobiology* **13**: 7–11.

De Graaff, G. (1981). *The Rodents of Southern Africa*. Butterworths: Durban.

Dempster, E.R., Dempster, R. & Perrin, M.R. (1992). A comparative study of the behaviour of six taxa of male and female gerbils (Rodentia) in intra- and interspecific encounters. *Ethology* **91**: 25–45.

Dempster, E.R., Dempster, R. & Perrin, M.R. (1993). Behavioural divergence in allopatric and sympatric gerbil species (Rodentia: Gerbillinae). *Ethology* **93**: 300–314.

Dempster, E.R. & Perrin, M.R. (1989a). A comparative study of agonistic behaviour in hairy-footed gerbils (Genus *Gerbillurus*). *Ethology* **83**: 43–59.

Dempster, E.R. & Perrin, M.R. (1989b). Male-female interactions in hairy-footed gerbils

(genus *Gerbillurus*). *Ethology* **83**: 326–334.

Ferkin, M.H. (1987). Reproductive correlates of aggressive behavior in female *Peromyscus melanophrys*. *Journal of Mammalogy* **68**: 698–701.

Gleason, P.E., Michael, S.D. & Christian, J.J. (1980). Aggressive behavior during the reproductive cycle of female *Peromyscus leucopus*: effects of encounter site. *Behavioral and Neural Biology* **29**: 506–511.

Grafen, A. & Hails, R. (2002). *Modern Statistics for the Life Sciences*. Oxford University Press: Oxford.

Granjon, L. & Duplantier, J.-M. (1993). Social structure in synanthropic populations of a murid rodent *Mastomys natalensis* in Sénégal. *Acta Theriologica* **38**: 39–47.

Gromov, V.S., Krasnov, B.R. & Shenbrot, G.I. (2001). Behavioural correlates of spatial distribution in Wagner's gerbil *Gerbillus dasyurus* (Rodentia, Gerbillinae). *Mammalia* **65**: 111–120.

Happold, M. (1976). Social behavior of the conilurine rodents (Muridae) of Australia. *Zeitschrift für Tierpsychologie* **40**: 113–182.

Harcourt, A.H., Harvey, P.H., Larson, S.G. & Short, R.V. (1981). Testis weight, body weight and breeding system in primates. *Nature* **293**: 55–57.

Hurst, J.L., Hall, S., Roberts, R. & Christian, C. (1996). Social organization in the aboriginal house mouse, *Mus spretus* Lataste: behavioural mechanisms underlying the spatial dispersion of competitors. *Animal Behaviour* **51**: 327–344.

Jarvis, J.U.M. (1981). Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science* **212**: 571–573.

Kenagy, G.J. & Trombulak, S.C. (1986). Size and function of mammalian testes in relation to body size. *Journal of Mammalogy* **67**: 1–22.

Kinahan, A.A. & Pillay, N. (2008a). Does differential exploitation of folivory promote coexistence in an African savanna granivorous rodent community? *Journal of Mammalogy* **89**: 132–137.

Kinahan, A.A. & Pillay, N. (2008b). Dominance status influences female reproductive strategy in a territorial African rodent *Rhabdomys pumilio*. *Behavioural Ecology and Sociobiology* **62**: 579–587.

Lott, D.F. (1991). *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge University Press: Cambridge.

Lötter, T.K. & Pillay, N. (2008). Reproduction and postnatal development of the bushveld gerbil *Gerbilliscus* (formerly *Tatera*) *leucogaster*. *Mammalian Biology* **73**: 430–437.

Martin, P. & Bateson, P. (2007). *Measuring Behaviour: An Introductory Guide*. (3rd ed.). Cambridge University Press: Cambridge.

Neal, B.R. (1990). Observations on the early post-natal growth and development of *Tatera leucogaster*, *Aethomys chrysophilus* and *A. namaquensis* from Zimbabwe, with a review of the pre- and post-natal growth and development of African Muroid rodents. *Mammalia* **54**: 245–270.

Neal, B.R. (1991). Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae: Rodentia), in Zimbabwe. *Zeitschrift für Säugetierkunde* **56**: 101–111.

Nel, J.A.J. (1975). Aspects of the social ethology of some Kalahari rodents. *Zeitschrift für Tierpsychologie* **37**: 322–331.

O'Riain, M.J. & Jarvis, J.U.M. (1997). Colony member recognition and xenophobia in the naked mole-rat. *Animal Behaviour* **53**: 487–498.

Ostfeld, R.S. (1985). Experimental analysis of aggression and spacing behavior in California voles. *Canadian Journal of Zoology* **63**: 2277–2282.

Parker, G.A. (1974). Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology* **47**: 223–243.

Perrin, M.R. & Swanepoel, P. (1987). Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life history theory. *South African Journal of Zoology* **22**: 218–227.

Pillay, N., Willan, K. & Cooke, J. (1995). Evidence of pre-mating reproductive isolation in two populations of the Vlei rat *Otomys irroratus*: experiments of intra- and interpopulation male-female encounters. *Zeitschrift für Säugetierkunde* **60**: 352–360.

Porter, R.H. (1976). Sex-differences in the agonistic behavior of spiny-mice (*Acomys cahirinus*). *Zeitschrift für Tierpsychologie* **40**: 100–108.

Razzoli, M. & Valsecchi, P. (2006). Different social bonds produce differential effects on behaviour and physiology in Mongolian gerbils. *Ethology Ecology & Evolution* **18**: 289–306.

Rice, W.R. (1989). Analyzing tables of statistical tests. *Evolution* **43**: 223–225.

Sachser, N., Schwarz-Weig, E., Keil, A. & Epplen, J.T. (1999). Behavioural strategies, testis size, and reproductive success in two Caviomorph rodents with different mating systems. *Behaviour* **136**: 1203–1217.

Salo, A.L., Shapiro, L.E. & Dewsbury, D.A. (1993). Affiliative behavior in different species of voles (*Microtus*). *Psychological Reports* **72**: 316–318.

Schradin, C., Kinahan, A.A. & Pillay, N. (2009). Cooperative breeding in groups of synchronously mating females and evolution of large testes to avoid sperm depletion in African striped mice. *Biology of Reproduction* **81**: 111–117.

Schradin, C. & Pillay, N. (2003). Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*): laboratory and field evidence. *Journal of Comparative Psychology* **117**: 317–324.

Schwaibold, U. & Pillay, N. (2006). Behavioral strategies of the African ice rat *Otomys sloggetti robertsi* in the cold. *Physiology and Behavior* **88**: 567–574.

Skinner, J.D. & Chimimba, C.T. (2005). *The Mammals of the Southern African Subregion*. (3rd ed.). Cambridge University Press: Cape Town.

Smithers, R.H.N. (1983). *The Mammals of the Southern African Subregion*. University of Pretoria: Pretoria.

Stamps, J.A. & Krishnan, V.V. (1994). Territory acquisition in lizards: II. Establishing

social and spatial relationships. *Animal Behaviour* **47**: 1387–1400.

StatSoft, Inc. (2001). *STATISTICA* (data analysis software system), *version 6*. www.statsoft.com.

Swanson, H.H. (1974). Sex differences in behaviour of the Mongolian gerbil (*Meriones unguiculatus*) in encounters between pairs of same or opposite sex. *Animal Behaviour* **22**: 638–644.

Vassallo, A.I. & Busch, C. (1992). Interspecific agonism between two sympatric species of *Ctenomys* (Rodentia: Octodontidae) in captivity. *Behaviour* **120**: 40–50.

Volodin, I.A. & Goltsman, M.E. (2002). Strategies of aggressive fighting reflect degree of sociality in three species of gerbils. In: Singleton, G.R., Hinds, L.A., Krebs, C.J. & Spratt, D.M. (eds). *Rats, Mice and People: Rodent Biology and Management*. ACIAR: Canberra.

Waage, J.K. (1988). Confusion over residency and the escalation of damselfly territorial disputes. *Animal Behaviour* **36**: 586–595.

Wolff, J.O. (2003). Laboratory studies with rodents: facts or artifacts? *Bioscience* **53**: 421–427.

Zuri, I. & Rado, R. (2000). Sociality and agonistic behavior in the lesser white-toothed shrew, *Crocidura suaveolens*. *Journal of Mammalogy* **81**: 606–616.

CHAPTER FOUR

Female aggression in the bushveld gerbil *Gerbilliscus leucogaster* during pregnancy and lactation: a case of infanticide prevention?

ABSTRACT

This study assessed the interactions of male–female pairs of bushveld gerbils *Gerbilliscus leucogaster* during pregnancy and lactation, and investigated whether tolerance levels changed with the changing reproductive condition of the female. This was achieved by observing the behaviour of familiar male–female pairs, and comparing behaviour before parturition with behaviour after parturition. Aggressive behaviour persisted throughout the study but I did not find clear changes in aggression levels over time, although there was a trend towards an increase in aggression immediately after parturition. Amicable behaviour ceased completely after parturition. Females were the aggressive sex, while males were cautious of females. I discuss possible reasons for aggression by females and suggest that protection against potential infanticide risk is a probable explanation. The behaviour of females and males in this study also suggests a lack of pair-bonding in bushveld gerbils.

Keywords: *Gerbilliscus leucogaster*; reproductive condition; female aggression; infanticide

INTRODUCTION

The social behaviour of animals is not fixed, and may change depending on factors such as the breeding condition of the female (Svare 1981). For example, in Brants' whistling rat *Parotomys brantsii*, an adult male can apparently live in a colony with several adult/subadult females in the non-breeding season, but females with offspring (suckling or newly weaned) are aggressive towards males entering their colony (Nel 1975). The interaction of males and females after mating is related to the social and mating system of a population/species. Many solitary species only tolerate one another during the mating period, and thereafter females become aggressive towards males (e.g. golden hamster *Mesocricetus auratus*: Lisk et al. 1983; pouched mouse *Saccostomus campestris*: Westlin 1996). In social species, particularly where there is a strong bond between the male and female, the female may not only tolerate the presence of the male during pregnancy,

parturition and lactation, but the male may also care for the offspring. For example, in the social northern hopping-mouse *Notomys alexis* male–female interactions during pregnancy and birth are amicable, with no repelling behaviour; males are present at parturition and exhibit paternal care (Happold 1976). Populations of the striped mouse *Rhabdomys pumilio* from the succulent karoo of South Africa are social, exhibiting communal breeding (Schradin & Pillay 2004) and paternal care, in which males display all parental behaviours, except nursing (Schradin & Pillay 2003).

There are a number of reasons that females may not tolerate males during pregnancy and lactation. For example, the female may be defending a territory containing resources such as food necessary to meet her energy demands during pregnancy and lactation (e.g. Ostfeld 1985, 1990). Alternatively (or in addition), female aggression towards males may serve to protect young from the risk of infanticide (Wolff 1985; Ostfeld 1990). Infanticidal males potentially benefit in several ways, including obtaining food resources and/or by producing their own offspring sooner through reducing the interbirth interval of the victimised female with whom they mate (reviewed in Ebensperger 1998; Ebensperger & Blumstein 2007). Obviously infanticide for these reasons is only beneficial if the male is not the father (Elwood et al. 1990), and certainty of paternity has been related to infanticide inhibition in a number of rodents (e.g. *Peromyscus* species: Wolff 1985; Wolff & Cicirello 1989). It has also been suggested that multi-male mating by females may prevent infanticide by confusing paternity (reviewed in Ebensperger & Blumstein 2007).

Reports of changes in maternal aggression during pregnancy differ: some strains of laboratory mice exhibit aggression only during lactation, while other strains show an increase in aggression with the progression of gestation, and the golden hamster shows a peak in aggression about 6 days before parturition (reviewed in Svare 1981). Studies of maternal aggression during lactation indicate that it is usually greatest early in the lactation period and decreases with time; maternal aggression in laboratory mice is highest when the young are 3–8 days old, and very low when they are 15–21 days old (e.g. Gandelman 1972; St. John & Corning 1973; reviewed in Svare 1981). Wolff (1985) investigated infanticide in two *Peromyscus* species and suggested that there is a critical period (between days 1 and 12–15) when young are particularly vulnerable to infanticide.

The bushveld gerbil *Gerbilliscus leucogaster* is a nocturnal, burrowing rodent, with a widespread occurrence from Tanzania and the Democratic Republic of Congo down to South Africa (Skinner & Chimimba 2005). The literature indicates that this species is tolerant of conspecifics (Choate 1972; De Graaff 1981; Dempster et al. 1993; Skinner &

Chimimba 2005) but a detailed study of their social behaviour suggests that, although same-sex interactions between familiar individuals may be relatively tolerant, male–female interactions are not particularly tolerant and persistent aggression is displayed mainly by females (Chapter 3). In addition, there is strong evidence for a promiscuous mating system, as suggested for this species by Neal (1991), and prolonged intersexual associations are unlikely, at least during the breeding season (Chapter 3).

The primary aim of this study was to investigate the social interactions between male and female *G. leucogaster* that were familiar with one another, in the context of pregnancy and lactation. Although males and females showed some amicable behaviour in the previous study, aggression persisted throughout the seven days of that study (Chapter 3). The current study aimed to investigate whether and how levels of aggression and amicability change with the changing reproductive condition of the female. If *G. leucogaster* is promiscuous and does not form prolonged male–female associations, the female should be unaccustomed to the presence of the male after mating. Consequently, I expected that interactions would be characterised by high levels of aggression and low amicability, and that females would be the more aggressive sex because of potential infanticide risk. Furthermore, I expected that female aggression would be highest early in the lactation period when this risk may be greatest.

MATERIALS AND METHODS

Study animals

The origin of study animals and the housing conditions are described elsewhere (Lötter & Pillay 2008, Chapter 2). Eight male–female pairs were used to investigate social interactions before and after the birth of the litter. Six of these were pairs from the previous male–female dyad encounters (Chapter 3), and two were additional pairs to increase the sample size. Due to logistical constraints, such as time and the number of wild-caught females (all females used in this study were wild-caught), and ethical considerations of maximising the use of animals, one of these two additional females was paired with a different male for the 'before birth' and 'after birth' parts of the experiment (± 3 months apart). Each male was the father of the offspring that the female was bearing/nursing at the time, and since this study focussed on changes in the reproductive condition of females, this female was treated as belonging to a single pair for the purpose of analyses (which involved a repeated measures design; see below). Furthermore, the data (below) for this

'pair' always fell within or close to (within 10% of) the range of the data for the other pairs, suggesting that the pairing procedure did not affect the data.

Experimental protocol

The six pairs from the male–female dyad encounters were transferred to different tank apparatus (below) after the initial 7-night dyad experiment. The remaining pairs were established at least 10 days prior to the start of experiments to ensure that males and females were familiar with one another. Initially (for the first two of the six pairs), both individuals were placed together in a large tank (855 x 305 x 350 mm), each with their own nest-box, water bottle and food dish. However, female aggression tended to be quite high, so consequently 0–4 days after the birth of the litter a small tank (465 x 310 x 350 mm) was attached to the large tank with an opaque PVC pipe (± 100–300 mm long, 45 mm diameter) to provide the male with an alternative place to nest. This small tank also had its own nest-box, water bottle and food dish. Thereafter, at the start of the experiment all pairs were provided with either one large tank connected to a smaller one, or two small tanks connected to each other. For ethical reasons, if injuries or weight-loss suggested high aggression or stress, the pair was separated by placing a steel barrier into the connecting pipe. The barrier was removed on those nights that behaviour was video-taped (below); this occurred on 12% of nights taped and involved four pairs. In two pairs, taping was restricted to fewer nights because of high aggression by females. Water and Epol® mouse cubes were available ad libitum and the diet was regularly supplemented with sunflower seeds, peanuts, mealworms and apple.

Pairs were video-taped for four hours per night, as described elsewhere (Chapter 3). Behaviour was not recorded on the first night when the pair was placed into their experimental tanks. Pairs were usually taped twice a week during pregnancy and lactation until young were about 2–3 weeks old; however, the number of nights taped differed between pairs (see Table 1 under data analysis). When scoring video tapes, focal sampling and a one–zero recording method with one minute intervals (Martin & Bateson 2007) were used to score the behaviours of each individual in the pair. Any behaviour was thus only scored once per individual per tank per minute. The behaviours used in this study included overt agonistic, ritualised agonistic, submissive, avoidance and amicable behaviour (see Chapter 3 for definitions). No sexual behaviour was observed during scoring sessions. For each minute, I also recorded whether or not the pair shared a tank during that minute. Scoring commenced 30 minutes after the start of the taping session (to increase the

likelihood that individuals would be active) and was conducted for the first 20 minutes of each hour thereafter. When an individual was not visible for a full minute, resulting in gaps in the data set, I assumed the behaviour and, where necessary, the tank position of the individual for that minute (as per Chapter 3). The number of minutes in which an individual was not visible for a full minute only amounted to approximately 1% of all minutes scored for males and females combined.

Data analysis

Data were analysed using STATISTICA 6.0 (StatSoft, Inc. 2001). All tests were two-tailed, with model-level significance determined at $\alpha = 0.05$. Alpha levels for individual tests were adjusted when several component tests were conducted (see below), and in these cases the adjusted alpha is provided below as well as in the Results for clarity; otherwise all tests were conducted at $\alpha = 0.05$. One value per minute was used for each behaviour (as per 1/0 recording), regardless of the tank in which the behaviour occurred. The effect of time relative to parturition was assessed by dividing the data from the video recordings into six time categories: 8–21 days; 4–7 days; 0–3 days before birth and 0–3 days; 4–7 days; 8–21 days after birth. Time was divided in this way in an attempt to detect changes in behaviour immediately before and after birth, as well as in the preceding/following weeks. Owing to the variation in the number of nights per category that pairs were taped (Table 1), all data were converted to proportions of the total number of minutes scored per category for each pair and then arcsine-transformed.

General Linear Models (GLMs) were used to assess the effect of time relative to birth on the variables below. All GLMs involved a repeated measures design since the same pairs were tested over a number of time categories. Fisher LSD post hoc tests were used to determine specific differences when categorical predictors/repeated measures factors had a significant effect. Although a multivariate design is appropriate when tests involve more than one dependent behaviour, the design of the input matrix in STATISTICA did not generate the degrees of freedom for a combined analysis of behaviours when this was necessary, and thus each behaviour was analysed separately with the alpha levels adjusted using the sequential Bonferroni technique (Rice 1989). The symbol—α'—refers to the first adjusted alpha in the sequence of the Bonferroni adjustment procedure. A number of time categories had one or more missing values, as per Table 1. To ensure that all the pairs (i.e. $n = 8$ pairs) were incorporated during repeated measures tests a mean substitution was performed on any missing values. The percentage

Table 1. Number of nights taped per time category for each pair three weeks before and three weeks after parturition. The resulting sample sizes (i.e. number of pairs taped) per time category are provided in parentheses.

Pair	Before birth			After birth		
	8–21 days (n = 8)	4–7 days (n = 6)	0–3 days (n = 5)	0–3 days (n = 7)	4–7 days (n = 6)	8–21 days (n = 7)
A	1	1	1	1	1	1
B	2	1	1	1	1	3
C	1	0	0	2	0	0
D	2	1	1	1	1	3
E	3	0	2	1	1	3
F	1	1	0	1	0	2
G	4	1	0	0	2	3
H	1	1	1	2	1	2

of data requiring mean substitutions ranged from 12.5–18.8% per test. All figures were generated without the mean substitutions to display the original data for comparison.

Aggressive and amicable behaviour

In order to obtain an overall impression of aggression versus amicability, I calculated one measure of aggression by combining the following forms of aggression: overt agonistic, ritualised agonistic and submissive behaviour, as well as where a nest-box was briefly co-occupied, but where this appeared aggressive rather than amicable. The sex of the dyad partners was not taken into account: for each minute, aggression and amicability were scored as occurring or not occurring (1/0 recording), regardless of the sex performing the behaviour. I therefore used one score for aggressive and one score for amicable behaviour per minute per pair. Changes in these behaviours were assessed using the six time categories as the repeated measures factor; there was no categorical predictor ($\alpha' = 0.025$).

Sex differences

I investigated sex differences in four socio-negative behaviours (overt agonistic, ritualised agonistic, submissive, avoidance), using the six time categories as the repeated measures factor and sex as a categorical predictor ($\alpha' = 0.013$).

Tank occupancy and sharing

I investigated whether one or both sexes was avoiding contact with the other by limiting their activity to one tank, or by avoiding sharing a tank: even if direct aggression levels were low, this could have been due to limited contact between the pair (Bronson 1964). I first calculated the number of minutes in which the two tanks were occupied by each sex to obtain an occupancy value for males and females for each tank. I then subtracted the occupancy value of one tank from the other to calculate the difference in occupancy between the two tanks for each sex. A large difference between the tanks would indicate that activity tended to be confined to one tank, whereas a small difference would suggest that the tanks were used more equally. I also examined the number of minutes in which each pair shared a tank. For both tests, there were extra missing data points under a number of time categories (as the first two pairs only had one tank for a while). To reduce the number of missing values I pooled the six time categories into two: 'before' and 'after' birth (resulting in two pairs with a missing value in the 'before' category), and used this pooled time as the repeated measures factor for both tests, with sex as the categorical predictor for the test involving the difference in tank occupancy.

RESULTS

Aggressive and amicable behaviour

Time was not a significant predictor of aggression, although there was a statistical trend in this regard ($F_{5,35} = 2.40$, $p = 0.057$) suggesting higher aggression just after birth compared to just before birth, with a subsequent decrease 4–7 days after birth (Figure 1). Time did significantly affect amicable behaviour ($F_{5,35} = 2.95$, $p = 0.025$, $\alpha' = 0.025$), owing mainly to higher amicability 8–21 and 0–3 days before birth compared to all time categories after birth (post hoc tests; Figure 1).

Sex differences

The results of the GLM analyses are given in Table 2. Sex significantly affected three of the four behaviours (overt agonistic, submissive, avoidance), with females exhibiting more overt agonistic behaviour and males displaying more submissive and avoidance behaviour (post hoc tests; Figure 2). The time categories did not affect any behaviour after sequential Bonferroni adjustments, nor did the interaction between time and sex.

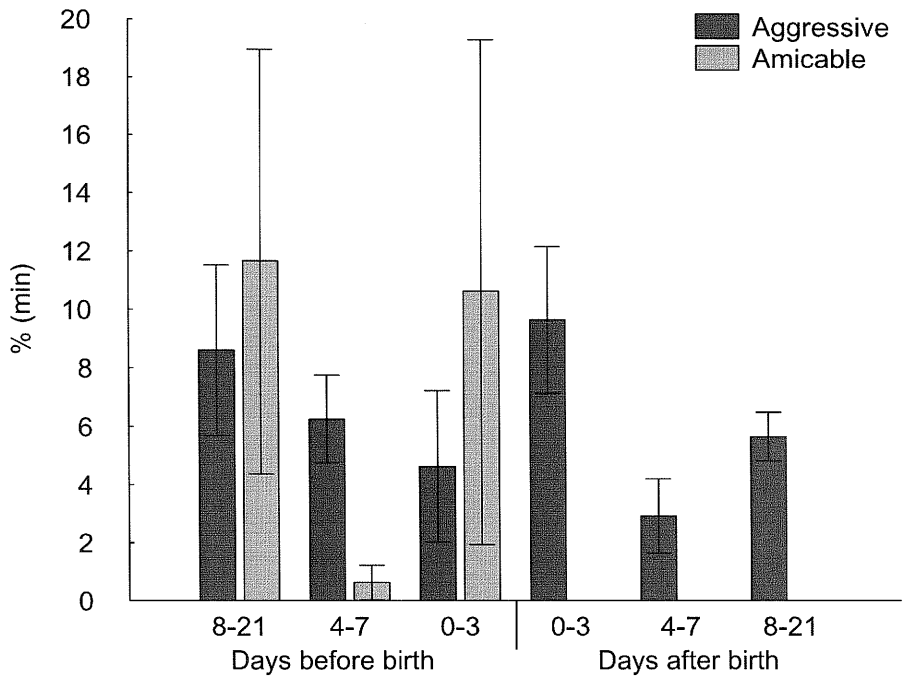


Figure 1. Changes in aggressive and amicable behaviour in relation to time before and after parturition, expressed as the mean (± SE) number of minutes in which these behaviours occurred in each of the six time categories (given as a percentage of the total number of minutes scored).

Table 2. Outcome of GLM analyses showing the effects of sex, the six time categories (8–21, 4–7, 0–3 days before birth and 0–3, 4–7, 8–21 days after birth) and the interactions between these on each socio-negative behaviour. Significant effects are shown in bold (α' = 0.013).

		Overt agonistic	Ritualised agonistic	Submissive	Avoidance
Sex	$F_{1,14}$	**151.02**	0.44	**210.60**	**36.31**
	p	**< 0.001**	0.520	**< 0.001**	**< 0.001**
Time	$F_{5,70}$	2.67	3.07	2.34	1.74
	p	0.029	0.015	0.050	0.136
Time x Sex	$F_{5,70}$	1.58	2.75	1.60	0.84
	p	0.177	0.025	0.170	0.524

Tank occupancy and sharing

Sex was a significant predictor of the difference in occupancy between the two tanks ($F_{1,14} = 46.02$, $p < 0.001$), with females exhibiting a smaller difference than males (post hoc tests; Figure 3), indicating that females used the tanks more equally, while males tended to remain in one tank. Time did not have a significant effect, although there was a statistical trend towards a greater difference after birth ($F_{1,14} = 4.18$, $p = 0.060$; Figure 3).

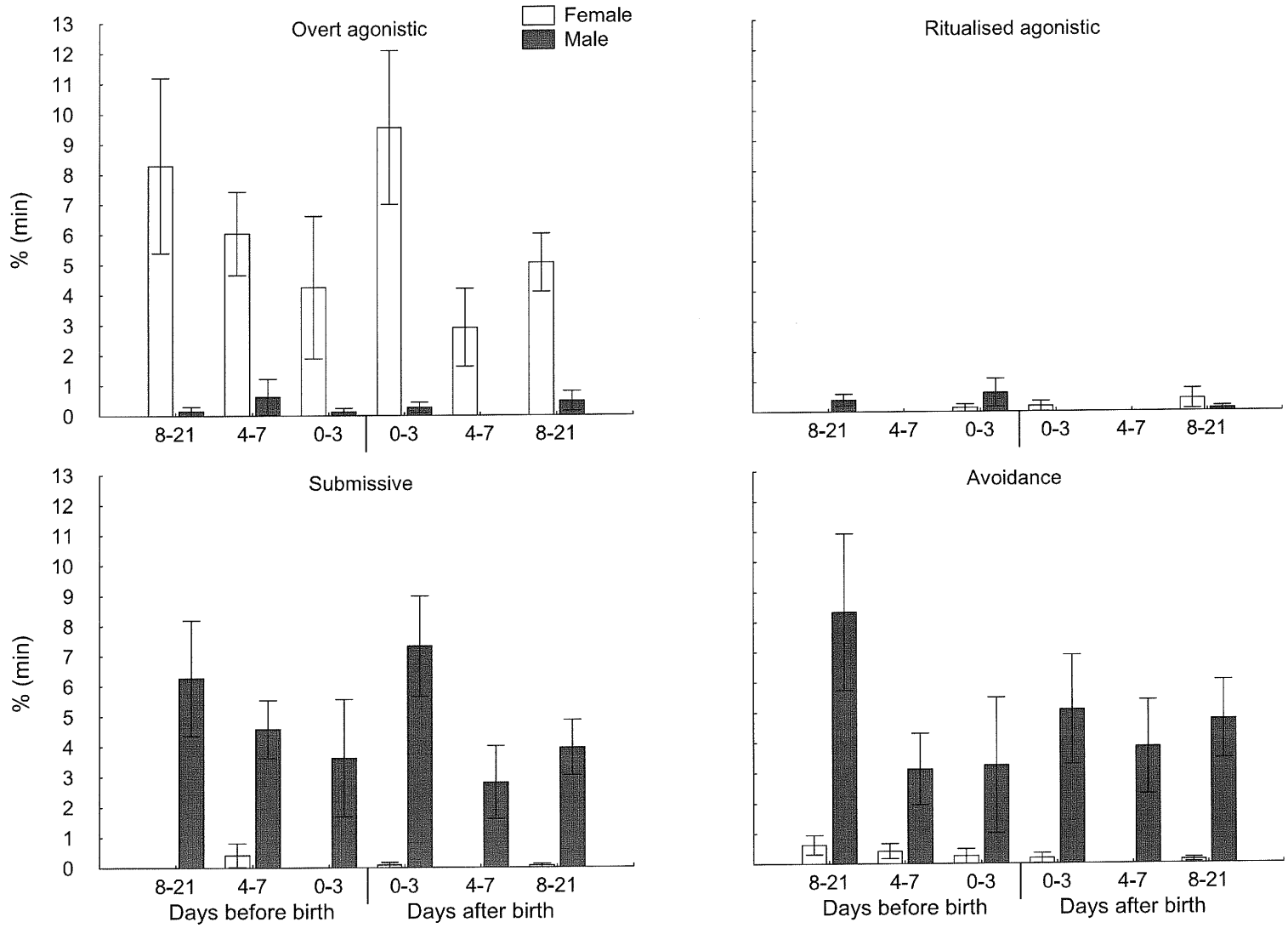


Figure 2. Changes in the four socio-negative behaviours, displayed by each sex in relation to time before and after parturition, expressed as the mean (± SE) number of minutes in which these behaviours were displayed in each of the six time categories (given as a percentage of the total number of minutes scored).

The interaction between time and sex had no effect ($F_{1,14} = 0.32$, $p = 0.582$). Finally, time had a near-significant effect on tank-sharing, with a strong statistical trend towards less sharing after birth ($F_{1,7} = 5.13$, $p = 0.058$; Figure 4).

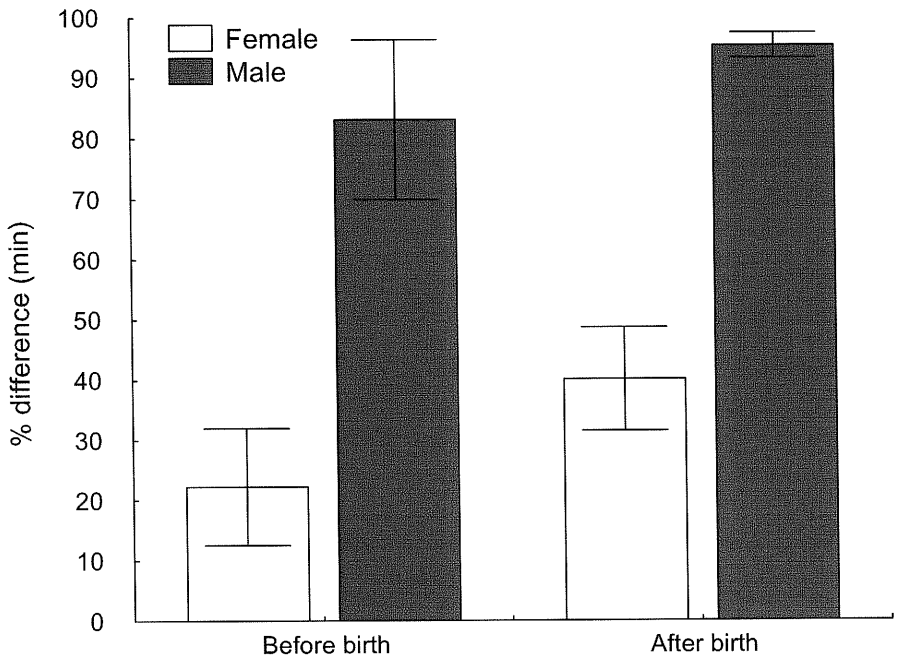


Figure 3. The difference in occupancy between the two tanks for each sex before and after parturition, expressed as the mean (± SE) difference in the number of minutes in which each tank was occupied by each sex (given as a percentage of the total number of minutes scored).

DISCUSSION

Pairs in the current study reached maximum mean aggression levels of around 9–10% of observation time for any time category, while in the week-long study of male–female dyads (Chapter 3), familiar dyads reached maximum mean aggression levels of about 6% for any night. This difference in maximum mean aggression levels is not significant ($p = 0.565$; Fisher exact test). It therefore seems that aggression between familiar pairs continues, but does not necessarily increase, during pregnancy and lactation (this study), compared with aggression before or just after mating (Chapter 3). The patterns of aggressive and amicable interactions between *G. leucogaster* pairs were not always as predicted. Although there was a trend towards higher aggression immediately after parturition, parturition did not affect aggression levels as much as expected. This may simply be a consequence of the relatively low sample sizes, but it is also possible that

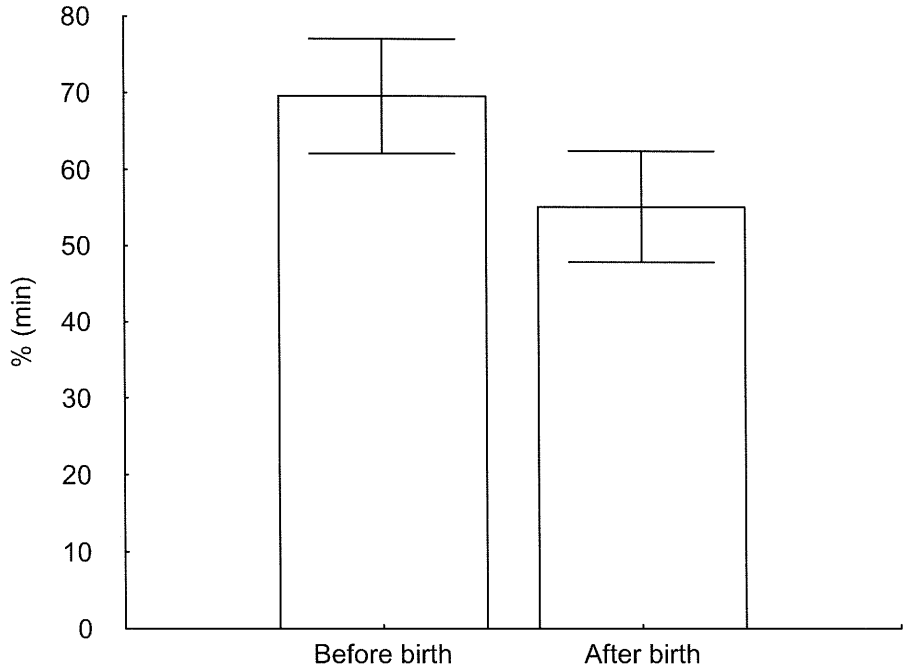


Figure 4. Mean (± SE) number of minutes in which pairs shared a tank before and after parturition (given as a percentage of the total number of minutes scored).

females encountered males less often after parturition due to investment in other behaviours such as lactation or feeding, or because of contact avoidance between the pair, resulting in fewer opportunities for direct aggression (avoidance may lead to lower direct aggression; Bronson 1964). This is supported by the finding that 1) males mostly confined their activities to one tank and 2) there was a trend towards less tank-sharing after birth. Consideration must also be given to the possibility of a postpartum oestrus (Lötter & Pillay 2008, Chapter 2), which would result in reduced aggression towards males after parturition for mating purposes since, as Happold (1976) points out, for mating to be successful the behaviour associated with copulation must at least not repel the individuals involved. However, only two of the eight females became pregnant with a second litter during the course of this study.

Amicable behaviour was surprisingly high before birth, but was extremely variable and attributable to only two pairs, as indicated by the large error bars in Figure 1. Parturition did appear to affect amicable behaviour: the two pairs that were amicable in this study displayed the greatest levels of amicability in the study of male–female dyads (Chapter 3), and it is interesting that parturition apparently resulted in the complete cessation of this behaviour, although the observation of more dyads displaying amicable

behaviour prior to parturition is necessary to confirm this suggestion. This is contrary to a study of *G. leucogaster* from Zimbabwe, where females frequently allowed males into the nest-boxes after birth (Choate 1972). In the brown desert mouse *Pseudomys desertor* males and females only appear to associate briefly for mating purposes, and the female behaves agonistically towards the male during pregnancy and parenthood (Happold 1976). Similarly, the persistent aggression during pregnancy and lactation, and the lack of amicable behaviour after birth in my study makes it unlikely that females and males nest together during the breeding season. However, it is possible that there is geographic variation in the level of tolerance between the sexes, given the observations by Choate (1972).

The high levels of overt agonistic behaviour by females, coupled with high levels of submissive and avoidance behaviour by males, indicate that females were the more aggressive sex, as predicted. Male wariness of females is also supported by the finding that males often limited their activity to one tank, whereas females used the two tanks much more equally. As already noted in the Introduction, female aggression towards males in the context of breeding may be due to a number of reasons, such as resource defence and/or infanticide. A previous study suggested that female–female dyads were more tolerant than male–female dyads, and that female home ranges could potentially overlap in nature (Chapter 3). This implies that resource defence is not the primary cause of female aggression towards males, since females should defend resources (such as food) against either sex. Indeed, food is considered the primary resource competed for among females (Ostfeld 1985). Furthermore, neither food nor nest-boxes were limiting in the laboratory, so it seems unlikely that females were defending these resources. Many studies report the occurrence of infanticide in rodents (see e.g. Labov et al. 1985; Ebensperger 1998; Ebensperger & Blumstein 2007) and it is possible that it occurs in bushveld gerbils, although, to my knowledge, this has not yet been documented. I found no evidence of infanticide in the laboratory: although the male was present with the female and her young, I never witnessed any clear aggression by males towards young and mortality of young appeared to be very low. Males generally seemed to ignore the young. Choate (1972) also found that male bushveld gerbils participated very little in the care of the young and that infanticide was rare.

Even if infanticide does occur in bushveld gerbils, it is possible that males in the laboratory were less likely to commit infanticide than their wild counterparts since their certainty of paternity may have been higher (although the mechanisms governing certainty

of paternity in bushveld gerbils would need to be elucidated before this could be confirmed), and it is well documented that males tend not to kill young if their certainty of paternity is high. For example, Wolf & Cicirello (1989) found that resident male white-footed mice *Peromyscus leucopus* (presumed to be fathers) did not commit infanticide within their own home range, but immigrant males and resident pre-reproductive subadults did kill infants. Although male Mongolian gerbils *Meriones unguiculatus* (which form stable pairs; Ågren 1984) may kill neonates under certain conditions, males that are part of an established pair do not harm their own pups (Elwood & Ostermeyer 1984). Although males tend not to kill their own offspring, several rodent studies report maternal aggression towards mates, even though the same species show paternal care under some conditions (see McGuire & Bemis 2007). This suggests that females may be aggressive towards their mates even when they have the potential to show paternal care (which would presumably be to the advantage of the female). McGuire & Bemis (2007) point out that female aggression directed at unfamiliar males could be seen as pup-defence but that it is unclear why females would react aggressively towards their mates.

Elwood & Ostermeyer (1984) suggest that female dominance over her mate during late pregnancy may be related to the inhibition of infanticide in Mongolian gerbils, and perhaps this partly explains female aggression towards mates in the current study. Furthermore, a promiscuous mating system may have certain consequences for infanticide and female aggression. Firstly, under natural conditions, male bushveld gerbils are very unlikely to remain with the female after mating (this study; Chapter 3) and perhaps females react aggressively towards all males, since a promiscuous mating system would lead to an increased frequency of encounters with males (Sandell & Liberg 1992; Pillay et al. 1995; Agrell et al. 1998), many of which may not have sired the female's offspring. Secondly, males of monogamous or polygynous species/populations would be more certain of their paternity than those with a promiscuous mating system (Mahady & Wolff 2002; Pillay & Kinahan 2009). Therefore, the risk of infanticide by mating partners, and thus female aggression towards them, may be highest in promiscuous species/populations. On finding that female giant kangaroo rats *Dipodomys ingens* mating exclusively with one male apparently weaned more offspring than those experiencing male competition, Randall et al. (2002) suggested that males from exclusive matings may be less likely to commit infanticide, although they did not provide reasons for this suggestion.

Compared to other South African rodents, female bushveld gerbils from my study appear to show intermediate tolerance towards their mates during breeding. Females from

promiscuous populations of the vlei rat *Otomys irroratus* are highly intolerant of their mates, not allowing them near the nest for a week before and after birth (N. Pillay, personal communication), whereas females from polygynous populations of the striped mouse are very tolerant of their mates, which display paternal care (Schradin & Pillay 2003, 2004). It is possible that, owing to the relatively longer gestation time in precocial versus altricial young (Sacher & Staffeldt 1974) and subsequent greater prenatal energy allocation required for precocial young (Boyce 1988), female vlei rats (whose young are precocial; Skinner & Chimimba 2005) are more protective of their young than female bushveld gerbils and striped mice (whose young are altricial; Skinner & Chimimba 2005). Interestingly, however, females from polygynous populations of the vlei rat are more tolerant of their mates than are females from promiscuous populations (Pillay 1993), which also suggests a tendency for less mate-tolerance within promiscuous populations.

Although paternal behaviour was not investigated directly in my study, there was no evidence of direct parental care, although certain indirect forms of care, such as defence of young (Kleiman & Malcolm 1981), would not have been observable under the current study conditions. The apparent lack of paternal care, as well as the generally low levels of amicable behaviour coupled with persistent female aggression towards males at all stages of pregnancy and lactation, strongly suggests that bushveld gerbils do not form prolonged male–female associations during the breeding season, supporting previous findings (Chapter 3). Although maternal aggression is not necessarily successful in preventing infanticide, it may be used together with other counter-strategies (Ebensperger 1998), and the combination of multi-male mating and postpartum aggression may increase the chances of neonate survival (Labov et al. 1985). Indeed, the high cost of infanticide to victimised females has probably resulted in natural selection favouring multiple counter-strategies to infanticide to enhance the fitness of females (Ebensperger & Blumstein 2007; Pillay & Kinahan 2009). It has been noted that intersexual territoriality/aggression in mammals is not common, but females of species where males are infanticidal display intersexual aggression (Agrell et al. 1998; Solomon & Keane 2007). Both multi-male mating and female aggression may be operating as counter-strategies in bushveld gerbils, if infanticide is indeed a risk. It would be of interest to investigate the responses of pregnant and lactating females towards adult males with whom they have not mated: if females are aggressive towards familiar males as in the current study, they should be highly intolerant of unfamiliar males if infanticide is a risk, owing to the potentially reduced certainty of

paternity in unfamiliar males (see discussion above). Higher aggression levels towards unfamiliar males would thus further support the infanticide hypothesis.

REFERENCE LIST

Agrell, J., Wolff, J.O. & Ylönen, H. (1998). Counter-strategies to infanticide in mammals: costs and consequences. *Oikos* **83**: 507–517.

Ågren, G. (1984). Pair formation in the Mongolian gerbil. *Animal Behaviour* **32**: 528–535.

Boyce, M.S. (1988). Evolution of life histories: theory and patterns from mammals. In: Boyce, M.S. (ed.). *Evolution of Life Histories of Mammals: Theory and Pattern.* Yale University Press: New Haven.

Bronson, F.H. (1964). Agonistic behaviour in woodchucks. *Animal Behaviour* **12**: 470–478.

Choate, T.S. (1972). Behavioural studies on some Rhodesian rodents. *Zoologica Africana* **7**: 103–118.

De Graaff, G. (1981). *The Rodents of Southern Africa.* Butterworths: Durban.

Dempster, E.R., Dempster, R. & Perrin, M.R. (1993). Behavioural divergence in allopatric and sympatric gerbil species (Rodentia: Gerbillinae). *Ethology* **93**: 300–314.

Ebensperger, L.A. (1998). Strategies and counterstrategies to infanticide in mammals. *Biological Reviews* **73**: 321–346.

Ebensperger, L.A. & Blumstein, D.T. (2007). Nonparental infanticide. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective.* The University of Chicago Press: Chicago.

Elwood, R.W., Nesbitt, A.A. & Kennedy, H.F. (1990). Maternal aggression in response to the risk of infanticide by male mice, *Mus domesticus*. *Animal Behaviour* **40**: 1080–1086.

Elwood, R.W. & Ostermeyer, M.C. (1984). Infanticide by male and female mongolian gerbils: ontogeny, causation, and function. In: Hausfater, G. & Hrdy, S.B. (eds). *Infanticide: Comparative and Evolutionary Perspectives.* Aldine Publishing Co.:

New York.

Gandelman, R. (1972). Mice: postpartum aggression elicited by the presence of an intruder. *Hormones and Behavior* **3**: 23–28.

Happold, M. (1976). Social behavior of the conilurine rodents (Muridae) of Australia. *Zeitschrift für Tierpsychologie* **40**: 113–182.

Kleiman, D.G. & Malcolm, J.R. (1981). The evolution of male parental investment in mammals. In: Gubernick, D.J. & Klopfer, P.H. (eds). *Parental Care in Mammals*. Plenum Press: New York.

Labov, J.B., Huck, U.W., Elwood, R.W. & Brooks, R.J. (1985). Current problems in the study of infanticidal behavior of rodents. *The Quarterly Review of Biology* **60**: 1–20.

Lisk, R.D., Ciaccio, L.A. & Catanzaro, C. (1983). Mating behaviour of the golden hamster under seminatural conditions. *Animal Behaviour* **31**: 659–666.

Lötter, T.K. & Pillay, N. (2008). Reproduction and postnatal development of the bushveld gerbil *Gerbilliscus* (formerly *Tatera*) *leucogaster*. *Mammalian Biology* **73**: 430–437.

Mahady, S.J. & Wolff, J.O. (2002). A field test of the Bruce effect in the monogamous prairie vole (*Microtus ochrogaster*). *Behavioural Ecology and Sociobiology* **52**: 31–37.

Martin, P. & Bateson, P. (2007). *Measuring Behaviour: An Introductory Guide*. (3rd ed.). Cambridge University Press: Cambridge.

McGuire, B. & Bemis, W.E. (2007). Parental care. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

Neal, B.R. (1991). Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae: Rodentia), in Zimbabwe. *Zeitschrift für Säugetierkunde* **56**: 101–111.

Nel, J.A.J. (1975). Aspects of the social ethology of some Kalahari rodents. *Zeitschrift für Tierpsychologie* **37**: 322–331.

Ostfeld, R.S. (1985). Limiting resources and territoriality in microtine rodents. *The American Naturalist* **126**: 1–15.

Ostfeld, R.S. (1990). The ecology of territoriality in small mammals. *Trends in Ecology and Evolution* **5**: 411–415.

Pillay, N. (1993). The evolution and socio-ecology of two populations of the vlei rat *Otomys irroratus*. PhD thesis. University of Natal: Durban.

Pillay, N. & Kinahan, A.A. (2009). Mating strategy predicts the occurrence of the Bruce effect in the vlei rat *Otomys irroratus*. *Behaviour* **146**: 139–151.

Pillay, N., Willan, K. & Cooke, J. (1995). Evidence of pre-mating reproductive isolation in two populations of the Vlei rat *Otomys irroratus*: experiments of intra- and interpopulation male-female encounters. *Zeitschrift für Säugetierkunde* **60**: 352–360.

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

Rice, W.R. (1989). Analyzing tables of statistical tests. *Evolution* **43**: 223–225.

Sacher, G.A. & Staffeldt, E.F. (1974). Relation of gestation time to brain weight for placental mammals: implications for the theory of vertebrate growth. *The American Naturalist* **108**: 593–615.

Sandell, M. & Liberg, O. (1992). Roamers and stayers: a model on male mating tactics and mating systems. *The American Naturalist* **139**: 177–189.

Schradin, C. & Pillay, N. (2003). Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*): laboratory and field evidence. *Journal of Comparative Psychology* **117**: 317–324.

Schradin, C. & Pillay, N. (2004). The striped mouse (*Rhabdomys pumilio*) from the succulent karoo, South Africa: a territorial group-living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology* **118**: 37–47.

Skinner, J.D. & Chimimba, C.T. (2005). *The Mammals of the Southern African Subregion.* (3rd ed.). Cambridge University Press: Cape Town.

Solomon, N.G. & Keane, B. (2007). Reproductive strategies in female rodents. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective.* The University of Chicago Press: Chicago.

St. John, R.D. & Corning, P.A. (1973). Maternal aggression in mice. *Behavioral Biology* **9**: 635–639.

StatSoft, Inc. (2001). *STATISTICA* (data analysis software system), *version 6.* www.statsoft.com.

Svare, B.B. (1981). Maternal aggression in mammals. In: Gubernick, D.J. & Klopfer, P.H. (eds). *Parental Care in Mammals.* Plenum Press: New York.

Westlin, L.W. (1996). Behavioural manifestation of conception 12 hours after mating in an asocial African rodent, *Saccostomus campestris. Journal of Zoology, London* **239**: 515–524.

Wolff, J.O. (1985). Maternal aggression as a deterrent to infanticide in *Peromyscus leucopus* and *P. maniculatus. Animal Behaviour* **33**: 117–123.

Wolff, J.O. & Cicirello, D.M. (1989). Field evidence for sexual selection and resource competition infanticide in white-footed mice. *Animal Behaviour* **38**: 637–642.

CHAPTER FIVE

Post-weaning social behaviour of the bushveld gerbil *Gerbilliscus leucogaster*: interactions with familiar and unfamiliar conspecifics

ABSTRACT

Social interactions between captive weaned bushveld gerbils *Gerbilliscus leucogaster* and familiar (mother/siblings) and unfamiliar (strange adult) conspecifics were studied to investigate natal dispersal in this species. Firstly, I examined the social interactions and space use of mother–offspring groups over several weeks to assess whether mothers and juveniles tolerate one another beyond weaning, and to investigate possible behavioural influences on dispersal. Each group was placed in a series of interconnecting tanks allowing juveniles free movement between tanks but restricting the movement of the mother. In two of the eight groups, the mother gave birth to a second litter during the study, which appeared to affect the behaviour of the group. The data suggest that mothers are intolerant of juveniles once a subsequent litter is born, and that dispersal at this point is possibly triggered by maternal aggression, although there appears to be some variation in maternal tolerance. If no subsequent litter is born the offspring probably disperse passively at around 5–6 weeks of age, although high tolerance within these groups indicates that philopatry and group formation is possible, which could be adaptive under some circumstances. Secondly, I examined the social interactions of juveniles and unfamiliar adults in staged dyad encounters over three nights to assess the extent to which adults tolerate juveniles under such circumstances. I tested all possible sex combinations to investigate sex differences in behaviour. I found large variation in the behaviour of adults towards juveniles and that adults can sometimes pose a serious risk; however, adults generally tolerated juveniles, especially after the first night. Adults did not seem to distinguish between male and female juveniles. Differences in the tolerance levels of adult males and females were unclear. Adult females appeared more aggressive than adult males initially, but it is also possible that juveniles avoided adult males more than adult females, such that that the actual response of adult males towards juveniles could not be fully assessed. I suggest that, although some adults may pose a threat, juveniles may often be tolerated by adults in nature, particularly over a period of time.

Keywords: *Gerbilliscus leucogaster*; mother–offspring interactions; natal dispersal, natal philopatry; adult–juvenile interactions

INTRODUCTION

It has often been suggested that social behaviour causes emigration or limits immigration (Brandt 1992). A number of studies suggest that social behaviour is implicated in the natal dispersal of various small mammal species. For example, mothers of the dasyurid marsupial genus *Antechinus* appear to initiate dispersal in their sons (Cockburn et al. 1985), while both parents and siblings probably influence the rate of natal dispersal in deer mice *Peromyscus maniculatus bairdi* (Savidge 1974). Aggressive and affiliative behaviour are both likely to affect dispersal (Brandt 1992), and parental aggression is one factor that may motivate dispersal (Savidge 1974; Lidicker & Stenseth 1992). Scheibler et al. (2006) found that reproductive male Mongolian gerbils *Meriones unguiculatus* were aggressive towards adult male offspring with elevated reproductive capacity (e.g. greater relative testes mass, increased fertility) and suggested that this could lead to dispersal of these offspring in nature. Although aggression has been implicated as a cause of dispersal, this is not necessarily the case (Bekoff 1977; Holekamp 1986). There is some debate over the role of aggression in dispersal, and Wolff (1993) concluded that no small mammal dispersal study has provided evidence for adult aggression as a cause of juvenile dispersal, but rather that juveniles disperse voluntarily in many mammal species.

During the process of leaving their natal site (even if they do not travel far), juveniles will encounter strange adult conspecifics, and the way that these adults interact with them will, to a large extent, determine their ability to settle in an area. Immigration may be limited by aggression associated with spacing (Brandt 1992), and thus the behaviour of strange adults may prevent juveniles from relocating. Reduced dispersal distances are sometimes seen under high population densities, and it is thought that this is due to aggression by residents (Ims & Hjermann 2001). Sadleir (1965) proposed that adult aggression towards juvenile deer mice *P. m. austerus* affected juvenile recruitment: both captive and field studies indicated that adults were intolerant of juveniles during the breeding season; after the breeding season juvenile recruitment increased, probably due to a seasonal decrease in adult aggression. Ferkin (1987) suggested that strange female plateau mice *P. melanophrys* may influence the survival and recruitment of weanlings. It is thus apparent that adult behaviour towards juveniles can have an important influence on juvenile survival and recruitment. On the other hand, Perrin et al. (2001) found that

aggressive behaviour by adults did not affect the survival and dispersal of young striped mice *Rhabdomys pumilio* and multimammate mice *Mastomys natalensis* in a grassland habitat in South Africa.

Very little, if anything, is known about dispersal in the bushveld gerbil *Gerbilliscus leucogaster*, and I am not aware of any published studies on the post-weaning social behaviour of mothers and offspring, or on the social interactions between strange adults and weaned juveniles. There are many aspects to dispersal (e.g. body size, population density, social structure; Ims & Hjermann 2001), and my study focused on several social factors in order to gain some insight into dispersal in bushveld gerbils.

My study aimed 1) to investigate the social and spacing behaviour of the mother and offspring to ascertain the levels of post-weaning tolerance and whether social interactions may influence dispersal, and 2) to investigate the social interactions between unfamiliar adults and juveniles to ascertain the level of tolerance that a dispersing juvenile might experience from strange adults. Specifically, I asked the following questions: 1a) Does the mother tolerate her offspring after weaning, or does maternal aggression increase with juvenile age? 1b) Do the juveniles tolerate one another or does sibling aggression increase with age? 1c) At what age do juveniles show independence from the mother and each other? 2a) Do adults tolerate unfamiliar juveniles and do tolerance levels change with increased familiarity? 2b) Does the sex of the adult/juvenile influence the tolerance levels of adults?

MATERIALS AND METHODS

The origin of study animals and housing conditions are described in Chapter 2 (Lötter & Pillay 2008).

Mother–offspring relationships

This experiment investigated the social interactions and space use of the mother and juveniles by using a series of interconnected tanks whereby juveniles were given the opportunity to leave the mother and natal nest area. For simplicity, the term 'juvenile' is used throughout this experiment even though some offspring may have reached sexual maturity during this time. Eight mother–juvenile groups resulting from pairs in a previous study (Chapter 4) were used in the current study. The general experimental protocol follows. When juveniles were about 20 days old (weaning = ± 24 days; Lötter & Pillay 2008, Chapter 2), they and their mother were individually marked by fur clipping. If not

already nesting in a large tank (855 x 305 x 350 mm), the mother and juveniles were placed into a large (termed 'natal') tank 0–3 days prior to the start of the experiment. When juveniles were a mean of 22 days old (range 21–27 days), small tanks (465 x 310 x 350 mm) were attached to the natal tank with flexible plastic pipes (± 40 mm diameter, 1170 mm long). The number of small tanks was equivalent to the litter size so that juveniles leaving the natal tank were not forced to share tanks. Litter sizes were as follows: 1 (one group), 3 (one group), 4 (four groups) and 5 (two groups). The experimental design allowed for a maximum of four small tanks to be attached; in the two groups in which litter size was five, one juvenile of the majority sex (a female in one group and a male in the other) was randomly chosen and removed at about 4 weeks old. Tanks were constructed as described previously (Chapter 3). A steel barrier with a 24 mm diameter hole in the middle was placed at the entrance to each pipe, thus preventing the mother from accessing the pipes and small tanks. When juveniles became too large to fit through the 24 mm holes, the barriers were replaced with ones containing holes 30 mm in diameter (juveniles occasionally struggled to fit through the 24 mm holes before these were changed; this was noted in 11% of nights when behaviour was taped; see below). Each tank was furnished with nest-boxes (one in the small tanks and two in the natal tank), a food dish and a water bottle, and contained wood shavings and hay. Water and Epol® mouse cubes were provided ad libitum. The diet was regularly supplemented (e.g. with sunflower seeds, peanuts, mealworms, apple); supplementary food was also available in the small tanks.

This experimental set-up was video-taped 1–3 times per week, beginning when juveniles were given access to the small tanks and continuing until they were about 7 weeks of age (i.e. for ± 4 weeks). Taping was conducted under red light (Dempster et al. 1992), beginning at 18h45, approximately 15 minutes prior to the dark phase of the light–dark cycle. Scoring of tapes commenced 30 minutes after the start of the tape and continued for 80 minutes, using a one–zero recording method with one minute intervals (Martin & Bateson 2007). Each tank was scored separately. Juveniles could not be individually distinguished on tapes and no attempt was made to score individual juveniles. The following three categories of affiliation were recorded: 'mother–juvenile', where the mother and one or more juveniles were in a tank simultaneously; 'juvenile–juvenile', where two or more juveniles were in a tank simultaneously; and 'alone', where the mother or a juvenile was alone in a tank (mother and juvenile scored separately). Under the mother–juvenile and juvenile–juvenile affiliations, the following three types of behaviours were scored: 'positive' (attracting social behaviour such as huddling/close proximity (i.e.

tolerance within ± 5 cm) and allogrooming); 'negative' (repelling behaviour such as lunging and chasing); and 'neutral' (where individuals shared a tank but were not behaving positively or negatively towards one another). When a positive or negative mother–juvenile affiliation was initiated, I recorded whether the mother or the juvenile was the initiator (once each per behaviour per minute). To explore changes in affiliations during the largely inactive diurnal period (i.e. who was nesting together) I recorded, where possible, which nest-box individuals occupied during the diurnal phase of the light–dark cycle on random days until tank configurations were dismantled. Tank configurations were often left set up beyond the end of taping, which enabled me to monitor the position of individuals during the diurnal phase for a longer period. Table 1 gives the age of juveniles when the tank configurations were dismantled, as well the number of times that the location of individuals was recorded during the day. These represent all attempts at recording nest-box position, which were not always successful (e.g. some individuals were awake and not occupying a nest-box at the time, or had scattered when I entered the room such that their nest-box position could not be determined).

Table 1. The age of juveniles when tank configurations were dismantled and the number of times that location was recorded during the diurnal phase for each of eight mother–juvenile groups.

Parameters	I	II	III	IV	V	VI	VII	VIII
Juvenile age (days)	67	64	83	51	63	69	74	61
Location (frequency)	24	22	38	8	34	41	32	31

Bushveld gerbils have a postpartum oestrus (Lötter & Pillay 2008, Chapter 2), and seven of the females used in the current study had the opportunity to mate after the birth of their first litter. However, only two females gave birth to a second litter (litter size = 2 for both second litters). This provided an opportunity to compare the effect of the presence of a second litter on the behaviour of the mother and first litter. The two second litters were born when the first litters of these groups were in the '3.5–4' and '4–4.5' week age categories (see data analysis). In one of these cases, I only set up the current experiment after the second litter was born, when the first litter (consisting of a single juvenile) was 27 days old. In this instance, the natal tank was a small tank containing a single nest-box, which was then joined to another small tank. In some mother–juvenile groups the mother was unavoidably able to access one or more small tanks at times, but this only affected 6.5% of nights taped and was taken into account where deemed necessary during data

analysis (see below). The complex tank set-up prevented all parts of tanks being visible on the tapes, and thus it was not always possible to keep track of all individuals throughout the scoring process, necessitating an estimation of their position/behaviour at times. However, I am confident that the general trends are still evident.

Unfamiliar adult–juvenile relationships

The second experiment investigated, by means of dyad encounters, the social interactions of adults and juveniles that had never shared a cage and were considered strangers. The following adult–juvenile combinations were investigated: adult male–juvenile male (M–m; n = 8); adult female–juvenile female (F–f; n = 7); adult male–juvenile female (M–f; n = 7); adult female–juvenile male (F–m; n = 7). Juvenile age ranged from 26–55 days old. For the purposes of this experiment, 'juvenile' refers to individuals that were not considered sexually mature: all males were younger than 9.9 weeks, which is the earliest age of sexual maturity (as per Lötter & Pillay 2008, Chapter 2), and all females were imperforate with two exceptions; however, vaginal smears of the latter revealed that they were anoestrus and they were therefore included in analyses.

The experimental set-up was very similar to that described previously (Chapter 3), with a few exceptions. As before, it consisted of three linearly arranged tanks connected with PVC pipes; each end tank served as a home tank for one individual, while the middle tank served as a neutral area separating the two end tanks. Tanks were furnished as described previously (Chapter 3). Additional food—sunflower seeds—was scattered into the middle tank once during the experiment (on the day before the last night of taping). Some items (e.g. bedding, mouse cubes, water bottle) from the lab-o-tec cage of the adult, in which the adult was housed prior to experiments, were transferred to their home tank to facilitate acceptance of the new tank. This was not necessary for juveniles, as the experiment was not investigating defence of an area by the juvenile. Dyad partners could be distinguished based on their size difference; thus no external markings were necessary. Individuals were weighed prior to experiments and were confined to their 'home' tanks two days before the commencement of video-taping (see below).

After the 2-day familiarisation period, the solid steel barriers in the interconnecting pipes were removed, and one with a central hole of 24–30 mm in diameter (depending on the size of the juvenile) was placed into the pipe leading to the juvenile's tank, so as to deny the adult access. This barrier was used for ethical reasons to allow the juvenile exclusive access to its home tank to escape any aggression by the adult. Dyad encounters

were run for three nights and video-taped under red light every other night for 8 hours on the first night and 4 hours on the third night, beginning at 18h45.

The behaviour of each dyad member was scored using focal sampling and a one–zero recording method with one minute intervals (Martin & Bateson 2007). Each behaviour was thus scored once per individual per tank per minute. The behavioural categories used in this study included overt agonistic, ritualised agonistic, submissive and amicable behaviour (see Chapter 3 for definitions). No sexual behaviour was seen during scoring sessions. The number of minutes in which dyads shared a tank was also recorded, using the same 1/0 method. Scoring of behaviour on the video tapes began 30 minutes after the start of the taping session (to increase the probability that individuals would be active) and was conducted for the first 20 minutes of each hour thereafter. Where an individual was not visible for a full minute, I assumed the behaviour and, where necessary, the tank position of the individual for that minute to complete the data set (as per Chapter 3). The number of minutes in which an individual was not visible for a full minute amounted to a range of ± 0.7 (F–f dyads) – 5.9% (M–m dyads) of all minutes scored for both dyad members (excluding those removed from analyses; see below). To investigate whether individuals were sharing a tank during the day when *G. leucogaster* is largely inactive, the location of each individual was recorded once daily for the three days of the experiment during the light phase of the light–dark cycle, typically between about 10h00 and 12h00. Vaginal smears were taken from most adult females—on the day prior to the first night of taping and the day after the final night of taping. Females were scored as being in oestrus or anoestrus, as described before (Chapter 3). If one individual was handled (e.g. to take vaginal smears) the dyad partner was also handled to reduce potential handling bias.

Data analysis

Data were analysed using STATISTICA 6.0 (StatSoft, Inc. 2001). All tests were two-tailed, with model-level significance determined at $\alpha = 0.05$. Alpha levels for individual tests were adjusted when several component tests were conducted (see below), and in these cases the adjusted alpha is given below as well as in the Results for clarity; otherwise all tests were conducted at $\alpha = 0.05$. All analyses, apart from those involving oestrus (below), were performed using General Linear Models (GLMs): a repeated measures design was used where the same groups/dyads were tested over a number of age categories/nights; a multivariate design was employed when dependent variables were not independent (unless otherwise specified); and Fisher LSD post hoc tests were used to determine specific

differences when categorical predictors/repeated measures factors had a significant effect. Where the input matrix for repeated measures tests contained missing data cells (as indicated in the Results section by deviations from the usual sample sizes), a mean substitution was performed on any missing values to ensure that the full data set was incorporated by the test. In tests involving mother–offspring relationships, the percentage of data requiring mean substitutions ranged from 2.8–11.1% per test where this was necessary, while in unfamiliar adult–juvenile relationships only 1.0% of data for one test required mean substitutions. All figures were generated without the mean substitutions to display the original data for comparison.

Mother–offspring relationships

The two groups where the mother gave birth to a second litter needed to be dealt with separately as it was clear that the presence of the second litter affected the behaviour of the group, particularly the mother. For this reason, the data were analysed using only the six groups where no second litter was present. Where appropriate, the graphs generated display the data for both the six 1-litter and the two 2-litter groups in order to provide an idea of the effect of the second litter despite the low sample size. Although the graphs incorporating the second litter (i.e. Figures 1 & 3) should be interpreted with caution, they show potentially important trends.

The effect of juvenile age on behaviour was investigated by dividing the total sampling time of ± 4 weeks into six age categories. It was expected that the greatest changes would occur earlier on in the experiment (i.e. in the first week or two after weaning), and for this reason the sampling time was divided into half-weeks for the first two weeks, and then into full weeks for the last two weeks, resulting in the following age categories: 3–3.5, 3.5–4, 4–4.5, 4.5–5, 5–6 and 6–7 weeks old. Sample sizes for each category are provided in the Results section. Where a group was taped for more than one night per category, the mean values were used for that category. Unless otherwise indicated, the data for all the tanks were used to generate one value per minute (as per 1/0 recording), regardless of which tank was involved.

Mother–juvenile affiliations

Changes in behaviours (neutral, positive, negative) were assessed using the six juvenile age categories as a repeated measures factor. The design of the input matrix in STATISTICA did not generate the degrees of freedom for a multivariate design, and thus

each behaviour was analysed separately with alpha levels adjusted using sequential Bonferroni adjustments (Rice 1989); $\alpha' = 0.017$ (α' refers to the first adjusted alpha in the sequence of the Bonferroni adjustment procedure).

To investigate which individual initiated positive and negative behaviours, I pooled the initiation data for all age categories (by calculating the mean for each mother–juvenile group), and performed a one-way multivariate ANOVA (i.e. MANOVA) with the frequencies of positive and negative initiations as the dependent factors and the initiator (i.e. mother or juvenile) as the categorical predictor.

Juvenile–juvenile affiliations

Changes in behaviours (neutral, positive, negative) with increasing age were assessed in the same way as for mother–juvenile affiliations above. Again, a multivariate design could not be employed, and each behaviour was analysed separately with alpha levels adjusted as before ($\alpha' = 0.017$).

Juvenile independence

I used the occupancy of the side tanks by the juveniles as one way of assessing their independence from the mother, as this involved their temporarily leaving the natal tank and thus the mother; to avoid skewing the results, I used only those tapes where the mother could not access a side tank (see Results for sample sizes). I pooled all the data for the occupancy of the side tanks into one value per minute (as per 1/0 recording), regardless of which side tank was used, with the six juvenile age categories as the repeated measures factor. Juvenile independence from the mother was also assessed by investigating the frequency that mothers were alone in a tank (i.e. those times that all juveniles had left the mother's tank), again with juvenile age as the repeated measures factor. As before, I used only those tapes where the mother could not access a side tank, so that this variable represented only those cases where the juveniles left the mother, rather than vice versa. Finally, I investigated juvenile independence from both siblings and the mother by analysing the frequency that a juvenile was alone in any tank, with juvenile age as the repeated measures factor.

Unfamiliar adult–juvenile relationships

Adults in three M–m and two M–f dyads were able to fit through the barrier and access the juvenile's tank. These dyads were removed from analyses to keep the

experimental protocol between dyad-types comparable. The sample size for M–m and M–f dyads was thus reduced to n = 5 each. One value per minute was calculated for each parameter analysed (as per 1/0 recording), regardless of the tank involved. Apart from the test analysing night 1 in isolation (see below), I summed the data for all the 20 minute scoring sessions for each night to give one value per behaviour per night. Unless otherwise stated, all analyses use only the first four scoring sessions of night 1 (i.e. 80 minutes) to allow a comparison between nights 1 and 3.

Aggressive and amicable behaviour

I combined the following forms of aggression into one behavioural category: overt agonistic, ritualised agonistic and submissive behaviour, as well as where co-occupation of a nest-box appeared aggressive rather than amicable. The age of the dyad partners was not taken into account i.e. for each minute, aggression and amicability were scored as occurring or not occurring (1/0 recording), regardless of whether the adult or the juvenile performed the behaviour, resulting in one score for aggressive and one score for amicable behaviour per minute per dyad. I assessed the effects of night (1, 3; repeated measures factor), and the sex of the adult (M, F) and juvenile (m, f; categorical predictors) on these behaviours. The effect of dyad-type (i.e. M–m, F–f, M–f, F–m) was incorporated in the interaction between adult sex and juvenile sex, but was considered less important as initial analyses suggested that adult sex had a greater influence on behaviour than dyad-type.

I then investigated night 1 in more detail by analysing the effect of adult sex and juvenile sex (categorical predictors) on aggressive and amicable behaviour using scoring session (all eight 20 minute scoring sessions) as the repeated measures factor.

Tank-sharing

The extent to which dyad partners shared a tank was analysed as a way of assessing whether juveniles were avoiding contact with adults. For example, direct aggression may have been low due to avoidance of the adult by the juvenile, rather than because the adult was tolerant of the juvenile (Bronson 1964). Tank-sharing was assessed using night as the repeated measures factor, with adult sex and juvenile sex as categorical predictors. The percentage of days in which dyads shared a tank during the diurnal period was also calculated.

Oestrus

The oestrous data were dichotomous, and hence Spearman rank correlations were used to test the effect of oestrus/anoestrus on aggressive and amicable behaviour, and on tank-sharing at night. Since the sample size was small for F–f dyads (n = 4; not all adult females were assessed), I combined the data for F–f and F–m dyads (total n = 11 adult females i.e. 22 oestrous measures). There was an unavoidable mismatch between the behavioural and oestrous data, as vaginal smears were first taken the day before night 1 but were only taken again after night 3. Therefore, for the analysis I had to use oestrous state before night 1 to assess behaviour on night 1, but oestrous state after night 3 to assess behaviour on night 3.

RESULTS

Mother–offspring relationships

For all results below, where results are given for both 1- and 2-litter groups, the statistical results for the 1-litter groups are presented first, so that the descriptive results for the 2-litter groups can be compared to these. Sample sizes are provided in each figure. The large error bars in the figures incorporating the data from 2-litter groups are owing to the low sample size for these groups (n = 2).

Mother–juvenile affiliations

Juvenile age did not appear to affect any behaviours in 1-litter groups (neutral: $F_{5,25}$ = 0.80, p = 0.557; positive: $F_{5,25}$ = 1.01, p = 0.431; negative: $F_{5,25}$ = 2.50, p = 0.057; α' = 0.017; Figure 1A). However, Figure 1 suggests that juvenile age may affect behaviour when there is a second litter. There was a tendency for both neutral and positive behaviours to decrease with juvenile age, suggesting that mothers and juveniles from 2-litter groups spent progressively less time sharing a tank. Compared to 1-litter groups, 2-litter groups also appeared to display much higher levels of negative behaviour, while 1-litter groups exhibited much higher levels of positive behaviour.

In 1-litter groups, the initiator of positive and negative behaviours was a significant predictor of the frequency with which these were initiated ($F_{2,9}$ = 14.88, p = 0.001, n = 6). Juveniles initiated more positive behaviour (mean ± SE frequency: mother = 6.83 ± 1.17, juveniles = 15.62 ± 1.02; post hoc tests), while only the mother initiated negative behaviour (mother = 0.41 ± 0.15, juveniles = 0.00 ± 0.00; post hoc tests). The tendency in the 2-litter groups (n = 2) was for juveniles to initiate substantially less positive behaviour

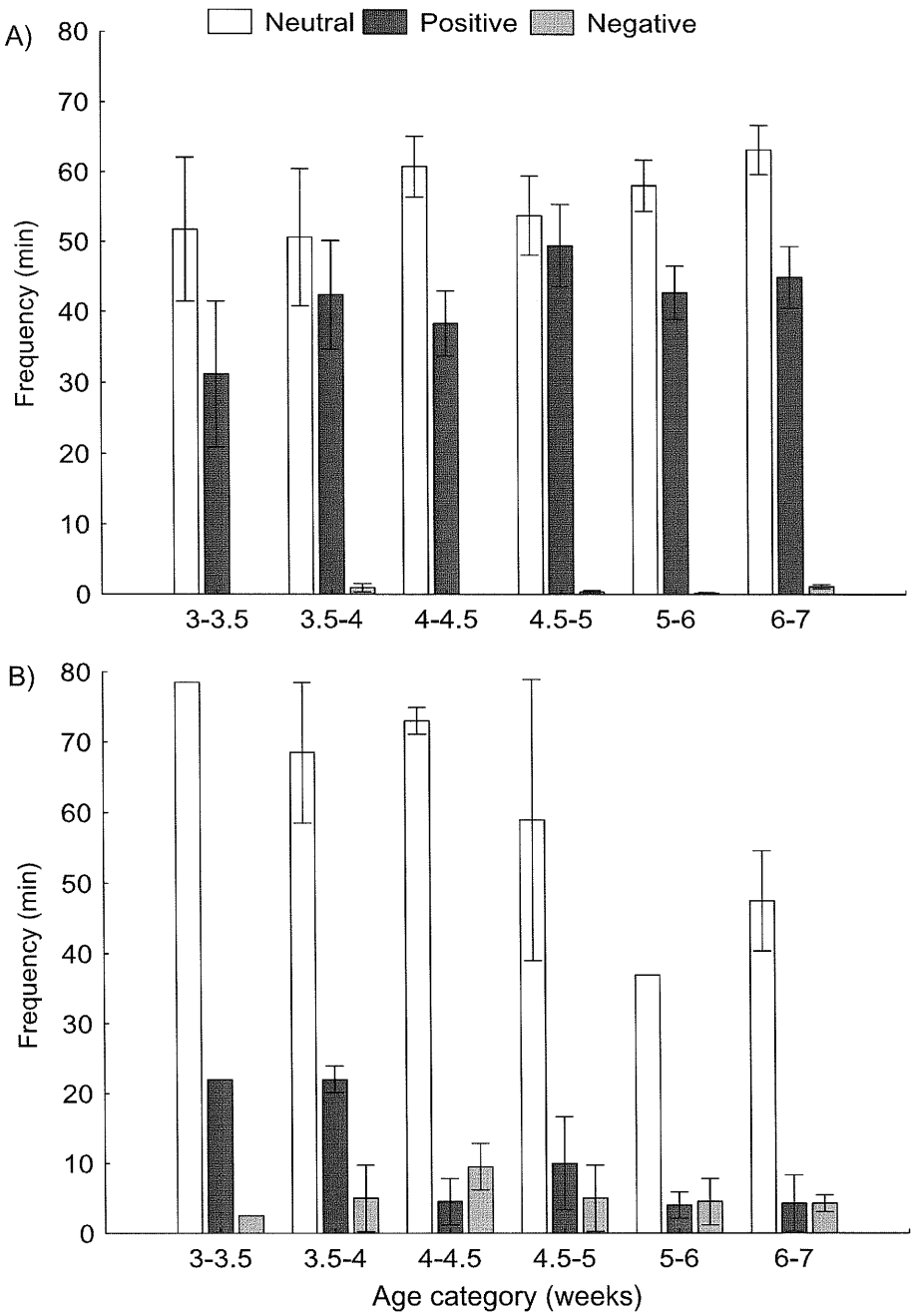


Figure 1. Changes in neutral, positive and negative behaviour during mother–juvenile affiliations with increasing juvenile age, expressed as the mean (± SE) number of minutes in which these behaviours occurred in each age category in A) 1-litter groups (n = 5 for 3–3.5 week age category; n = 6 for the other 5 age categories) and B) 2-litter groups (n = 1 for 3–3.5 week age category; n = 2 for the other 5 age categories). Maximum minutes = 80.

than those from 1-litter groups (mother = 3.90 ± 0.40, juveniles = 2.19 ± 1.89), while the mother initiated much more negative behaviour than in 1-litter groups (mother = 5.25 ± 1.25, juveniles = 0.00 ± 0.00).

Juvenile–juvenile affiliations

Juvenile age significantly affected two of the three behaviours in 1-litter groups ($\alpha' = 0.017$): neutral behaviour ($F_{5,25} = 3.71$, $p = 0.012$), which was mainly due to lower levels in the 3–3.5 week age category than most other categories, and positive behaviour ($F_{5,25} = 7.16$, $p < 0.001$), where the 3–3.5 week age category showed higher levels than all other categories (post hoc tests; Figure 2). Negative behaviour among juveniles only appeared after 4.5 weeks of age, was very rare, and was not affected by age ($F_{5,25} = 0.97$, $p = 0.457$; Figure 2). Figure 2 does not include the 2-litter groups because no juvenile–juvenile affiliations could be recorded for the group with only one juvenile in the first litter.

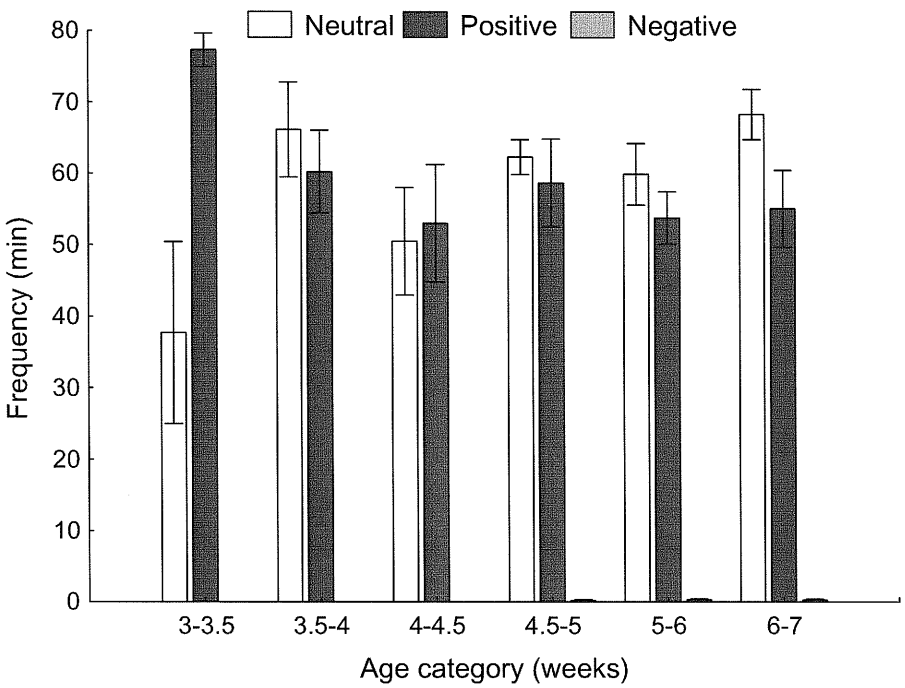


Figure 2. Changes in neutral, positive and negative behaviour during juvenile–juvenile affiliations with increasing juvenile age, expressed as the mean (± SE) number of minutes in which these behaviours occurred in each age category; 1-litter groups only (n = 5 for 3–3.5 week age category; n = 6 for the other 5 age categories). Maximum minutes = 80.

Juvenile independence

Juveniles first started entering the side tanks from about 23–24 days old (i.e. after 3 weeks of age), although some entered the pipes as early as 21 days old (the start of the experiment for some groups). Side tank use increased significantly with age in 1-litter

groups ($F_{5,25} = 16.63$, $p < 0.001$), specifically after 3.5 weeks and again after 4.5 weeks (post hoc tests; Figure 3A). The trend in side tank use was similar for 1- and 2-litter groups (Figure 3A). In 1-litter groups, juvenile age also significantly affected the frequency that the mother was alone in the natal tank ($F_{5,25} = 3.12$, $p = 0.025$), which generally increased with juvenile age, apart from the 6–7 week age category where it decreased again, but was very low overall (post hoc tests; Figure 3B). Mothers with two litters appeared to spend substantially more time alone in the natal tank than those with one litter, particularly after juveniles were 5 weeks old (Figure 3B).

Juvenile age in 1-litter groups also had a significant effect on the frequency that a juvenile was alone in a tank ($F_{5,25} = 10.63$, $p < 0.001$), with frequency increasing significantly after 3.5 weeks and again after 4.5 weeks (post hoc tests; Figure 4). Again, the data for 2-litter groups are not included owing to the group with only one juvenile.

The earliest that a juvenile from a 1-litter group was found in a nest-box without the mother during diurnal observations was at 41 days old. Thereafter, juveniles were very erratic in the amount of time spent apart from the mother and she was seldom alone during the day: usually at least one juvenile was nesting with her. One group remained in the experimental set-up until juveniles were 83 days old, and one or more were found nesting with the mother until the end. The two 2-litter groups differed from each other. The group with one juvenile from the first litter was always found nesting with the mother and second litter during the day. However, all four juveniles from the other group consistently nested separately from the mother and second litter from 33 days old (when the second litter was 1 day old) until 61 days old (when the second litter was ± 1 month old). Thereafter, juveniles from the first litter were occasionally found nesting with the mother and second litter. At 37 days old, a juvenile from the second litter was found nesting separately from the mother with a juvenile from the first litter. In general (for all eight groups), juveniles did not show any clear patterns of nesting with or without their siblings during the day.

Unfamiliar adult–juvenile relationships

In spite of attempting to give juveniles a means of escaping aggression, three juveniles were killed/severely injured by adults (one adult male and two females killed/injured their juvenile male partners on the first night). These dyads were not included in analyses, and additional dyads were established to maintain sample sizes. There were no deviations from the sample sizes given previously (i.e. M–m: n = 5; F–f: n = 7; M–f: n = 5; F–m: n = 7) except for the analysis involving all eight scoring sessions on

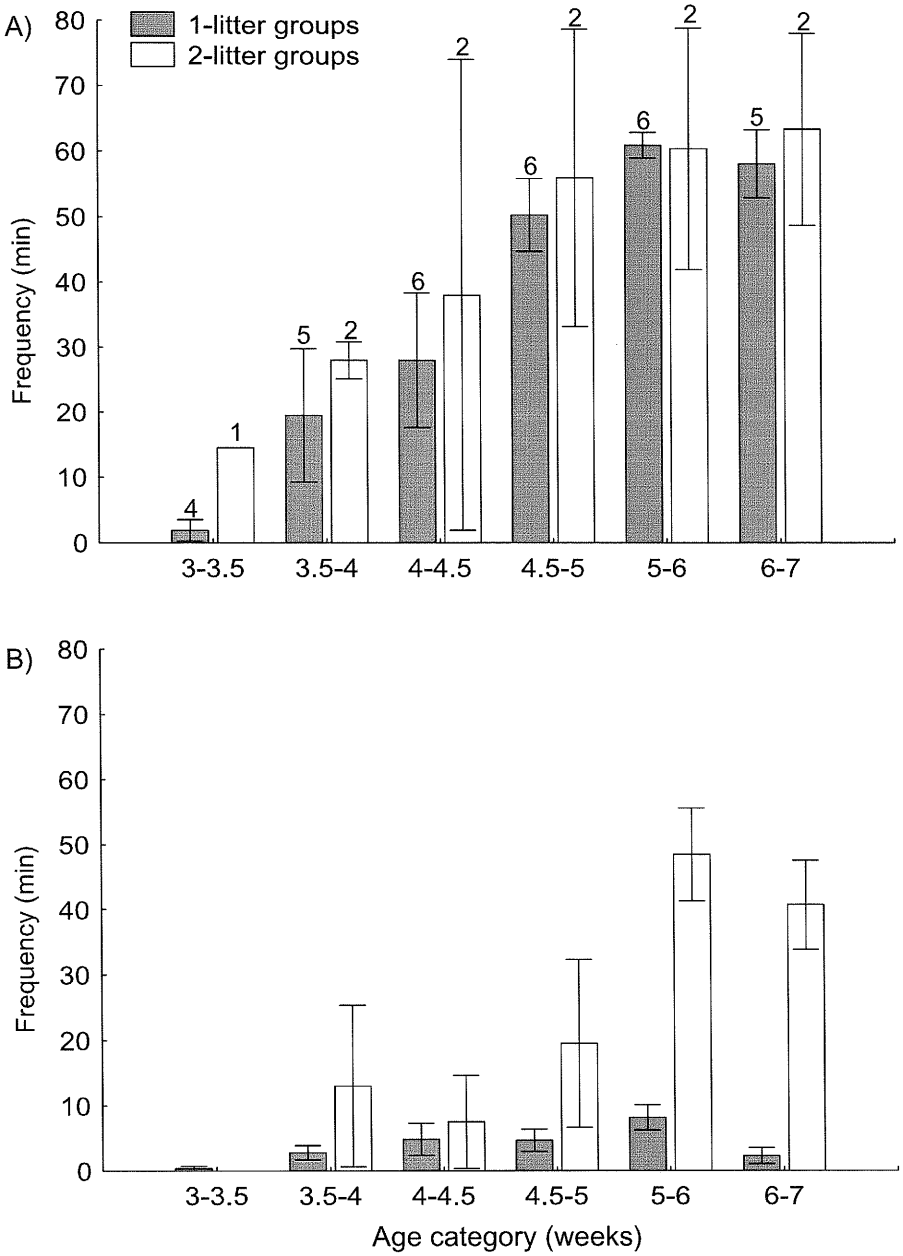


Figure 3. The relationship between juvenile age and time spent away from the mother in 1- and 2-litter groups, as illustrated by the mean (± SE) number of minutes per age category in which A) juveniles occupied the side tanks (sample sizes above bars) and B) the mother was alone in the natal tank (sample sizes as for A). Maximum minutes = 80.

night 1 (see below): one F–f dyad was only taped for 6 hours instead of 8 hours, resulting in n = 6 for sessions 7 and 8. In all dyads where overt agonistic behaviour was recorded, this behaviour was almost always performed by adults (juveniles performed overt agonistic behaviour in only three of the 209 minutes (1.4%) in which I recorded this behaviour).

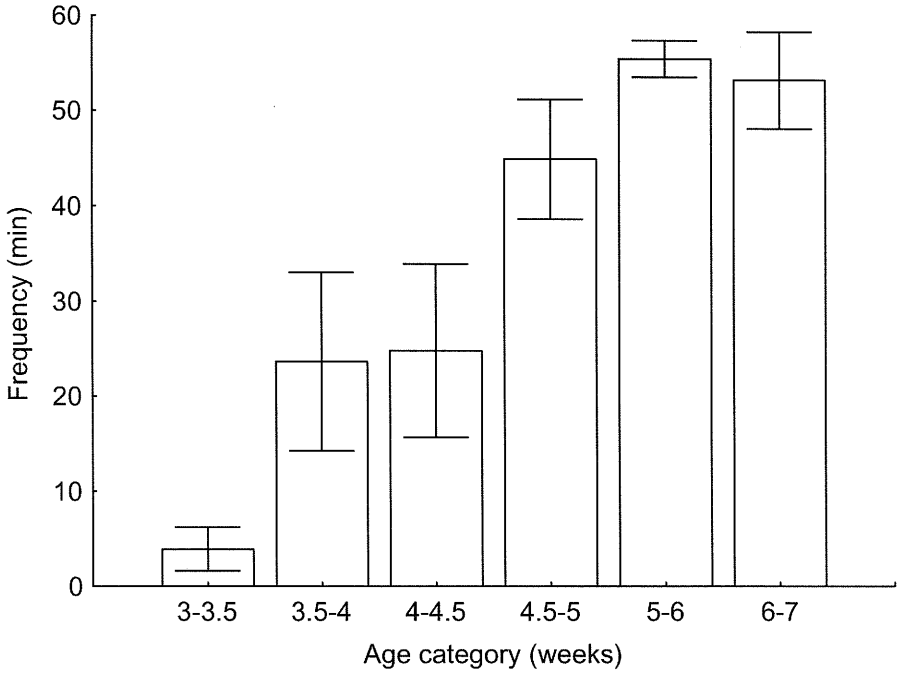


Figure 4. The relationship between juvenile age and time spent away from siblings and the mother, as illustrated by the mean (± SE) number of minutes per age category in which a juvenile was alone in a tank; 1-litter groups only (n = 5 for 3–3.5 week age category; n = 6 for the other 5 age categories). Maximum minutes = 80.

Aggressive and amicable behaviour

Variation in the levels of aggressive, and particularly amicable, behaviour was very high (Figure 5). Within each dyad-type some dyads displayed no amicable behaviour, while others were highly amicable. Some dyad-types also showed large ranges in aggression levels. Only adult sex, night and the interaction of these significantly affected behaviour (Table 2). High aggression on the first night was attributable to dyads with adult females. In addition, these dyads showed similar levels of amicable behaviour on nights 1 and 3, whereas those with adult males showed very low amicability on night 1 versus night 3 (Table 2; Figure 5).

In the analysis of the eight 20 minute scoring sessions of night 1, only the sex of the adult was a significant predictor of behaviour ($F_{2,19} = 4.42$, $p = 0.027$): dyads with adult females had higher aggression levels than those with adult males (post hoc tests; Figure 6). There was no effect of juvenile sex, scoring session or any interactions on behaviour ($p > 0.225$). Although dyads with adult females displayed more aggression than those with adult males, Figure 6 shows a trend towards their aggression levels dropping after the first few scoring sessions, and amicable levels rising sooner than in dyads with adult males. In

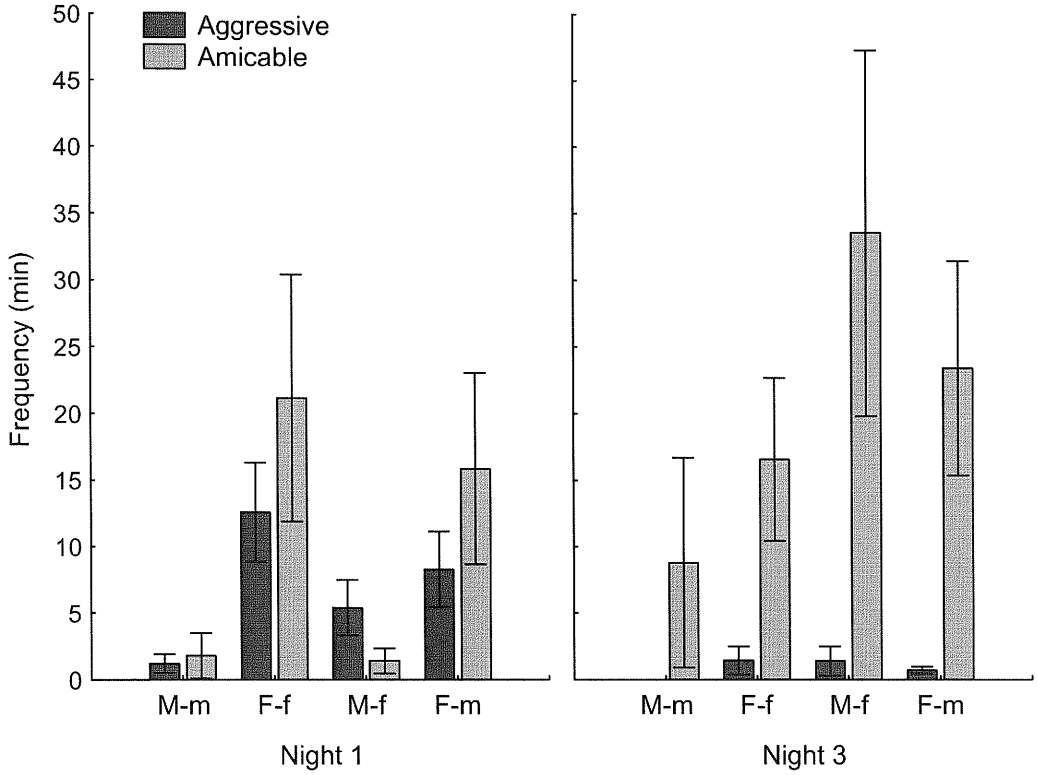


Figure 5. Changes in aggressive and amicable behaviour from night 1 to night 3 as displayed by each dyad-type, expressed as the mean (± SE) number of minutes in which these behaviours were displayed per night (M–m: n = 5; F–f: n = 7; M–f: n = 5; F–m: n = 7). M = adult ♂; F = adult ♀; m = juvenile ♂; f = juvenile ♀. Maximum minutes = 80.

Table 2. Outcome of the GLM analysis showing the effects of adult sex, juvenile sex, night (1, 3) and the interactions between these on aggressive and amicable behaviour. Significant effects are shown in bold, and the corresponding significant post hoc results are also provided.

	$F_{2,19}$	p	Post hoc results
Adult sex	**4.50**	**0.025**	Aggressive: ♀ > ♂
Juvenile sex	2.28	0.129	
Adult sex x Juvenile sex	0.44	0.647	
Night	**7.92**	**0.003**	Aggressive: night 1 > night 3 Amicable: night 3 > night 1
Night x Adult sex	**7.16**	**0.005**	Aggressive: night 1, ♀ > all others Amicable: night 1, ♂ < night 3, ♂ & night 3, ♀
Night x Juvenile sex	0.62	0.548	
Night x Adult sex x Juvenile sex	3.29	0.059	

addition, Figure 6 suggests that the very low amicability of adult male dyads on night 1 compared to night 3 in the previous analysis (Figure 5) is because they only became more amicable after 4 hours, which is not reflected in the previous test. As in Figure 5, the large error bars for amicable behaviour in Figure 6 reflect the high level of variation in amicability among the dyads.

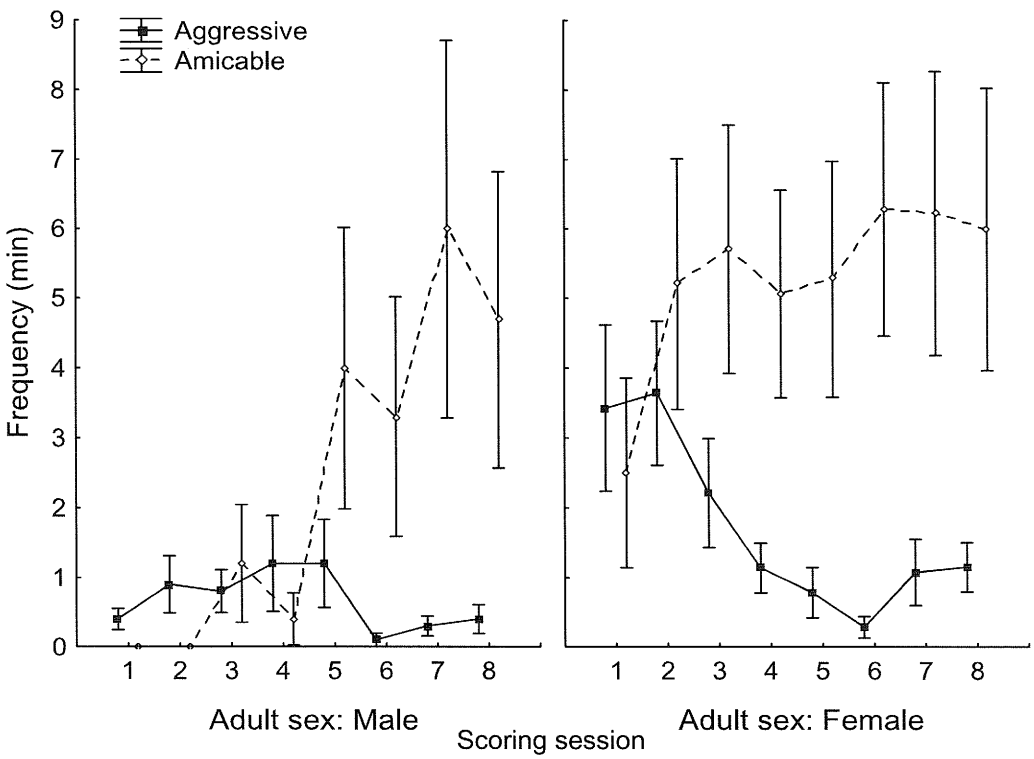


Figure 6. Changes in aggressive and amicable behaviour over all eight 20 minute scoring sessions of night 1, as displayed by dyads with adult males versus those with adult females, expressed as the mean (± SE) number of minutes in which these behaviours were displayed per session (dyads with adult males: n = 10 for all sessions; dyads with adult females: n = 14 for sessions 1–6, n = 13 for sessions 7–8).

Tank-sharing

Only night and its interaction with adult sex significantly affected tank-sharing (Table 3). More tank-sharing took place on night 3 than on night 1 (post hoc tests; Figure 7). Dyads with adult males showed an increase in tank-sharing on night 3 compared to night 1, whereas those with adult females displayed similar levels of sharing over the two nights (post hoc tests; Figure 7). The relatively large error bars indicate a fairly high level

of variation in tank-sharing within each dyad-type. Tank-sharing during the diurnal period was as follows: M–m dyads shared a tank on 13% of days; F–f dyads = 43%; M–f dyads = 33%; F–m dyads = 43%.

Table 3. Outcome of the GLM analysis showing the effects of adult sex, juvenile sex, night (1, 3) and the interactions between these on tank-sharing. Significant effects are shown in bold.

	$F_{1,20}$	p
Adult sex	1.09	0.309
Juvenile sex	1.28	0.272
Adult sex x Juvenile sex	0.38	0.543
Night	**8.81**	**0.008**
Night x Adult sex	**4.68**	**0.043**
Night x Juvenile sex	0.48	0.496
Night x Adult sex x Juvenile sex	0.23	0.633

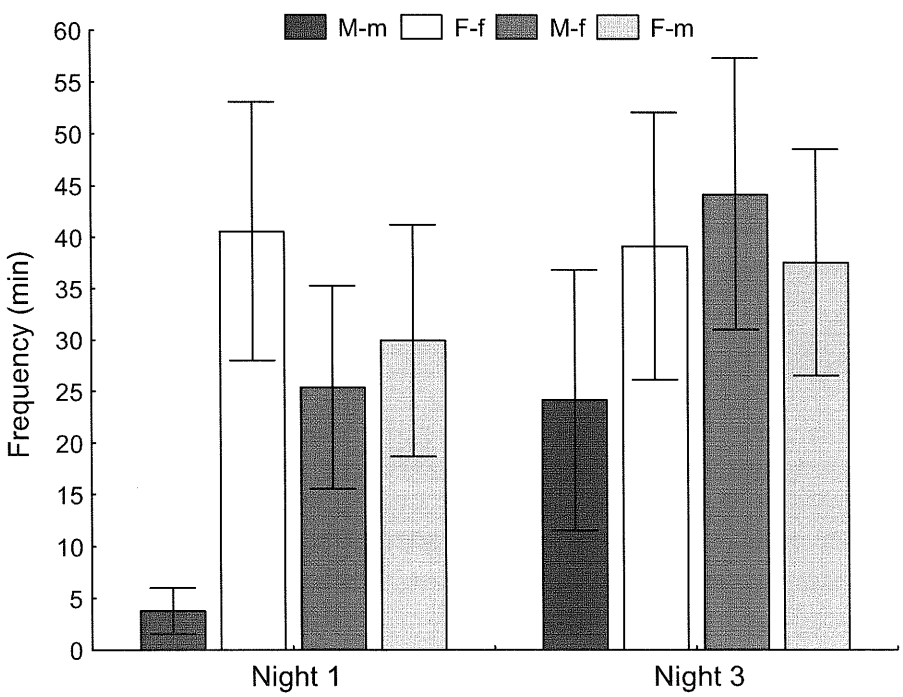


Figure 7. Change in tank-sharing by each dyad-type from night 1 to night 3, expressed as the mean (± SE) number of minutes per night in which dyads shared a tank (M–m: n = 5; F–f: n = 7; M–f: n = 5; F–m: n = 7). M = adult ♂; F = adult ♀; m = juvenile ♂; f = juvenile ♀. Maximum minutes = 80.

Oestrus

I detected no relationship between the oestrous stage of adult females and aggressive or amicable behaviour, or tank-sharing at night (Spearman $r = -0.25$, 0.35 and 0.26 respectively, $p > 0.050$ in all cases).

DISCUSSION

Mother–offspring relationships

I first asked whether the mother tolerates her offspring after weaning, or whether maternal aggression increases with juvenile age (question 1a). It appears that the mother's tolerance of her offspring may be dependent on whether or not she has a subsequent litter. My data indicate that mothers can be tolerant of their offspring well beyond weaning, as suggested for 1-litter groups by the relatively high levels of positive (i.e. attracting), combined with low levels of negative (i.e. repelling), behaviour in mother–juvenile affiliations, as well as the high frequency with which mothers and juveniles shared a tank. It is possible, however, that this situation changes if the mother produces a subsequent litter, given the substantially lower levels of positive social behaviour and increased frequency of negative social behaviour in 2-litter groups, although clearly a bigger sample of 2-litter groups is needed to explore this further. Question 1b) aimed to investigate juvenile tolerance of one another and whether sibling aggression increased with age. Siblings showed a very high affinity for one another in the first 3.5 weeks after parturition, and even after this time positive behaviour remained high. In Brants' whistling rat *Parotomys brantsii* reciprocal aggression between mothers and pups increased substantially when pups became independent, while aggression between siblings increased but remained relatively low (Jackson 2000). Hinze (2005) found that both sibling and mother–offspring aggression in ice rats *Otomys sloggetti robertsi* increased as female offspring reached sexual maturity, which promoted dispersal in this species.

With regard to question 1c), I asked at what age juveniles show independence from the mother and each other. Juveniles started displaying independence around the same age as weaning, as illustrated by their use of the side tanks from 23–24 days old. Juveniles used the side tanks more frequently and spent more time alone as they aged, with both these factors increasing substantially after 4.5 weeks of age. Before 4.5 weeks of age, side tank use and time spent alone by juveniles from 1-litter groups was more variable, as evidenced by the relatively large error bars in Figures 3 and 4. Similarly, sandrat *Psammomys obesus* siblings tended to spend less time in bodily contact with one another with increasing age

(Daly & Daly 1975). Although juveniles from 1-litter groups spent more time away from the mother as they aged, she was seldom alone in a tank, indicating that there was no clear breakdown of the mother–offspring bond, even by 7 weeks of age. The earliest that juveniles from 1-litter groups appeared to be nesting away from the mother during the day was close to 6 weeks of age (although an individual from a second litter was first found nesting away from the mother at just over 5 weeks old). However, juveniles from 1-litter groups never seemed to make a complete transition from nesting with the mother to nesting away from her, even after nearly 12 weeks. Animals often begin to disperse before or when they reach sexual maturity (Bekoff 1977; Waser & Jones 1983). Jackson (2000) found that Brants' whistling rat pups dispersed from their natal nest area after 5 weeks, when they had developed all important adult behaviours; this was also the age at which females could become sexually mature. A previous study of bushveld gerbils suggested that the earliest that females reached sexual maturity was 6.6 weeks (Lötter & Pillay 2008, Chapter 2). The fact that juveniles from 1-litter groups kept returning to the mother was probably a consequence of the laboratory situation, but also reinforces the very high level of post-weaning tolerance. This contrasts with vlei rats *O. irroratus*, where tolerance after weaning decreases steadily until sexual maturity, regardless of whether or not there is a subsequent litter (N. Pillay, personal communication).

Again, the situation differed in the 2-litter groups, where the mother was alone more often. The data suggest that the mother may or may not tolerate the juveniles once a subsequent litter is born. Perhaps the mother that allowed the first litter in the nest after the birth of the second litter did so because her combined litter size was only three (litter size of 1st litter = 1, 2nd litter = 2), versus six in the other group (1st litter = 4, 2nd litter = 2), and thus the single juvenile from her first litter may not have significantly increased her energy investment (see discussion of parent–offspring conflict below). There was, however, still more negative behaviour in this group compared to 1-litter groups. The juveniles from the other 2-litter group made a very sudden and consistent change from nesting with the mother to nesting away from her at about 4.5 weeks old shortly after the second litter was born. It is also possible that individual mothers respond differently to the first litter when a subsequent litter is present. Savidge (1974) found that *P. m. bairdi* mothers could be classed as aggressive or non-aggressive: juveniles left their natal site at greater rates when they had an aggressive mother with a subsequent litter, whereas non-aggressive mothers with subsequent litters did not have this effect; this difference was not apparent if there was no subsequent litter.

As discussed previously, the role of aggression in dispersal is debatable. Holekamp (1986) suggests that, although conspecific aggression is often unrelated to dispersal, it appears to apply to some situations, such as parental aggression in the case of a subsequent pregnancy/litter in some species, as reported for *P. m. bairdi* (Savidge 1974) and Chinese hamsters *Cricetulus griseus* (Dasser 1981). Similarly, in the Cape short-tailed gerbil *Desmodillus auricularis* the mother only tolerates the young if she fails to conceive after the postpartum oestrus, and will continue to do so until she becomes pregnant again (Keogh 1973). The theory of parent–offspring conflict predicts that conflict should exist over the extent of parental investment, and that the offspring should attempt to elicit greater investment from the parent than the parent is prepared to give (Trivers 1974). Thus, the optimal timing of natal dispersal may differ for parents and their offspring. This conflict should be greatest if the mother is expecting a subsequent litter due to the greater energy demands of the new offspring, and thus it is not surprising that parental aggression can appear more prevalent in this situation. Furthermore, in the current study, the finding that juveniles were largely responsible for initiating positive mother–juvenile affiliations in 1-litter groups is also consistent with parent–offspring conflict: Trivers (1974) explains that as the conflict of interests between parent and offspring increases, the offspring must increasingly obtain any parental investment by their own initiation.

Happold (1976) suggests that the breakdown of bonds may occur either passively, through a reduction in attracting behaviour, or actively through repelling behaviour. It appears that the breakdown of mother–offspring bonds in bushveld gerbils, which would ultimately lead to dispersal, occurs passively if there is no second litter but potentially more actively if there is one. The very low levels of negative behaviour among siblings in the current study also suggest that any breakdown of sibling bonds is passive. In sandrats the breakdown of sibling and mother–pup bonds leading to dispersal is a passive process with apparently no aggression, although the demands of a subsequent litter may hasten the decline of mother–pup contact (Daly & Daly 1975).

An alternative explanation for aggression by mothers towards juveniles in my study involves the theory of abandonment. Montane voles *Microtus montanus* may abandon their litter on weaning, although this is not restricted to females who are expecting a subsequent litter (Jannett 1978). Dasser (1981) found that pregnant Chinese hamsters shifted burrows to give birth to their subsequent litter and did not tolerate their previous offspring near the new burrow. Rowell (1961) suggested that aggression by golden hamster *Mesocricetus auratus* mothers towards their offspring may be a laboratory artefact where the mother is

unable to move away from her offspring. Thus, it is possible that dispersal in bushveld gerbils is not initiated by maternal aggression, but rather by maternal 'abandonment'.

The high degree of tolerance between *G. leucogaster* mothers and offspring in the absence of a subsequent litter suggests that there exists the potential for philopatry and thus the formation of family groups (Solomon 2003). In the striped mouse in the succulent karoo, parents are tolerant of their offspring well beyond weaning, and natal philopatry can result in the formation of large groups (Schradin & Pillay 2004). It is unlikely that bushveld gerbils form family groups during the breeding season when the female is probably pregnant for much of the time, but it is possible that the last litter of the season remains with the female until the following breeding season. This may have several advantages, for example thermoregulatory benefits from huddling (see review in Ebensperger 2001); the highveld, from where gerbils used in my study originated, can get very cold, and I recorded minimum temperatures as low as –4°C during my fieldwork. Furthermore, tolerance between mothers and offspring (and between siblings) would allow the formation of groups under high-density conditions when the habitat may become saturated and opportunities for successful dispersal are lower (Jones et al. 1988). Even among species that are not social, Lambin et al. (2001) note that a number of studies provide evidence of reduced dispersal and greater kin association when density is high. Since *G. leucogaster* can experience considerable population fluctuations (De Graaff 1981), the possibility of group formation is potentially adaptive as it would allow individuals to exist in close proximity with minimal aggression when density is high (see Chapter 6 for further discussion of this concept).

Unfamiliar adult–juvenile relationships

The section on unfamiliar adult-juvenile relationships aimed to address two questions. Firstly, do adults tolerate unfamiliar juveniles and do tolerance levels change with increased familiarity (question 2a)? And secondly, does the sex of the adult/juvenile influence the tolerance levels of adults (question 2b)? The results were not always clear, and unfortunately relatively low sample sizes coupled with high variation make interpretation of the data difficult. It appears that adults, specifically females, can be intolerant of unfamiliar juveniles, but that tolerance does increase with greater familiarity. However, as I suggest below, there may be other factors leading to apparently higher aggression by adult females compared to adult males. Although the sex of the adult influenced aggression on night 1, the sex of the juvenile had no effect on behaviour on

either night, suggesting that adults do not distinguish between male and female juveniles. Similarly, juvenile sex did not affect the aggressive behaviour of adults towards strange juveniles in *P. m. austerus* (Halpin 1981) or meadow voles *Microtus pennsylvanicus* (Boonstra 1984). Adult bushveld gerbils did seem to differentiate between same- and opposite-sex adult dyad partners, with male–female dyads exhibiting less tolerance than same-sex, especially female–female, dyads (Chapter 3). That adults apparently did not differentiate between male and female juveniles in the current study is probably because of the immature state of the juveniles. Dasser (1981) speculated that adult male Chinese hamsters were unable to distinguish between male and female juveniles owing to a lack of appropriate sex-specific olfactory cues in the juvenile males.

Higher initial aggression on night 1 compared to subsequent nights is similar to the results obtained in adult–adult dyads (Chapter 3), although it appears that adult-juvenile dyads (especially those with adult females) showed greater levels of amicable behaviour on the first night compared to adult-adult dyads. This suggests that adult-juvenile dyads displayed tolerance sooner. However, I also observed a tendency for juveniles to be more active than adults, and they may therefore have made contact with adults sooner than adults made contact with one another, thus facilitating the earlier display of amicable behaviour. Interestingly, Perrin et al. (2001) found that adults of the striped mouse and the multimammate mouse in a grassland habitat were less aggressive and more amicable towards subadult than towards adult conspecifics. A similar higher tolerance for younger animals may exist in bushveld gerbils.

Apart from higher aggression levels on night 1 than night 3, the higher level of tolerance displayed by adults towards familiar juveniles is also reflected in the greater degree of tank-sharing on the third compared to the first night. Interestingly, it was dyads with adult males that significantly increased tank-sharing from night 1 to night 3. Dyads with adult males also displayed the least amount of tank-sharing during the day. It is possible that juveniles avoid adult males more than adult females (particularly strangers). If this is true, the apparently higher initial aggression in dyads with adult females could be the result of increased interaction between adult females and juveniles, rather than higher aggression in itself. Furthermore, it could explain the trend towards dyads with adult females becoming amicable sooner than those with adult males, despite showing higher initial aggression. Low levels of initial interaction in adult male dyads would also explain why these dyads showed low amicability on night 1 compared to night 3, whereas adult female dyads were similarly amicable on both nights. Dasser (1981) suggested that

avoidance of resident adults rather than aggression by adults, influenced dispersal patterns in young male Chinese hamsters. The situation in bushveld gerbils is unclear, since avoidance of adult males seemed mainly applicable to the first night, after which amicable behaviour and tank-sharing increased, although variation in these parameters was high.

The literature on adult–juvenile relationships indicates great variation in the responses of adult males and females towards unfamiliar juveniles. Sadleir (1965) found that resident adult *P. m. austerus* were generally very aggressive towards intruding juveniles, while Healey (1967) suggested that adult males of this subspecies were more aggressive towards juveniles than adult females. Halpin (1981), however, could not find any such sex differences in *P. m. austerus*. In contrast to the more aggressive *P. m. austerus*, an island population of deer mice *P. m. saturatus* showed almost no aggression by adults towards any juveniles (Halpin 1981). In a study of Chinese hamsters (spanning a number of days), Dasser (1981) found that strange adult males tolerated juveniles throughout the observation period, while adult females did not. Adult female plateau mice were also more aggressive than adult males towards strange weanlings (Ferkin 1987). It has been suggested that aggression by adults of some *Peromyscus* species may affect juvenile survival and recruitment (Sadleir 1965; Healey 1967; Halpin 1981; Ferkin 1987). Although the results of the current study suggest that, like some of the above studies, adult female bushveld gerbils may be more aggressive towards strange juveniles than adult males, it is more likely that juveniles interact less with adult males. It is uncertain, however, why juveniles should avoid adult males as there is little evidence for male territoriality (as per the findings of Chapters 3 & 6, although more studies are necessary for confirmation), but it is possible that they pose an infanticide risk (see Chapter 4).

Ims & Hjermann (2001) point out that inhibition of immigration due to competition with residents, particularly at high densities, should be greatest in, for example, territorial populations, whereas dispersal should be less inhibited where interference by individuals is less direct. If bushveld gerbils are not territorial (see Chapters 3 & 6), dispersing juveniles may not experience high levels of interference by resident adults in general, although my study suggests that there is variation in this regard. It is noteworthy that in some dyads both adult males and adult females tolerated juveniles within a few hours of night 1, as evidenced by the relatively high levels of amicable behaviour. The high level of variation in my data, including tank-sharing, suggests that some adults are more tolerant than others and that perhaps there is also individual variation in juvenile avoidance of adults. In addition, the fact that some adults killed/severely injured their juvenile dyad partners

indicates that adults of both sexes can pose a very serious threat to strange juveniles. Individual variation in behaviour among rodents is not unusual. Healey (1967) classified some male *P. m. austerus* as docile and others as aggressive, and found that juvenile growth and survival were better when juveniles had contact with docile compared with aggressive males. This is similar to the distinction made by Savidge (1974) between aggressive and non-aggressive mothers in *P. m. bairdi*: aggressive females attacked strange weanlings whereas non-aggressive females did not. Perhaps the ability of *G. leucogaster* juveniles to immigrate into a population is partly determined by individual variation in behaviour: both their own and that of the adults in the population.

Conclusion

My study has investigated how social interactions may influence dispersal in *G. leucogaster*. Obviously, in a study such as this one, there is always the danger that small sample sizes influence the outcomes of the study, and therefore further studies with larger sample sizes are needed to confirm the trends. The trends in my study suggest that young may begin to disperse passively from the natal nest at around 5–6 weeks old but that mothers with subsequent litters may not tolerate weaned young, resulting in earlier dispersal. The formation of family groups is also possible, particularly if there is no subsequent litter (e.g. at the end of the breeding season). Once they have left the natal nest, the question of how adults respond to juveniles attempting to enter an existing population is unclear. My study suggests that aggression levels by strange adults could occasionally pose a serious risk to juveniles, but that there is great variation in tolerance levels and that juveniles may often be accepted into an existing population, particularly over a period of time. While more research is needed to understand the effect of adult bushveld gerbils on juvenile recruitment/immigration, my study suggests that adults may not affect juveniles to the extent argued for some other rodents. Adults do not appear to differentiate between male and female juveniles, but sex differences in the tolerance levels of adults towards juveniles are unclear and further studies would also help to clarify these differences. Finally, Ims & Hjermann (2001) point out that a number of conditions affecting dispersal may act simultaneously, possibly leading to interactive effects, and so there is a need for multifactorial studies to be carried out in relation to dispersal.

REFERENCE LIST

Bekoff, M. (1977). Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *The American Naturalist* **111**: 715–732.

Boonstra, R. (1984). Aggressive behavior of adult meadow voles (*Microtus pennsylvanicus*) towards young. *Oecologia* **62**: 126–131.

Brandt, C.A. (1992). Social factors in immigration and emigration. In: Stenseth, N.C. & Lidicker, W.Z. Jr (eds). *Animal Dispersal: Small Mammals As a Model*. Chapman & Hall: London.

Bronson, F.H. (1964). Agonistic behaviour in woodchucks. *Animal Behaviour* **12**: 470–478.

Cockburn, A., Scott, M.P. & Scotts, D.J. (1985). Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae). *Animal Behaviour* **33**: 908–915.

Daly, M. & Daly, S. (1975). Behavior of *Psammomys obesus* (Rodentia: Gerbillinae) in the Algerian Sahara. *Zeitschrift für Tierpsychologie* **37**: 298–321.

Dasser, V. (1981). Dispersal tendencies and social behaviour of young Chinese hamsters (*Cricetulus griseus*). *Behaviour* **78**: 1–20.

De Graaff, G. (1981). *The Rodents of Southern Africa*. Butterworths: Durban.

Dempster, E.R., Dempster, R. & Perrin, M.R. (1992). A comparative study of the behaviour of six taxa of male and female gerbils (Rodentia) in intra- and interspecific encounters. *Ethology* **91**: 25–45.

Ebensperger, L.A. (2001). A review of the evolutionary causes of rodent group-living. *Acta Theriologica* **46**: 115–144.

Ferkin, M.H. (1987). Parental care and social interactions of captive plateau mice, *Peromyscus melanophrys*. *Journal of Mammalogy* **68**: 266–274.

Halpin, Z.T. (1981). Adult-young interactions in island and mainland populations of the deermouse *Peromyscus maniculatus*. *Oecologia* **51**: 419–425.

Happold, M. (1976). Social behavior of the conilurine rodents (Muridae) of Australia. *Zeitschrift für Tierpsychologie* **40**: 113–182.

Healey, M.C. (1967). Aggression and self-regulation of population size in deermice. *Ecology* **48**: 377–392.

Hinze, A. (2005). Social behaviour and activity patterns of the African ice rat *Otomys sloggetti robertsi*. PhD thesis. University of the Witwatersrand: Johannesburg.

Holekamp, K.E. (1986). Proximal causes of natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). *Ecological Monographs* **56**: 365–391.

Ims, R.A. & Hjermann, D.Ř. (2001). Condition-dependent dispersal. In: Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds). *Dispersal*. Oxford University Press: New York.

Jackson, T.P. (2000). Female nesting behaviour, pup growth and ontogeny in Brants' whistling rat (*Parotomys brantsii*). *Journal of Zoology, London* **251**: 417–425.

Jannett, F.J. Jr (1978). The density-dependent formation of extended maternal families of the montane vole, *Microtus montanus nanus*. *Behavioral Ecology and Sociobiology* **3**: 245–263.

Jones, W.T., Waser, P.M., Elliott, L.F., Link, N.E. & Bush, B.B. (1988). Philopatry, dispersal, and habitat saturation in the banner-tailed kangaroo rat, *Dipodomys spectabilis*. *Ecology* **69**: 1466–1473.

Keogh, H.J. (1973). Behaviour and breeding in captivity of the Namaqua gerbil *Desmodillus auricularis* (Cricetidae: Gerbillinae). *Zoologica Africana* **8**: 231–240.

Lambin, X., Aars, J. & Piertney, S.B. (2001). Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. In: Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds). *Dispersal*. Oxford University Press: New York.

Lidicker, W.Z. Jr & Stenseth, N.C. (1992). To disperse or not to disperse: who does it and why? In: Stenseth, N.C. & Lidicker, W.Z. Jr (eds). *Animal Dispersal: Small Mammals As a Model*. Chapman & Hall: London.

Lötter, T.K. & Pillay, N. (2008). Reproduction and postnatal development of the bushveld gerbil *Gerbilliscus* (formerly *Tatera*) *leucogaster*. *Mammalian Biology* **73**: 430–437.

Martin, P. & Bateson, P. (2007). *Measuring Behaviour: An Introductory Guide*. (3rd ed.). Cambridge University Press: Cambridge.

Perrin, M.R., Ercoli, C. & Dempster, E.R. (2001). The role of agonistic behaviour in the population regulation of two syntopic African grassland rodents, the striped mouse *Rhabdomys pumilio* (Sparrman 1784) and the multimammate mouse *Mastomys natalensis* (A. Smith 1834) (Mammalia Rodentia). *Tropical Zoology* **14**: 7–29.

Rice, W.R. (1989). Analyzing tables of statistical tests. *Evolution* **43**: 223–225.

Rowell, T.E. (1961). The family group in golden hamsters: its formation and break-up. *Behaviour* **17**: 81–94.

Sadleir, R.M.F.S. (1965). The relationship between agonistic behaviour and population changes in the deermouse, *Peromyscus maniculatus* (Wagner). *Journal of Animal Ecology* **34**: 331–352.

Savidge, I.R. (1974). Social factors in dispersal of deer mice (*Peromyscus maniculatus*) from their natal site. *American Midland Naturalist* **91**: 395–405.

Scheibler, E., Weinandy, R. & Gattermann, R. (2006). Male expulsion in cooperative Mongolian gerbils (*Meriones unguiculatus*). *Physiology and Behavior* **87**: 24–30.

Schradin, C. & Pillay, N. (2004). The striped mouse (*Rhabdomys pumilio*) from the succulent karoo, South Africa: a territorial group-living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology* **118**: 37–47.

Solomon, N.G. (2003). A reexamination of factors influencing philopatry in rodents. *Journal of Mammalogy* **84**: 1182–1197.

StatSoft, Inc. (2001). *STATISTICA* (data analysis software system), *version 6*. www.statsoft.com.

Trivers, R.L. (1974). Parent-offspring conflict. *American Zoologist* **14**: 249–264.

Waser, P.M. & Jones, W.T. (1983). Natal philopatry among solitary mammals. *The Quarterly Review of Biology* **58**: 355–390.

Wolff, J.O. (1993). What is the role of adults in mammalian juvenile dispersal? *Oikos* **68**: 173–176.

CHAPTER SIX

Breeding and space use patterns of free-living bushveld gerbils *Gerbilliscus leucogaster*

ABSTRACT

This study investigated the breeding and space use patterns of bushveld gerbils *Gerbilliscus leucogaster* in a highveld grassland region in northern South Africa. The purpose of the study was to provide demographic information (related to breeding season) from this region for comparison with *G. leucogaster* studies from other regions, and to provide information on space use to complement laboratory studies on the social and mating system of the species. The study primarily made use of capture–mark–recapture techniques using permanent trapping grids, but also incorporated some radio-tracking. Data were collected from September 2002–January 2004, and some unpublished data from 1997 and 1998 were also included in the data set. Population density was very low during 2002–2004 (minimum number alive ranged from 0.49–4.69/ha), which may have been related to poor rainfall and/or possibly suboptimal habitat. Despite the often small sample sizes and other related limitations of this study, some interesting trends were still evident: breeding was associated with the summer rainfall season, although the duration of the breeding season appeared to be longer in 1997 and 1998 compared to 2002–2004; there was no sexual dimorphism in body mass; males travelled further than females in summer but similar distances in winter; male home ranges were larger than those of females; home ranges could overlap with multiple members of the opposite sex; and home ranges of males sometimes overlapped with one another but female ranges did not overlap with other females. The data from this field study provide some support for laboratory studies, which suggested a promiscuous mating system and a lack of territoriality, particularly in males. There was some discrepancy between the laboratory data on females, which indicated relatively high intrasexual tolerance levels, and the field data, which implied a lack of female–female overlap. Although reasons for this are unclear, I suggest that females may occupy exclusive areas under some conditions, such as when population density is low and/or food is limited, but are able to tolerate one another under high density conditions.

Keywords: *Gerbilliscus leucogaster*, breeding season, population density, home range

INTRODUCTION

This study aimed to provide field data on the reproduction and sociality of bushveld gerbils *Gerbilliscus leucogaster*, and was not designed to provide information on community structure or exhaustive population demography. The information generated here was mainly used to support the behavioural data provided in the preceding chapters, to attempt to generate a socio-ecological assessment for *G. leucogaster*.

Rodents are typically very difficult to study under natural conditions, especially if they are nocturnal (Nel 1975; Bondrup-Nielsen et al. 1993). Thus many rodent studies take place in the laboratory, where it is much easier to conduct controlled experiments. Laboratory studies have been questioned as to their relevance to animals living in the wild (Wolff 2003; Tang-Martínez 2003). Although it is often not feasible to investigate some aspects of small mammal biology in the field (Sherman & Wolff 2007), it is important to undertake field studies to complement laboratory research (Wolff 2003; Tang-Martínez 2003), for example as conducted by Schradin & Pillay (2003) to investigate whether paternal care in captive striped mice *Rhabdomys pumilio* also occurs in nature.

In the field, researchers often make use of indirect methods such as the capture–mark–recapture (CMR) technique to investigate various aspects of small mammal biology (e.g. Ascaray et al. 1991; Keesing 1998; Milstead et al. 2007). Radiotelemetry is also widely used and provides several advantages over CMR studies when investigating space use (Andreassen et al. 1993). I define space use for this chapter as the way an animal uses the space available to it, both in terms of how much space it uses (e.g. home range size) and the way it shares this space with conspecifics. Space use data can provide important information on the biology of secretive species (Andreassen et al. 1993), such as inferring social organisations and mating systems (e.g. Kraus et al. 2003; Schradin & Pillay 2005).

Gerbilliscus leucogaster is a nocturnal, burrowing rodent inhabiting a wide variety of habitats including open grassland, open woodland, thornveld and bushveld (De Graaff 1981; Smithers 1983). Several field studies have investigated various features of the biology of bushveld gerbils. Most detailed studies have focussed on the breeding biology and diet (Perrin & Swanepoel 1987; Neal & Alibhai 1991; Neal 1991; Neal 1996). Chidumayo (1980) studied various aspects of the population ecology in addition to the breeding biology, while Odhiambo et al. (2008) report on abundance in relation to season, habitat (maize fields versus fallow lands) and crop stages, in addition to the breeding biology and diet. Many studies describe the breeding season, with reports ranging from seasonal and associated with rainfall (e.g. Chidumayo 1980; Perrin & Swanepoel 1987;

Neal 1991; Odhiambo et al. 2008) to apparently year-round breeding (e.g. Smithers 1971; Wilson 1975). However, I am not aware of any studies investigating space use in this species. Very little is known about the mating system of *G. leucogaster* but Neal (1991) suggested promiscuity, which was supported by a laboratory study (Chapter 3).

The current field study investigated the breeding and space use patterns of bushveld gerbils from the highveld grassland region where those used in laboratory studies (Chapters 2–5) originated. To my knowledge, this biome has not been considered previously in any detailed study of bushveld gerbils. The primary aims were 1) to assess breeding patterns by investigating specific demographic aspects of bushveld gerbils (i.e. age and reproductive structure) from this region in order to place these into the broader context of *G. leucogaster* breeding patterns as reported in the literature, and 2) to investigate space use and sexual dimorphism in *G. leucogaster* in an attempt to complement the laboratory studies of the social and mating system of the species (Chapters 3–5).

MATERIALS AND METHODS

Study site

My study was conducted at Ezemvelo Nature Reserve (25°42.451′S; 29°00.999′E), situated near Bronkhorstspruit, South Africa. The reserve covers about 11 000 ha with an elevation of approximately 1 375 m above sea level. It falls within a summer rainfall region; the average annual rainfall for Bronkhorstspruit from 1980–2008 was 644 mm, with rain falling mainly from October to March. For the purposes of this study, I regard September–March as summer months and April–August as winter months. Excluding a particularly cold spell in September 2002, minimum and maximum temperatures during fieldwork from September 2002 to January 2004 averaged approximately 14/30°C in summer and 6/25°C in winter. The reserve is comprised of two vegetation types: Rand Highveld Grassland and Loskop Mountain Bushveld (Mucina et al. 2005). My study was conducted in the Rand Highveld Grassland vegetation type. Vegetation data were only available for the enlarged trapping grid (see below), where the most common grasses were *Trachypogon spicatus*, *Loudetia* spp. and *Tristachya rehmannii*, while the herbaceous shrub *Fadogia tetraquetra* was also common; the area was scattered with *Burkea africana* trees.

Demography and space use

I investigated the demography and space use of *G. leucogaster* primarily by using CMR techniques. Initially, three 8 x 8 trapping grids were set up consisting of 64 permanent trap stations (marked with metal stakes) located 10 m apart, such that each grid was 6 400 m^2 in size (80 x 80 m, including a 5 m edge i.e. half the distance between trap stations was added around the grid to calculate grid size; see Korn 1987). Grids were located a minimum of 2 km apart. Trapping was conducted monthly, excluding December, from September 2002 to March 2003 on two grids and from September 2002 to February 2003 on the third grid. The third grid was not sampled in March 2003 as the previous four trapping sessions had yielded only a single bushveld gerbil per session. This initial trapping yielded poor success and it was suspected that gerbil home ranges during the study period might have been large relative to the size of the grids, such that only a few individuals could be trapped within each grid. Therefore, the size of one of the three grids was enlarged to 40 950 m^2 (195 x 210 m, including a 7.5 m edge) with 182 trap stations located 15 m apart, resulting in a 13 x 14 grid. The decision regarding which grid to enlarge, and by how much to enlarge it, was based on trapping success on the original three grids, including extra trapping conducted beyond the edge of the grids. Trapping was conducted on this enlarged grid during May, June, July, October 2003 and January 2004, thus covering all four seasons.

One PVC live trap (29 x 6 x 7 cm; or occasionally a metal live trap, 25 x 7.5 x 8 cm), baited with a mixture of sunflower seeds, oats, raisins, peanut butter, oil and salt, was placed at each trap station. In an effort to increase trapping success, I infrequently baited some traps with sorghum beer or added banana to the usual bait mixture, but this did not seem to affect trapping success. To reduce the risk of trap mortality due to overheating or cold, traps were covered with grass in all seasons and cottonwool was sometimes placed inside traps, especially during the colder months. The grids were typically trapped for four consecutive nights per trapping session. I occasionally deviated from the usual methodology by placing additional traps outside burrows, placing additional traps outside of the grids, or increasing the number of nights trapped. This was done in an attempt to increase trapping success and to assess which grid to enlarge, and also when trapping for radio-tracking purposes (see below). Trapped individuals were weighed to the nearest gram using a spring balance and reproductive status was recorded as follows: males—scrotal (testes descended/partially descended) or non-scrotal (testes in abdominal cavity); females—vaginal orifice perforate or imperforate. Animals were individually marked by

toe-clipping, a standard procedure in small mammal studies (Spinks et al. 2000; Schradin & Pillay 2004; Massawe et al. 2006) and one that has been shown to have no deleterious effects on survival (Wood & Slade 1990; Braude & Ciszek 1998); toe-clipping was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand. Toe wounds were disinfected with antiseptic liquid, and individuals were released close to the capture station.

In order to obtain a different estimate of space use, a small number of individuals were radio-tagged on the enlarged grid in June 2003. Radio-tracking was performed with an AOR 8000 wide-range receiver and a Telonics RA-14K antenna. Individuals were equipped with MD-2C radio transmitters weighing 2.5 g including the collar, which represented ± 4% of the body mass of the animals tagged. Due to poor trapping success, only one female and two males were radio-tagged, although the female's transmitter failed shortly after tagging and thus data from only the two males were used. Tracking was performed from 18h30–05h00 on the first night and then from approximately 18h30–24h45 for five consecutive nights thereafter, as gerbils appeared to be more active during the first part of the night. Fixes were taken with a GPS, usually about an hour apart (range: 40 minutes–1 hour 45 minutes), excluding the first night when time between fixes was longer (range: 35 minutes–3 hours 25 minutes). In addition, fixes were taken during the day on two or three days to determine the location of burrow sites. Including these day fixes, radio-tracking spanned a period of 9 and 6 days for each male respectively.

Data analysis

Data from the three smaller trapping grids were always combined during calculations. Some unpublished data from 1997 and 1998 (N. Pillay, unpublished data) were available for an area of highveld grassland 5 km north of my study site, and I included these data in my results where possible to increase the sample size. The size of the trapping grid for this unpublished study was 100 x 100 m^2 (traps set 10 m apart) and trapping usually took place every month for five consecutive nights per month; other methodology was similar to my study.

Demography

The additional traps/trap nights made it difficult to calculate population density accurately, but I estimated the minimum number alive (Krebs 1966) per hectare for each trapping session using only those individuals captured on my grids. Other methods for

calculating density were not used because of the small sample sizes on my grids; the 'minimum number alive' method has been favoured over mark–recapture population models owing to the sensitivity of the latter to small sample sizes (Manor & Saltz 2008).

The percentage of adults and juveniles captured per trapping session, and the reproductive status of adults per trapping session, was compared graphically rather than statistically, owing to the low sample sizes in some of the months trapped. These data included individuals caught both on and off my trapping grids and a few extra individuals trapped elsewhere on the reserve for laboratory purposes (Chapters 2–5), as well as the unpublished data from 1997/1998. Juveniles were approximately separated from subadults/adults based on mass (< 49 g; after Chidumayo 1980); the term 'adults' in this study includes subadults.

Sexual dimorphism was assessed (using only my 2002–2004 data) by comparing the mass of adult males and females during winter using a General Linear Model (GLM) in STATISTICA 6.0 (StatSoft, Inc. 2001); $\alpha = 0.05$. Since breeding appeared to occur mainly in summer during 2002–2004 (see below), I used winter mass to avoid any bias caused by pregnant females. Data included adults trapped both on and off grids as well as extra individuals trapped elsewhere for the laboratory. Individuals were only included once and the mass on first capture of winter was used (unless this was < 49 g, in which case the first 'adult' mass (i.e. ≥ 49 g) for the individual was used).

Space use

Space use was assessed using my trapping and radio-tracking data from 2002–2004 and the unpublished trapping data from 1997–1998. The average maximum distance travelled was calculated per season for males and females (the 2002–2004 data included three juveniles). Distances that spanned more than one season were not included. Pooling the data from different years, differences in maximum distance travelled between the sexes and between seasons were assessed using a GLM in STATISTICA 6.0, with sex and season as categorical predictors; Fisher LSD post hoc tests were used to determine specific differences when categorical predictors had a significant effect, and α was set at 0.05: only the 1997/1998 data were analysed in this way owing to the small sample sizes in 2002–2004. Where an adult was trapped at least three times at three or more different locations, the home range was estimated using the minimum convex polygon (MCP) method, a widely used method in home range calculations (Keesing 1998; Priotto et al. 2002; Schradin & Pillay 2005; Lancaster 2009). Since the MCP method has been criticised on a

number of levels (see Nilsen et al. 2008), the kernel density estimator (KDE, 95% fixed kernel; Ranges6) was also used to calculate home range size for the 1997/1998 data only (owing to the larger sample sizes for these data, both in terms of number of individuals and number of trap locations per individual). The home ranges of the two adult males that were radio-tracked were estimated by plotting the GPS co-ordinates in the program ArcView 3.3 (ESRI 2002), which then calculated home range using minimum convex polygon. Potential intra- and intersexual overlap in space use by adults was assessed by examining the number of individuals caught within approximately 15 m of one another within each trapping session.

RESULTS

Demography

Gerbilliscus leucogaster was the most common species trapped in 2002–2004, but even so the number of individuals captured per trapping session was very low. Of the total number of captures for the 2002–2004 study (i.e. 146, which does not include any individuals removed for laboratory studies), 78% were *G. leucogaster*, while 95% of captures on the enlarged grid (i.e. 69 of 73) comprised *G. leucogaster*. Other genera/species trapped (i.e. 22% of captures) included *Aethomys* spp., *Dendromus mesomelas*, *Elephantulus myurus*, *Gerbilliscus brantsii*, *Mastomys* spp., *Mus minutoides* and *Otomys angoniensis*. Of the 114 *G. leucogaster* captures, 48 were first captures and 66 were recaptures. Maximum trapping success for *G. leucogaster* (including recaptures) was less than 2%, whether or not I included the additional trap nights in the calculations. Table 1 gives the minimum number of *G. leucogaster* alive per hectare for each trapping session. Surprisingly, trapping a single larger area (i.e. enlarged grid; from May 2003) yielded even fewer individuals per hectare than when trapping was conducted on the three smaller grids prior to this. Although the occasional use of different traps and bait could have potentially influenced trapping success, it is unlikely that this was the case during my study, as bushveld gerbils were caught using both plastic and metal traps, and all types of bait. Furthermore, regular traps and bait were always available on the grids (in abundant excess of the number of bushveld gerbils captured).

Figure 1 gives the percentage of adult males, adult females and juveniles trapped in each trapping session. I estimate that the breeding season during my trapping period (i.e. 2002–2004) began in September and ended in March/April. A pregnant female caught for laboratory studies gave birth near the beginning of October 2003, and thus she must have

Table 1. Minimum number of bushveld gerbils alive (MNA) during each trapping session at Ezemvelo Nature Reserve.

	Total area of grids (ha)	MNA per ha
September 2002	1.920	3.65
October 2002	1.920	3.13
November 2002	1.920	4.69
January 2003	1.920	4.69
February 2003	1.920	1.04
March 2003	1.280	4.69
May 2003	4.095	1.22
June 2003	4.095	0.98
July 2003	4.095	0.49
October 2003	4.095	1.47
January 2004	4.095	0.98

conceived in September (gestation = 21–22 days; Lötter & Pillay 2008, Chapter 2). The last new juvenile trapped was in early May 2003, and therefore the latest it could have been born was early April (weaning = ± 24 days; Lötter & Pillay 2008, Chapter 2). The 1997/1998 data (Figure 1B) indicate that a new juvenile was trapped in August each year and thus that the breeding season can start earlier than indicated by my data. Figure 2 gives the reproductive status of adults. Figure 2A indicates that, overall, the majority of adults during 2002–2004 were in breeding condition (scrotal/perforate) during summer with fewer such adults present in winter. However, these data should be interpreted with caution given the low sample sizes, especially in winter. Similarly, in 1997/1998 (Figure 2B) the majority of adults were in breeding condition in summer; however, adults in breeding condition were also trapped in many winter months, suggesting again that the breeding season was possibly longer than in 2002–2004 but, as before, low samples sizes make interpretation difficult.

There was no difference between adult male and female mass during winter ($F_{1,15}$ = 0.05, p = 0.824; mean ± SE: males = 67.33 ± 4.59 g, n = 9; females = 65.63 ± 6.14 g, n = 8). The overall adult mass during 2002–2004, including summer data, was: males = 80.03 ± 2.45 g (n = 34, range = 51–106 g); females = 71.39 ± 4.07 g (n = 18, range = 51–110 g).

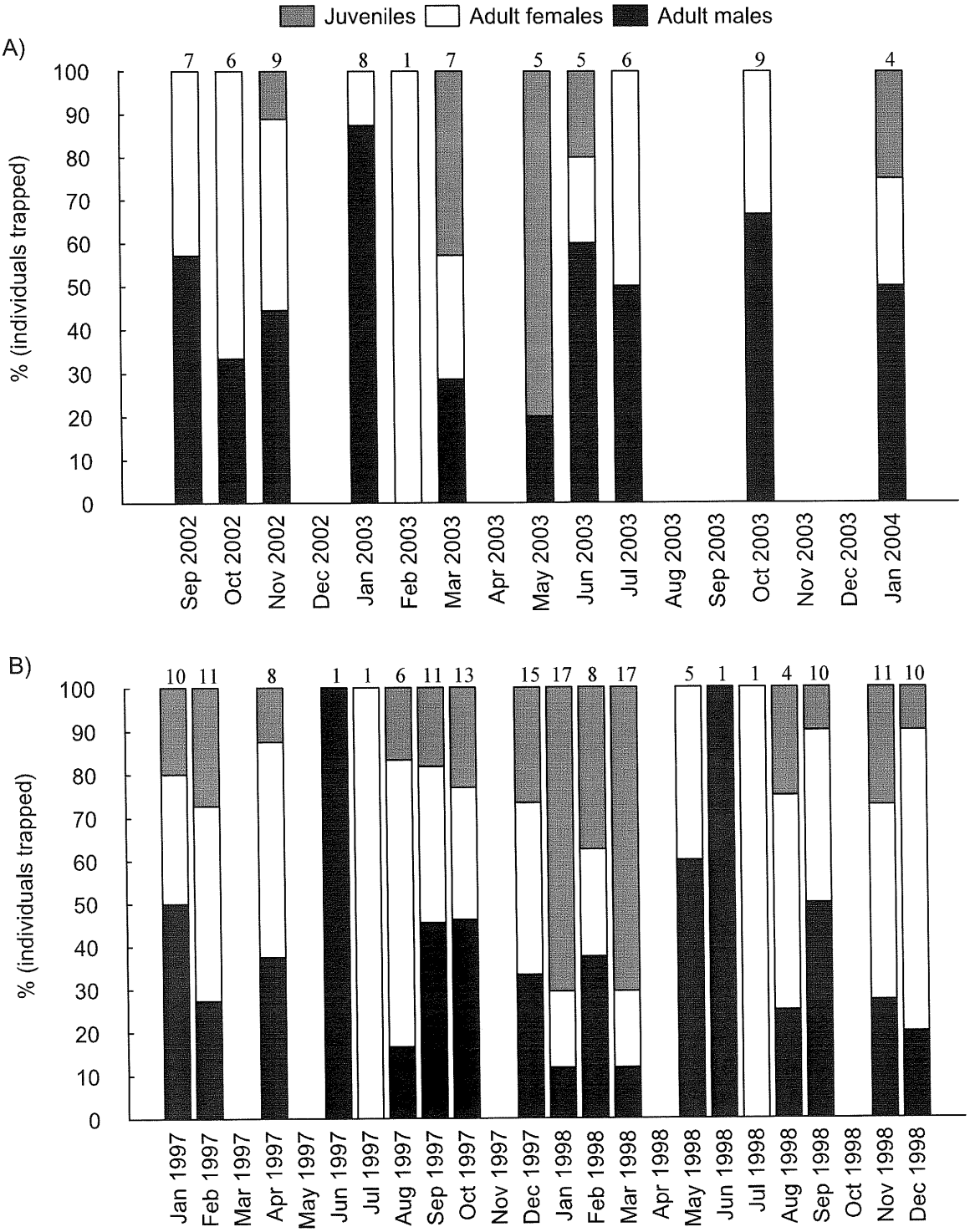


Figure 1. Number of adult males, adult females and juveniles captured each trapping session as a percentage of the total number of individuals captured per trapping session: A) 2002–2004 data B) 1997/1998 unpublished data. Sample sizes above bars.

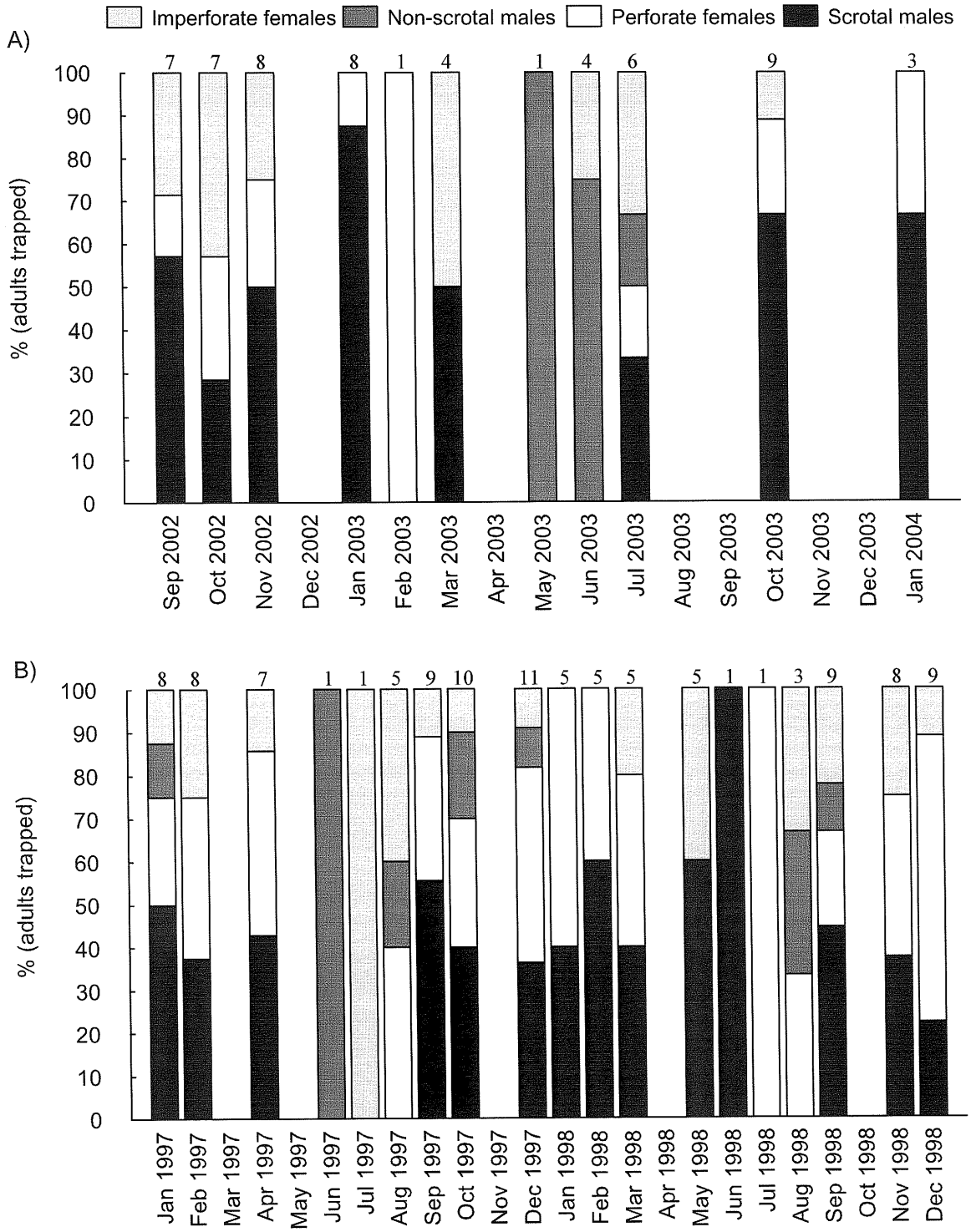


Figure 2. Reproductive status of adult males and females captured each trapping session as a percentage of the total number of adults captured per trapping session: A) 2002–2004 data B) 1997/1998 unpublished data. Sample sizes above bars (in Oct 2002, 6 adults were captured, but 1 female was scored twice as she was both imperforate and perforate during this month).

Space use

The mean (± SE) maximum distance travelled is given in Table 2. It is unclear from the 2002–2004 data whether males or females travel further, since females travelled further in summer 2002/2003 and winter 2003, while males travelled further in summer 2003/2004; clearly the low sample sizes confound these results. However, the 1997/1998 data suggest that males travelled about double the distance compared to females during summer, but similar distances in winter. The statistical analysis supports this: although season did not have a significant effect ($F_{1,68} = 3.04$, $p = 0.086$), both sex ($F_{1,68} = 6.32$, $p = 0.014$) and the interaction between season and sex ($F_{1,68} = 9.12$, $p = 0.004$) significantly affected the maximum distance travelled. Males travelled further than females in summer, but equivalent distances in winter (post hoc tests). Unfortunately, not many individuals were trapped at three or more different locations in 2002–2004, and thus very few home ranges could be calculated. Home ranges for two males were 149.91 m^2 and 49.98 m^2, while those of two females were 1 200.15 m^2 and 650.00 m^2. The data from the two radio-tracked males yielded home ranges of 3 131.01 m^2 and 1 960.27 m^2, which is probably a more accurate reflection of male home range size. Using the MCP method, mean ± SE male home range during 1997/1998 was 1 770.48 ± 386.32 m^2 (range = 987.21–3 111.78 m^2, n = 5), while that of females was 615.73 ± 171.41 m^2 (121.34–1 254.21 m^2, n = 7). Using the KDE method, mean ± SE male home range during 1997/1998 was 1738.36 ± 410.36 m^2 (range = 961.20–3210.10 m^2, n = 5), while that of females was 598.99 ± 164.52 (165.40–1234.20 m^2, n = 7). There were no significant differences between the MCP and KDE home range values for either males or females (paired t-test for males: $t_4 = 0.70$, $p = 0.522$; females: $t_6 = 0.53$, $p = 0.616$; STATISTICA 6.0). Table 3 gives the number of individuals whose ranges potentially overlapped with those of other individuals: a number of males overlapped with one another, while no females overlapped with other females; males and females overlapped with up to three individuals of the opposite sex.

DISCUSSION

Population density of *G. leucogaster* in my study was often lower than reported for other studies, although other studies also report low densities at times. For example, in Zambia the population estimate peaked at 9.7/ha in June 1974 but had crashed to less than 0.2/ha by February 1976 (Chidumayo 1980), while in Zimbabwe monthly densities in miombo woodland (considered preferred habitat in this study) ranged from 1.2–9.7/ha over about a year, but were lower in other habitats (Linzey & Kesner 1997). Density in various

Table 2. Mean ± SE maximum distance travelled (m) per season for male and female bushveld gerbils in a highveld grassland region. Sample sizes in parentheses.

	Males	Females
Summer 2002/2003	17.09 ± 7.33 (n = 7)	38.96 ± 9.77 (n = 5)
Winter 2003	25.50 ± 25.50 (n = 3)	37.50 ± 22.50 (n = 2)
Summer 2003/2004	35.98 ± 8.64 (n = 4)	18.25 ± 9.79 (n = 3)
Summer 1996/1997	101.75 ± 11.79 (n = 7)	53.99 ± 8.72 (n = 7)
Winter 1997	50.36 ± 11.29 (n = 9)	51.87 ± 10.82 (n = 9)
Summer 1997/1998	76.68 ± 11.91 (n = 9)	40.16 ± 9.24 (n = 9)
Winter 1998	53.32 ± 8.73 (n = 11)	58.96 ± 10.80 (n = 11)

Table 3. Number of individuals overlapping with 1, 2 or 3 other individuals (i.e. caught within ± 15 m of one another, both intra- and intersexually); n = total number of individuals that could have overlapped with one or more others.

	♂♂ overlap				♀♀ overlap				♂ overlap with ♀				♀ overlap with ♂			
Overlapping with	1	2	3	n	1	2	3	n	1	2	3	n	1	2	3	n
2002–2004	4	6	0	21	0	0	0	5	8	0	0	19	3	1	1	8
1997–1998	1	3	2	6	0	0	0	10	1	3	2	6	2	6	2	10

habitats in a reserve in Limpopo Province, South Africa ranged from 2–25/ha (Korn 1987). High density was reported in the Northern Cape Province, South Africa, where Perrin & Kotler (2005) estimated 35.5 animals/ha. It should be noted that the above studies made use of different techniques for calculating density, but the trends are still of interest. Odhiambo et al. (2008) report an overall trapping success of 4.9% for *G. leucogaster* in Tanzania, which is substantially higher than my maximum success of less than 2% (although they removed animals from their grids, and thus their trapping success does not include recaptures, which would have potentially resulted in an even higher success rate). It is possible that my study population was declining when I commenced the study and had not yet recovered by the end of the study.

The population decline in the study by Chidumayo (1980) was associated with a shortened breeding season, a lower pregnancy rate in some age groups, and poor pre- and post-weaning survival. Chidumayo (1980) speculated that, although a direct relationship between rainfall and demography was unlikely, decreasing rainfall over the study period

may have affected food and vegetation cover. In my study, the average monthly rainfall for Bronkhorstspruit in 2002 and 2003 was 42.14 and 32.01 mm respectively, compared to an overall monthly average of about 55 mm from 1980–2008. The reason for the low density in my study is not clear, but breeding in bushveld gerbils is known to be associated with rainfall (Perrin & Swanepoel 1987; Neal 1991) and the overall below-average rainfall during my study may have affected breeding in the population. Whereas juveniles were present during all summer trapping sessions in 1997/1998, I did not capture juveniles in a number of summer trapping sessions during my 2002–2004 study, suggesting that recruitment was lower during this period. This could either be attributed to lower reproductive output or increased juvenile mortality, or a combination of both.

Apart from the low rainfall, the habitat may not have been optimal for bushveld gerbils, also potentially resulting in low population density. Although they do not appear to be associated with a specific type of vegetation (Smithers 1983), Rautenbach (1982), in his study of mammals of the old Transvaal Province (northern South Africa), suggests that optimum habitat for this species is open scrubland with minimal grass. The grassland vegetation at my study site may therefore not have been ideal, and the habitat was also relatively dense from grass/moribund material and herbaceous shrubs. Bushveld gerbils appear to select more open habitats (Rautenbach 1982; Monadjem 1999), and although detailed studies investigating habitat preferences in bushveld gerbils are lacking, the results of several studies imply a tendency towards selecting open habitats. For example, Linzey & Kesner (1997) conducted trapping in five different habitats in Zimbabwe, and found the highest densities in miombo woodland, which had a poorly developed shrub layer. Korn (1987) conducted trapping in five habitats in Limpopo Province, South Africa, and found the highest densities in an area of *Acacia* savanna that had been burnt the previous year, compared to low densities in an area of unburnt *Acacia* savanna. Kern (1981), in a study of the effect of fire on small mammal populations, concluded that bushveld gerbils tend to be found in areas with relatively low cover and litter. It is thus possible that the degree of openness of the habitat at my study site was not optimal, but of course detailed vegetation analyses allowing habitat and population density comparisons of my study site with other bushveld gerbil localities would be necessary to assess this suggestion.

Bushveld gerbils appear to breed seasonally in the highveld grassland region reported by the current study. Rautenbach (1982) suggests a summer breeding season for *G. leucogaster* in northern South Africa (the old Transvaal Province; summer rainfall region) and Perrin & Swanepoel (1987) note that the species breeds seasonally in an area about

250 km north of my study site, with breeding usually occurring between October and March but that breeding may extend into April, May, August and September. This is very similar to the pattern suggested by the current study, where breeding during 2002–2004 seemed to fall more or less within the typical summer breeding season given by Perrin & Swanepoel (1987), while the breeding season was possibly longer in 1997/1998. Variation in the length of the breeding season has been reported frequently in the literature for *G. leucogaster* (e.g. Zambia: Chidumayo 1980; South Africa: Perrin & Swanepoel 1987; Zimbabwe: Neal 1991). Alternatively, the differences between the two periods reported in the current study might simply be attributable to low sample sizes and/or gaps in the months sampled. The current study and others reporting seasonal breeding contrast with studies from regions reporting more or less year-round breeding (e.g. Botswana: Smithers 1971; another part of Zimbabwe: Wilson 1975).

The lack of sexual dimorphism in this study is consistent with the literature on bushveld gerbils (Smithers 1983; Skinner & Chimimba 2005). This supports a promiscuous mating system: Boonstra et al. (1993) proposed that, for microtines, the greatest sexual dimorphism in body mass should occur in polygynous species, followed by promiscuous species and then those that exhibit obligate monogamy. Since monogamy is unlikely in bushveld gerbils based on low levels of male–female tolerance in captivity (Chapters 3 & 4), a lack of sexual dimorphism suggests promiscuity. The data on space use also revealed patterns consistent with a promiscuous mating system. The maximum distance travelled by males during summer in 1997/1998 was about double that of females. Furthermore, male home range size in general appeared to be more than twice that of females, which, as noted by Schradin & Pillay (2005), is a pattern is typical of solitary rodents mating promiscuously. In their research of the striped mouse, they imply a promiscuous mating system for a grassland population in which male home ranges were much larger than those of females, whereas there was no intersexual difference in home range size in an apparently polygynous desert population (Schradin & Pillay 2004, 2005). In the congener of *G. leucogaster*, the highveld gerbil *G. brantsii*, which Neal (1991) suggests is probably promiscuous, males also have larger home ranges than females: 4 900 m^2 versus 1 900 m^2 (De Moor 1969).

The home ranges of both sexes of *G. leucogaster* potentially overlapped with more than one individual of the opposite sex at times, also indicating a promiscuous, as opposed to a polygynous, system. Further support of this is given by the possibility that male home ranges sometimes overlapped with one another, suggesting a lack of male territoriality

(Ostfeld 1990), as proposed previously from investigations of social behaviour in captivity (Chapter 3). The space use patterns suggested by the current study are similar to those of two *Peromyscus* species where male home ranges were larger than those of females and intrasexual overlap was greater for males than females; the authors note that these patterns are consistent with a promiscuous mating system (Ribble & Stanley 1998). A promiscuous mating system was also suggested for long-tailed singing mice *Scotinomys xerampelinus*, where there was a tendency for the home ranges of both sexes to overlap with multiple members of the opposite sex and for males to show greater intrasexual overlap than females; there was also no sexual size dimorphism in this species (Blondel et al. 2009).

Even if female ranges overlap with those of multiple males and male ranges overlap with one another, it is possible that a dominance system exists whereby only the dominant male mates with the females in his home range, making the system polygynous (Oka 1992). Only genetic data would confirm paternity and thus the type of mating system. The current study also did not test the possibility that males display temporal territoriality, as was found in the ice rat *Otomys sloggetti robertsi*, where colony members displayed a high degree of spatial overlap but very little temporal overlap above-ground (Hinze 2005), or that males only defend an area around their burrows, overlapping in other parts of their range, as generally appears to occur in the genera *Perognathus* and *Dipodomys* (discussed by Eisenberg 1975).

That no females appeared to overlap with one another in the current study is surprising given the relatively high tolerance observed in female–female dyads in captivity (Chapter 3). The overlap data are suggestive of female territoriality (Ostfeld 1990), which was not indicated by dyad encounters, although females did seem to show a stronger preference than males for their home tanks during the day (Chapter 3), when they would be resting/sleeping in their burrows in nature. Increased population density may lead to increased overlap by individuals (e.g. Ostfeld et al. 1985), particularly if they are not territorial (Kraus et al. 2003). The low density during 2002–2004 may have resulted in females being more dispersed than normal and one would need to investigate spatial distribution under higher density to better understand female space use. Females are more dependent on food resources than males (Ostfeld 1985) and food appears to be a particularly important factor affecting the breeding pattern of *Gerbilliscus* females (Neal 1982). Thus, it is possible that *G. leucogaster* females prefer to occupy exclusive areas, especially during periods of low rainfall or in suboptimal habitat when food may be limited, but are able to tolerate one another when forced to live in close proximity, for

example as occurred in dyad encounters (Chapter 3) or during population eruptions in nature (Choate 1972; De Graaff 1981). Since I did not measure food availability, it is not possible to assess whether or not food was limited in my study, but the low rainfall may have resulted in a reduction in food supplies, as suggested by Chidumayo (1980). In two species of *Peromyscus*, high densities were associated with an increase in intrasexual home range overlap, with a corresponding increase in aggression (Wolff 1985). The evolution of pacifism in the *Spalax ehrenbergi* superspecies (blind mole-rats) has been related to selection for decreased aggression in desert habitats to minimise overheating and water loss, and to save energy (reviewed in Nevo 2007). Similarly, tolerance of conspecifics under high population density is potentially adaptive in bushveld gerbils if lower aggression leads to increased fitness through, for example, decreased energy expenditure.

This study has provided very simple data from free-living bushveld gerbils in order to provide some comparison with the literature and to support previous laboratory studies on sociality. There are obvious limitations to the study owing primarily to the poor capture success. It was not the intention to conduct a detailed ecological study since, although such a study is certainly warranted, the low capture success of the present study rendered a detailed study unfeasible at the time. Clearly, more detailed studies incorporating higher sample sizes are necessary to further investigate the trends highlighted here. The results presented here for *G. leucogaster* are generally in concordance with the laboratory results reported previously. They support the suggestion of a promiscuous mating system and a lack of territoriality, at least in males. The reasons for the discrepancy between the overlap and behaviour data in females are not clear, and again more studies are needed to further understand female behaviour and space use. Radiotelemetry generally provides more suitable data for estimating space use patterns than CMR techniques (Andreassen et al. 1993) and future studies should attempt to use this method to confirm the present findings and to investigate space use in bushveld gerbils in greater detail. It was not possible in the current study to assess the extent of overlap between individuals, and future studies incorporating this would give further insight into space use patterns. Since rodents may change their reproductive strategies under varying population densities (Wolff & Cicirello 1990), it is also important to conduct studies under a range of population densities. Finally, there are several ecological conditions affecting space use patterns in rodents that could not be investigated in the present study (such as vegetation cover and food availability; Schradin & Pillay 2006; Hayes et al. 2007), and these also need to be incorporated into

future studies to understand how social and ecological factors interact to influence space use in bushveld gerbils.

REFERENCE LIST

Andreassen, H.P., Ims, R.A., Stenseth, N.C. & Yoccoz, N.G. (1993). Investigating space use by means of radiotelemetry and other methods: a methodological guide. In: Stenseth, N.C. & Ims, R.A. (eds). *The Biology of Lemmings*. Academic Press, Harcourt Brace and Company: London.

Ascaray, C.M., Perrin, M.R., McLachlan, A. & Els, S.F. (1991). Population ecology of the Hairy-footed gerbil, *Gerbillurus paeba*, in a coastal dunefield of South Africa. *Zeitschrift für Säugetierkunde* **56**: 296–305.

Blondel, D.V., Pino, J. & Phelps, S.M. (2009). Space use and social structure of long-tailed singing mice (*Scotinomys xerampelinus*). *Journal of Mammalogy* **90**: 715–723.

Bondrup-Nielsen, S., Lambin, X. & Fredga, K. (1993). An overview of dyadic behaviour encounters with an example: behaviour of female wood lemmings (*Myopus schisticolor*). In: Stenseth, N.C. & Ims, R.A. (eds). *The Biology of Lemmings*. Academic Press, Harcourt Brace and Company: London.

Boonstra, R., Gilbert, B.S. & Krebs, C.J. (1993). Mating systems and sexual dimorphism in mass in microtines. *Journal of Mammalogy* **74**: 224–229.

Braude, S. & Ciszek, D. (1998). Survival of naked mole-rats marked by implantable transponders and toe-clipping. *Journal of Mammalogy* **79**: 360–363.

Chidumayo, E.N. (1980). Population ecology of *Tatera leucogaster* (Rodentia) in southern Zambia. *Journal of Zoology, London* **190**: 325–335.

Choate, T.S. (1972). Behavioural studies on some Rhodesian rodents. *Zoologica Africana* **7**: 103–118.

De Graaff, G. (1981). *The Rodents of Southern Africa*. Butterworths: Durban.

De Moor, P.P. (1969). Seasonal variation in local distribution, age classes and population density of the gerbil *Tatera brantsi* on the South African highveld. *Journal of*

Zoology, London **157**: 399–411.

Eisenberg, J.F. (1975). The behavior patterns of desert rodents. In: Prakash, I. & Ghosh, P.K. (eds). *Rodents in Desert Environments*. Dr W. Junk: The Hague.

ESRI. (2002). *ArcView, version 3.3*. Environmental Systems Research Institute: Redlands.

Hayes, L.D., Chesh, A.S. & Ebensperger, L.A. (2007). Ecological predictors of range areas and use of burrow systems in the diurnal rodent, *Octodon degus*. *Ethology* **113**: 155–165.

Hinze, A. (2005). Social behaviour and activity patterns of the African ice rat *Otomys sloggetti robertsi*. PhD thesis. University of the Witwatersrand: Johannesburg.

Keesing, F. (1998). Ecology and behavior of the pouched mouse, *Saccostomus mearnsi*, in central Kenya. *Journal of Mammalogy* **79**: 919–931.

Kern, N.G. (1981). The influence of fire on populations of small mammals of the Kruger National Park. *Koedoe* **24**: 125–157.

Korn, H. (1987). Densities and biomasses of non-fossorial southern African savanna rodents during the dry season. *Oecologia* **72**: 410–413.

Kraus, C., Künkele, J. & Trillmich, F. (2003). Spacing behaviour and its implications for the mating system of a precocial small mammal: an almost asocial cavy *Cavia magna*? *Animal Behaviour* **66**: 225–238.

Krebs, C.J. (1966). Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* **36**: 239–273.

Lancaster, J.L. (2009). Population and life history characteristics of coexisting small mammal species in a grassland habitat. PhD thesis. University of the Witwatersrand: Johannesburg.

Linzey, A.V. & Kesner, M.H. (1997). Small mammals of a woodland-savannah ecosystem in Zimbabwe. I. Density and habitat occupancy patterns. *Journal of Zoology, London* **243**: 137–152.

Lötter, T.K. & Pillay, N. (2008). Reproduction and postnatal development of the bushveld

gerbil *Gerbilliscus* (formerly *Tatera*) *leucogaster*. *Mammalian Biology* **73**: 430–437.

Manor, R. & Saltz, D. (2008). Conservation implications of competition between generalist and specialist rodents in Mediterranean afforested landscape. *Biodiversity and Conservation* **17**: 2513–2523.

Massawe, A.W., Rwamugira, W., Leirs, H., Makundi, R.H. & Mulungu, L.S. (2006). Do farming practices influence population dynamics of rodents? A case study of the multimammate field rats, *Mastomys natalensis*, in Tanzania. *African Journal of Ecology* **45**: 293–301.

Milstead, W.B., Meserve, P.L., Campanella, A., Previtali, M.A., Kelt, D.A. & Gutiérrez, J.R. (2007). Spatial ecology of small mammals in north-central Chile: role of precipitation and refuges. *Journal of Mammalogy* **88**: 1532–1538.

Monadjem, A. (1999). Geographic distribution patterns of small mammals in Swaziland in relation to abiotic factors and human land-use activity. *Biodiversity and Conservation* **8**: 223–237.

Mucina, L., Rutherford, M.C. & Powrie, L.W. (eds). (2005). *Vegetation Map of South Africa, Lesotho and Swaziland, 1:1 000 000 scale sheet maps.* South African National Biodiversity Institute: Pretoria.

Neal, B.R. (1982). Reproductive biology of three species of gerbils (Genus *Tatera*) in East Africa. *Zeitschrift für Säugetierkunde* **47**: 287–296.

Neal, B.R. (1991). Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae: Rodentia), in Zimbabwe. *Zeitschrift für Säugetierkunde* **56**: 101–111.

Neal, B.R. (1996). Reproductive response of *Tatera leucogaster* (Rodentia) to supplemental food, water, and 6-methoxybenzoxazolinone. *Mammalia* **60**: 651–666.

Neal, B.R. & Alibhai, S.K. (1991). Reproductive response of *Tatera leucogaster* (Rodentia) to supplemental food and 6-methoxybenzoxazolinone in Zimbabwe. *Journal of Zoology, London* **223**: 469–473.

Nel, J.A.J. (1975). Aspects of the social ethology of some Kalahari rodents. *Zeitschrift für*

Tierpsychologie **37**: 322–331.

Nevo, E. (2007). Evolution of pacifism and sociality in blind mole-rats. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective.* The University of Chicago Press: Chicago.

Nilsen, E.B., Pedersen, S. & Linnell, J.D.C. (2008). Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? *Ecological Research* **23**: 635–639.

Odhiambo, R.O., Makundi, R.H., Leirs, H. & Verhagen, R. (2008). Demography, reproductive biology and diet of the bushveld gerbil *Tatera leucogaster* (Rodentia: Gerbillinae) in the Lake Rukwa valley, south-western Tanzania. *Integrative Zoology* **3**: 31–37.

Oka, T. (1992). Home range and mating system of two sympatric field mouse species, *Apodemus speciosus* and *Apodemus argenteus*. *Ecological Research* **7**: 163–169.

Ostfeld, R.S. (1985). Limiting resources and territoriality in microtine rodents. *The American Naturalist* **126**: 1–15.

Ostfeld, R.S. (1990). The ecology of territoriality in small mammals. *Trends in Ecology and Evolution* **5**: 411–415.

Ostfeld, R.S., Lidicker, W.Z. Jr & Heske, E.J. (1985). The relationship between habitat heterogeneity, space use, and demography in a population of California voles. *Oikos* **45**: 433–442.

Perrin, M.R. & Kotler, B.P. (2005). A test of five mechanisms of species coexistence between rodents in a southern African savanna. *African Zoology* **40**: 55–61.

Perrin, M.R. & Swanepoel, P. (1987). Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life history theory. *South African Journal of Zoology* **22**: 218–227.

Priotto, J., Steinmann, A. & Polop, J. (2002). Factors affecting home range size and overlap in *Calomys venustus* (Muridae: Sigmodontinae) in Argentine agroecosystems. *Mammalian Biology* **67**: 97–104.

Rautenbach, I.L. (1982). Mammals of the Transvaal. *Ecoplan Monograph* **1**: 1–211.

Ribble, D.O. & Stanley, S. (1998). Home ranges and social organization of syntopic *Peromyscus boylii* and *P. truei*. *Journal of Mammalogy* **79**: 932–941.

Schradin, C. & Pillay, N. (2003). Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*): laboratory and field evidence. *Journal of Comparative Psychology* **117**: 317–324.

Schradin, C. & Pillay, N. (2004). The striped mouse (*Rhabdomys pumilio*) from the succulent karoo, South Africa: a territorial group-living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology* **118**: 37–47.

Schradin, C. & Pillay, N. (2005). Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy* **86**: 99–107.

Schradin, C. & Pillay, N. (2006). Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. *Behavioral Ecology* **17**: 452–458.

Sherman, P.W. & Wolff, J.O. (2007). Conclusions and future directions. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

Skinner, J.D. & Chimimba, C.T. (2005). *The Mammals of the Southern African Subregion*. (3rd ed.). Cambridge University Press: Cape Town.

Smithers, R.H.N. (1971). The mammals of Botswana. *Memoirs of the National Museums of Rhodesia* **4**: 1–340.

Smithers, R.H.N. (1983). *The Mammals of the Southern African Subregion*. University of Pretoria: Pretoria.

Spinks, A.C., Bennett, N.C. & Jarvis, J.U.M. (2000). A comparison of the ecology of two populations of the common mole-rat, *Cryptomys hottentotus hottentotus*: the effect of aridity on food, foraging and body mass. *Oecologia* **125**: 341–349.

StatSoft, Inc. (2001). *STATISTICA* (data analysis software system), *version 6*. www.statsoft.com.

Tang-Martínez, Z. (2003). Emerging themes and future challenges: forgotten rodents, neglected questions. *Journal of Mammalogy* **84**: 1212–1227.

Wilson, V.J. (1975). Mammals of the Wankie National Park, Rhodesia. *Museum Memoir of the National Museums and Monuments of Rhodesia* **5**: 1–147.

Wolff, J.O. (1985). The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*. *Canadian Journal of Zoology* **63**: 2657–2662.

Wolff, J.O. (2003). Laboratory studies with rodents: facts or artifacts? *Bioscience* **53**: 421–427.

Wolff, J.O. & Cicirello, D.M. (1990). Mobility versus territoriality: alternative reproductive strategies in white-footed mice. *Animal Behaviour* **39**: 1222–1224.

Wood, M.D. & Slade, N.A. (1990). Comparison of ear-tagging and toe-clipping in prairie voles, *Microtus ochrogaster*. *Journal of Mammalogy* **71**: 252–255.

CHAPTER SEVEN

GENERAL DISCUSSION

The bushveld gerbil *Gerbilliscus leucogaster* represents an African rodent for which we have little detailed information. My study, which invoked various laboratory and field techniques, thus aimed to add to the existing knowledge of the species. The primary aim was to investigate the social and mating system in greater detail, and thus to propose a model of sociality for the species. A secondary aim was to investigate the reproductive biology of the species. Since providing information on species from understudied regions is one of the challenges for studies of rodent sociality (Tang-Martínez 2003), my study represents an important contribution to our knowledge of this field, as well as adding to our general knowledge of the species.

REPRODUCTIVE BIOLOGY

The investigation of the reproductive biology of bushveld gerbils (Lötter & Pillay 2008, Chapter 2) found that postnatal development was slow for an altricial rodent, and that this characteristic is possibly phylogenetically constrained. It was suggested that this slow development may be related to high energy demands during lactation, but also that slow development may be beneficial by increasing the survival of juveniles, especially considering that bushveld gerbils have a relatively small litter size. As discussed, the slower development could also be related to the fact that the species has well-developed hind limbs (a characteristic of the family Gerbillinae; Skinner & Chimimba 2005). Finally, it was noted that the slow development may also reflect the increased protection afforded by the use of burrows. Similarly, the water rat *Dasymys incomtus* appears to compensate for small litter size and low reproductive potential through well-developed maternal care and the construction of a complex nest, offering increased protection to the mother and young (Pillay 2003).

In *G. leucogaster*, it appears that some features of reproduction such as litter size and breeding season vary with geographic location, and may reflect local adaptation to differing environmental variables (Lötter & Pillay 2008, Chapter 2). The field study of bushveld gerbils, conducted in a highveld grassland region, suggested that they breed seasonally in this area, mainly in summer, but that the length of the breeding season may

vary (Chapter 6). These and previous studies indicate that bushveld gerbils display some level of flexibility in their breeding patterns. The flexible nature of bushveld gerbils is illustrated by a 13 year study in the central Namib Desert, where gerbil species (namely the Cape short-tailed gerbil *Desmodillus auricularis*, the bushveld gerbil and the hairy-footed gerbils *Gerbillurus paeba*, *G. tytonis*, *G. setzeri*, *G. vallinus*) were found to be opportunistic feeders and breeders (Griffin 1990). Here, bushveld gerbils were able to expand their distribution after good rains, but as conditions became more arid, they were only marginally present in the area (Griffin 1990).

SOCIALITY AND MATING SYSTEM

Comparison with the literature

Most literature on *G. leucogaster* suggests that it is a relatively social species, living communally in burrows occupied by pairs or families/several adults (e.g. Choate 1972; Wilson 1975; De Graaff 1981; Rautenbach 1982; Skinner & Chimimba 2005), with promiscuity being the proposed mating system (Neal 1991). However, few detailed studies have been conducted to corroborate these findings, and my study thus aimed to investigate the social and mating system in greater detail. I achieved this mainly through laboratory observations of the behaviour (especially the social interactions) of combinations of individuals varying in age, sex and reproductive condition in different temporal and spatial contexts. Although I had to conduct primarily laboratory work owing to poor trapping success at my field site, I also incorporated some field data to complement the laboratory investigations.

My findings regarding the mating system strongly support promiscuity, as proposed in the literature. The three principal mating systems described in rodents are monogamy, polygyny and promiscuity (Waterman 2007). Since the interactions between male and female bushveld gerbils suggested that monogamy is very unlikely, the remaining options are polygyny and promiscuity. The large relative testes size and lack of sexual dimorphism, combined with behaviour data from the laboratory and space use data from the field, all point to a promiscuous rather than a polygynous mating system (Chapters 3 & 6).

My study does, however, contradict reports that *G. leucogaster* burrows are occupied by a pair (Skinner & Chimimba 2005), since the findings suggest that, at least during the breeding season, males and females do not form pair-bonds and do not associate except for mating purposes. Amicable behaviour between males and females that were familiar with

one another was limited, apart from one pair that showed unusually high levels of amicability. Furthermore, aggressive behaviour persisted from the time of pairing, and continued throughout pregnancy and lactation, with amicable behaviour ceasing completely after parturition. Initial aggression by females towards males may have been related to mate choice (Ferkin 1987), but later aggression was possibly a counter-strategy to infanticide (Wolff 1985; reviewed in Ebensperger 1998). Since my study was mainly concerned with male–female interactions in the context of breeding, it is possible that interactions are more amicable during the non-breeding season, similar to meadow voles *Microtus pennsylvanicus*, which display seasonal variation in social organisation depending on the tolerance levels of adult females (Madison & McShea 1987). Such variation might explain the discrepancy with the literature. My data also contrast with that of Dempster et al. (1993), but this may be related to different experimental techniques, as discussed previously (Chapter 3). The comparisons of social behaviour in same-sex versus opposite-sex dyads suggest that the former are more tolerant than the latter. Interactions between adult females appeared to be particularly amicable, although even here there was substantial variation in the levels of amicable behaviour displayed by the different dyads. Perhaps the reports of groups of adults occupying a burrow result from group formation by females, as the above laboratory study has shown that females can co-exist amicably. Alternatively, these may be family groups resulting from sibling associations or philopatric offspring (see below).

In spite of the apparent possibility of group formation, I found little field evidence to support this. The literature reports that *G. leucogaster* frequently inhabits warrens, which can be extensive (Smithers 1971; Wilson 1975; Smithers & Wilson 1979; De Graaff 1981; Rautenbach 1982), although Smithers (1971) notes that solitary burrows are sometimes found. The majority of burrows at my field site did not appear to be aggregated (i.e. as warrens), but rather were relatively spread out. Furthermore, when conducting trapping outside of burrows I sometimes set two or more traps per burrow but seldom, if ever, caught more than one individual, which suggests that burrows were occupied singly. Similarly, trapping conducted at a site near to mine in 1997 and 1998 only ever yielded one individual per burrow (N. Pillay, unpublished data). During the dry non-breeding season in Zimbabwe, Neal & Alibhai (1991) and Neal (1996) found that most burrows were occupied singly. Together with the above literature, this suggests some variation in burrow occupation by bushveld gerbils, but whether this is related to the breeding season is not known. My study covered all seasons and I did not notice a seasonal difference in this

regard. Apart from contradictions with much of the literature, I also found some conflict between my field and laboratory studies: female home ranges did not appear to overlap in the field, but laboratory data suggested relatively high tolerance between adult females.

There are a number of possible reasons for the discrepancy between my results and those of the literature (some of which have been discussed above), and between my field and laboratory results. Social structure can vary according to population density (Nel 1975; Lott 1991). The population density was very low during my fieldwork and this may account for individuals being more dispersed than suggested by the literature; it is possible that bushveld gerbils are more social under conditions of higher population density. Ågren et al. (1989) also suggested that sociality may vary according to fluctuating population densities in the Mongolian gerbil *Meriones unguiculatus*, and social structure is density-dependent in the great gerbil *Rhombomys opimus* (Randall et al. 2005; see below). Furthermore, Randall (2007) notes that semifossorial desert rodents are usually solitary, but that high density conditions can lead to a group situation. Although I am not aware of any studies relating population density to sociality in bushveld gerbils, Choate (1972) found that they could tolerate crowded conditions in captivity, thus demonstrating the potential for sociality under high density conditions.

As discussed (Chapter 6), the low density at my study site could have been due to lower than average rainfall in the region and/or the habitat may not have been optimal for bushveld gerbils. Rautenbach (1982) points out that solitary burrows are encountered more frequently in less favourable habitat. I suggest that both suboptimal habitat and low rainfall were responsible for the low population density at my study site, although these suggestions lack the support of a detailed habitat/food availability investigation. I discovered a number of apparently abandoned burrows, suggesting that the area was possibly more suitable at one time. Unfavourable habitat alone was unlikely to be responsible for the low density of bushveld gerbils as one would then expect to find higher numbers of other rodent species better adapted to the habitat (i.e. grasslands); however, *G. leucogaster* was the most common species trapped overall. During the same period, numbers of the Namaqua rock mouse *Micaelamys namaquensis* were far more abundant in the rocky outcrops (Lancaster 2009), suggesting that this habitat was less affected by the low rainfall, or that it was better able to support rodents for some other reason. The total rainfall for Bronkhorstspruit in 2003 was only 384 mm, compared to an average of 644 mm over 29 years. Bushveld gerbils are able to occupy relatively arid regions (Smithers 1983) and show physiological adaptations associated with hot and arid environments

(Webb & Skinner 1996). Furthermore, Perrin & Kotler (2005) found that bushveld gerbils were able to forage efficiently at a lower resource density than their competitor, the striped mouse *Rhabdomys pumilio*, in a semi-arid region of South Africa. Perhaps, although population numbers were limited, the above characteristics of bushveld gerbils explain why they were the most common species in the grasslands in my study during the period of low rainfall.

Flexibility

I have discussed earlier how bushveld gerbils show flexibility in some aspects of their reproduction. The discrepancies between my laboratory study, the field study and the literature suggest that there is also flexibility in the social structure of *G. leucogaster*. In the laboratory, females, and to a lesser extent males, showed relatively high levels of tolerance towards same-sex partners, sometimes sharing tanks (and even nests) during the day, as did some adult–juvenile dyads. This would be unexpected for a solitary species. Gromov (2007) points out that individuals cannot co-exist without tolerant relationships, and thus the fact that there was tolerance in my behavioural studies suggests that there is potential for sociality in *G. leucogaster*, as indicated in the literature. Bushveld gerbils are known to experience population eruptions (Choate 1972; Smithers 1975; De Graaff 1981), and Choate (1972) hypothesizes that the tendency of rodents, including *G. leucogaster*, to erupt may be linked to social tolerance. Wolff (2002) points out that the social behaviour of rodents must be flexible enough to adapt to the changing social environments caused by changes in population density. For example, the great gerbil has been described as facultatively social, with most females living in groups under high densities when conditions are favourable for survival and reproduction, but with more living solitarily and dispersed when food is limited, mortality is high and density is low (Randall et al. 2005). Most of my experiments revealed large variation in the levels of aggressive and amicable behaviour between individuals/pairs, indicating flexibility in the social behaviour of bushveld gerbils. Behavioural variation is not unusual and, although it may affect statistical significance, the variation itself may be important as the behaviour of the variant individuals would affect others in the population (Sadleir 1965). Indeed, Jacobs (2009) notes that there has recently been increased focus on the adaptive significance of individual variation in behaviour.

My results suggest that the dispersal strategy of *G. leucogaster* is also flexible, with juveniles having the potential to remain with the mother under some circumstances.

Mother–offspring relationships after weaning have been shown to be related to social organisation, as reported in studies of conilurine rodents (Happold 1976a, b) and voles (McGuire & Novak 1984): the more social species continued to exhibit attracting behaviour (even after the birth of a subsequent litter), whereas mothers of the more solitary species seemed to initiate a breakdown of the mother–offspring bond. Although there are some exceptions, dispersal patterns in gerbils also tend to reflect their level of sociality, such that the highly social species remain as philopatric non-breeders until the following breeding season, while the solitary species tend to disperse around maturation (Tchabovsky & Bazykin 2004). The results of my study suggest that mother–offspring relationships and dispersal patterns in bushveld gerbils can reflect either a more solitary or a more social way of life. This may depend on the social environment at the time; for example, the presence or absence of a subsequent litter (which may affect the behaviour of the mother towards her weaned offspring) or possibly the population density (which could promote group formation under high density conditions; see Chapters 5 & 6 and below).

Solomon (2003) notes that species displaying facultative philopatry may adjust their philopatric behaviour to short-term changes in the environment, and thus social groups may form and break up under different ecological and demographic conditions. It is not known whether *G. leucogaster* displays facultative philopatry or not, but my study suggests that it is possible, and that flexible maternal tolerance of offspring may allow family groups to form. Such flexibility would be beneficial if dispersal opportunities were limited because of, for example, high population density, or if there were other advantages to overwintering in the natal nest at the end of the breeding season (costs and benefits of philopatry reviewed in Solomon 2003; see also Chapter 5). Schradin et al. (2010) found that, during the breeding season, striped mice in the succulent karoo lived in family groups when population density was high, but were solitary when population density was low. They suggest that, even though solitary living should be favoured in the breeding season when there is reproductive competition within groups, high population density results in habitat saturation; this limits offspring dispersal, resulting in the formation of family groups. In the banner-tailed kangaroo rat *Dipodomys spectabilis*, dispersing individuals experienced lower overwinter survival than philopatric individuals at high population density, but this was reversed at low population density (Waser & Jones 1989). The above two studies illustrate that the ability to adjust dispersal behaviour according to the prevailing environmental conditions can be of great benefit. My study suggests that the behaviour of adult *G. leucogaster* towards strange juveniles is highly variable and that

adults can sometimes pose a serious risk to juveniles. This risk may be highest when the population density is high, making philopatry especially advantageous under high density conditions; Boonstra (1978) found that juvenile survival was negatively correlated with adult female density in Townsend voles *Microtus townsendii*.

Randall (2007) has observed that desert rodents seem to display particularly opportunistic and flexible behaviour. She notes that harsh environments appear to elicit opportunistic responses in both group formation and reproductive strategies, and that even the most social species seem to show social flexibility. Even though bushveld gerbils are generally found in areas of southern Africa with a mean annual rainfall of over 250 mm, they do occur in more arid areas (mean annual rainfall of less than 100 mm; Skinner & Chimimba 2005) and have been recorded from the central Namib Desert (Griffin 1990). As mentioned previously, they also show physiological adaptations associated with arid environments (Webb & Skinner 1996) and are able to forage efficiently at a low resource density (Perrin & Kotler 2005). Perhaps the behavioural flexibility that they exhibit is partly owing to the harsh environments in which they sometimes occur, where resources and consequently population densities may fluctuate unpredictably (as tends to occur in desert environments; see Randall 2007). Indeed, Jacobs (2009) notes that selection is likely to favour flexibility in a changing environment as this would allow an animal to respond to new situations. In bushveld gerbils, flexibility would confer an advantage, not only in arid/semi-arid environments, but also in mesic environments when conditions such as poor rainfall result in a harsher environment than normal, as was probably the case in the highveld grassland region during my field study.

Proposed social structure and mating system of *G. leucogaster*

Based on the information I have obtained during my study together with that in the literature (as discussed above and in the previous chapters highlighted below), a model of social organisation is proposed for *G. leucogaster* that is flexible and may depend on population density, among other factors. Neither sex appears to be territorial although this is unclear at present, and during the breeding season males probably wander in search of oestrous females, their home ranges overlapping with a number of females and with other males (Chapter 3 & 6). Apart from mating, females appear to be generally intolerant of and aggressive towards males: this may function as a mate choice mechanism during courtship, but it appears that aggression continues during pregnancy and lactation, which is possibly related to infanticide prevention (Chapter 3 & 4). Female home ranges may overlap with

several males, and females possibly encourage multi-male mating as a deterrent to infanticide by confusing paternity (Chapters 4 & 6). The resulting mating system would be promiscuous for both sexes, and males most likely use other strategies, such as sperm competition, to compete for females, rather than overt aggression (Chapters 1, 3, 4 & 6).

It appears that strangers are less tolerant of one another than are familiar individuals (Chapters 3 & 5). At a low population density, as occurred during my fieldwork, individuals may be widely dispersed, with females maintaining separate ranges from one another, which could serve to maximise access to resources, particularly if the conditions are suboptimal (Chapter 6). Females most likely raise their offspring alone, with these dispersing when a subsequent litter is born, while the last litter of the season may remain for a longer period with the mother (Chapters 4 & 5). Most dispersing individuals probably integrate into an existing population without too much interference from adults, although there may be variation in this regard (Chapter 5). At a high population density, individuals may be able to co-exist through group formation or simply tolerance of one another at close proximity (Chapters 3, 5 & 6). During the breeding season, females probably seldom tolerate males for extended periods under any density conditions, and any affiliations during periods of high density are most likely between same-sex (particularly female) individuals, between mothers and their philopatric offspring, or between siblings (Chapters 3, 4 & 5). This flexible social strategy would allow for the dispersed spacing of individuals when population density is low and conditions may be suboptimal, while also allowing for co-existence with minimal aggression during high population density (Chapters 5 & 6).

OTHER MEMBERS OF THE SOUTHERN AFRICAN GERBILLINAE

The social systems of gerbils around the world vary greatly from solitary, such as the pallid gerbil *Gerbillus perpallidus* (Volodin & Goltsman 2002), to highly social species such as the Mongolian gerbil (Ågren et al. 1989). The three genera of gerbils occurring in southern Africa also appear to display a variety of social systems, as discussed below.

Desmodillus auricularis is described as asocial/solitary by Nel (1975). Nel & Stutterheim (1973) found that the male was often killed by the female, and suggest that the male is only tolerated briefly during mating and does not show any paternal care. The aggressive, solitary nature of *D. auricularis* was supported by the behavioural studies of Dempster et al. (1993) who found that male–female interactions revealed high levels of agonistic and low levels of amicable behaviour, despite the attempted induction of oestrous behaviour. This contrasted with comparatively lower levels of agonistic and higher levels

of amicable behaviour in the Cape gerbil *Gerbilliscus afra* and in *G. leucogaster* (Dempster et al. 1993).

Intra- and intersexual behavioural encounters suggest that the four *Gerbillurus* species range in social structure from aggressively solitary (*G. paeba paeba*, *G. p. exilis* and *G. tytonis*), where females dominate males, to the more tolerant *G. setzeri* and *G. vallinus*, where the sexes are equally aggressive, with *G. vallinus* being the most social of the genus (Dempster & Perrin 1989a, b). This is supported by De Graaff (1981) who reports that *G. vallinus* is gregarious and that burrows are often interconnected, while Griffin (1990) states that *G. setzeri* is found singly or in small family groups. Randall (2007), however, suggests that rather than being social per se, *G. vallinus* probably forms groups under high population density. There may thus be similarities with bushveld gerbils in this regard, if my suggestions regarding group formation and population density in bushveld gerbils are correct. Within the taxon *G. paeba*, the two subspecies studied appear to differ in social tolerance, with *G. p. exilis* being more tolerant than *G. p. paeba* (Dempster & Perrin 1989a, b), although a later study revealed greater tolerance by *G. p. paeba* than previous studies, indicating behavioural plasticity (Dempster et al. 1992). The authors suggest that the widespread distribution of *G. p. paeba* is indicative of a generalist, and that this behavioural plasticity may be confirmation of its generalist status (Dempster et al. 1992). Bushveld gerbils also have a widespread distribution (Skinner & Chimimba 2005) and exhibit behavioural plasticity, suggesting that they too are generalists. Similarly, the occupation of a wide range of habitats in the genus *Rhabdomys* has been attributed to social flexibility (Schradin & Pillay 2003). Both phylogeny and habitat have been implicated in the social systems of the genus *Gerbillurus* (Dempster & Perrin 1989a).

There is still much to understand about the social systems of the four southern African *Gerbilliscus* species, but they do not appear to exhibit behavioural/social differences as great as those described in the genus *Gerbillurus* above. It is reported that *G. afra* occupies extensive burrows which often intercommunicate, while the highveld gerbil *G. brantsii* occurs in small colonies, occupying intercommunicating warrens (De Graaff 1981). According to Nel (1975), female *G. brantsii* occupy burrows singly, with males only co-occupying the burrow briefly during oestrus. The Gorongosa gerbil *G. inclusus* is apparently more solitary than *G. leucogaster* and does not form warrens; burrows are occupied singly, by a pair or by a female with young (Skinner & Chimimba 2005). Dempster et al. (1993) compared male–female interactions in three species. Overall, they found that male *G. brantsii* performed more upright boxing and female *G. brantsii*

displayed more motionless watching of their partners compared to *G. afra* and *G. leucogaster*. Male *G. leucogaster* nasal sniffed and huddled more than male *G. brantsii*. There were no differences in male or female behaviour frequencies between *G. afra* and *G. leucogaster*. Under conditions of attempted oestrous behaviour induction, the behaviour patterns in staged male–female encounters (Dempster et al. 1992, 1993) suggest that *G. brantsii* is less tolerant of conspecifics than *G. leucogaster* and *G. afra*. Similar to *G. leucogaster* in my study, females of both *G. brantsii* (Dempster et al. 1992) and *G. afra* (Dempster et al. 1993) were more aggressive than males, although females from my study only showed this effect when the first night was excluded from analyses. This similarity between all three species suggests that phylogeny may be implicated in the social structure of the genus. However, more studies using similar methodologies are needed to assess this further, especially considering that Dempster et al. (1993) did not find sex differences in aggression in *G. leucogaster*.

Lötter & Pillay (2008, Chapter 2) noted that the slow postnatal development of the three *Gerbilliscus* species for which there is postnatal data (i.e. *G. afra*, *G. brantsii* and *G. leucogaster*) may be due to phylogenetic constraints. Postnatal studies of five *Gerbillurus* taxa, namely *G. paeba exilis* (Ascaray & McLachlan 1991), *G. p. paeba*, *G. tytonis* (Dempster & Perrin 1989c), *G. setzeri* and *G. vallinus* (Dempster & Perrin 1991), reveal that these also exhibit relatively slow development, as illustrated by the age at which the eyes open. This ranges from 17 days in *G. p. exilis*, 14–18 days in *G. p. paeba*, 22–24 days in *G. tytonis*, ca. 18 days in *G. setzeri* and 16–20 days in *G. vallinus*. These approximate the ranges for the three *Gerbilliscus* species (see Lötter & Pillay 2008, Chapter 2). Since the genus *Gerbillurus* is very closely related to the southern clade of *Gerbilliscus* (i.e. *G. afra*, *G. brantsii*, *G. leucogaster*; Colangelo et al. 2007), the slow development of *Gerbillurus* supports the argument for phylogenetic constraints on postnatal development in this group.

FUTURE STUDIES

As discussed previously (Chapter 1), reproductive traits may be associated with social and mating systems. Although my study did not specifically investigate the breeding biology of *G. leucogaster* in relation to the social and mating system, future studies can use the baseline information provided here to examine whether some of the associations found in other species also occur in bushveld gerbils (see Chapter 1).

Social groupings can change with, for example, oestrus or pregnancy (Nel 1975), and therefore studies using behaviour to elucidate social structure should be undertaken in a variety of contexts. While my study provided several different contexts in which to investigate behaviour (e.g. age, sex, pregnancy etc.), there are many more contexts that one could provide. For example, since the effect of oestrus on behaviour was not specifically investigated in my study, future studies could examine this in greater detail. Intrasexual female interactions could also be investigated under different breeding conditions: Zuri & Rado (2000) have suggested that differences in aggression levels between females of the lesser white-toothed shrew *Crocidura suaveolens* may be attributed to breeding condition. Such studies would give a greater understanding of the social structure and tolerance levels of bushveld gerbils under conditions different from those provided in the current study.

As indicated earlier, there is a need to compare social structure in the breeding versus non-breeding seasons. For example, Schradin et al. (2010) found that social structure in striped mice from the succulent karoo was affected by a combination of season and population density. Similarly, Randall (2007) notes that studies of various species of gerbils (genus *Meriones*) indicate that social behaviour varies with season and density. One method of investigating seasonal differences in behaviour, where direct observations are difficult, is to observe dyads of newly captured individuals in each season: either in cages in the field (to simulate residency, similar to that conducted by Hinze 2005) or in neutral cages indoors. Interactions between familiar versus unfamiliar individuals could be staged by pairing individuals caught nearby with those captured in different areas (Hinze 2005). If females are more tolerant of males in the non-breeding season it would also provide support for the infanticide hypothesis to explain female aggression (since female aggression typically increases during breeding and is often associated with infanticide prevention; Ebensperger & Blumstein 2007).

The model of sociality proposed for *G. leucogaster* allows for the tolerant co-existence of individuals under varying population densities. Although I propose that population density is one factor influencing social structure in bushveld gerbils, there are many other factors that may be involved. Ebensperger (2001) reviewed some of the causes of rodent sociality. Owing to a lack of comprehensive information, I am not in a position to comment in any detail on these hypotheses in relation to the apparent variability in the social structure of bushveld gerbils. I can, however, make some suggestions based on my study and the literature. Of the eight hypotheses reviewed by Ebensperger (2001) I will briefly discuss the four that I believe have the most potential to influence sociality in *G.*

leucogaster. Future studies can test the predictions of these hypotheses (see Ebensperger 2001) to better understand the reasons behind the flexible social structure of this species. It should be remembered that these hypotheses are not mutually exclusive and that some predictions are shared between hypotheses (Ebensperger 2001). Therefore a number of these hypotheses (or alternatives that are not included here) may apply to *G. leucogaster*.

1) The resource-defence hypothesis states that group-living individuals can defend abundant and patchy resources better than solitary individuals. However, if resources are scarce and uniformly distributed solitary living is preferred. If resources were scarce during my fieldwork (e.g. owing to poor rainfall; Chapter 6) it may explain why individuals appeared to be relatively dispersed. It is possible that, as abundance and distribution of resources varies with changing environmental conditions, bushveld gerbils may benefit from communal resource defence. Testing this hypothesis would require a thorough understanding of the nature of the resources utilised by *G. leucogaster*. 2) Under the predatory risk hypothesis, group-living reduces the risk of predation. Since bushveld gerbils seem to select more open habitats (Rautenbach 1982; Monadjem 1999), group-living under these conditions may be beneficial if the open habitat increases vulnerability to predators. In my study, the habitat was relatively dense from grass/moribund material and herbaceous shrubs, and in some cases trees, which may also have reduced any such benefits of group-living. 3) The water energy-stress hypothesis predicts that aggression should be lower in arid areas due to the need to conserve water and energy. Since *G. leucogaster* has a very wide distribution and is able to inhabit regions receiving less than 100 mm of mean annual rainfall (Skinner & Chimimba 2005), it would be of interest to compare sociality in populations from more arid regions with those from more mesic areas. Under this hypothesis I would predict that, for similar population densities, bushveld gerbils from arid areas would be more tolerant of conspecifics than those from mesic areas. However, if mesic areas allow for greater population densities than arid areas owing to better resources, I would expect to find greater sociality in mesic areas (because of, for example, group formation resulting from habitat saturation; Schradin et al. 2010). 4) Finally, the burrow-sharing hypothesis maintains that species utilising limited refuges or constructing costly burrows may need to live in groups to share burrows or to reduce the cost of burrow construction. Since bushveld gerbils usually inhabit areas with sandy soils (Smithers 1983), burrow construction may not necessarily be very costly. However, they can occupy areas of hard ground, where they do not appear to excavate burrows but rather

utilise existing holes (Smithers 1983). It would be interesting to investigate whether group-living is more common, or if group size increases, in these areas.

CONCLUSIONS

Differences in social organisation are related to differences in tolerance levels towards conspecifics (Eisenberg 1967). The finding that tolerance is displayed by *G. leucogaster* at times suggests that the species is not strictly solitary and can display some sociality, particularly compared to other known solitary rodents in southern Africa, such as the vlei rat *Otomys irroratus* (Pillay 1993) and the water rat (Pillay 2003). On the other hand, it does not seem to be highly social either, but rather to lie along a social continuum (see review in Lacey & Sherman 2007), its position varying along this continuum. Bushveld gerbils appear to be opportunists, with the potential to adjust their behaviour and thus their social structure, as well as aspects of their reproduction (e.g. litter size and breeding season), to changing environmental/demographic conditions; this plasticity appears to be reflected in their widespread distribution, as discussed above. Bushveld gerbils may show some similarities to great gerbils, in that the ability of great gerbils to tolerate conspecifics when space is limited allows them to be flexible and adapt to unpredictable environments and changing population densities (Randall et al. 2005).

My study has added valuable information to our knowledge of the reproductive biology, sociality and mating system of an African rodent for which there was little information on these subjects, particularly the latter two aspects. It has also shown the importance of conducting investigations that allow the expression of spatial, and particularly temporal, variation in behaviour. However, it should be remembered that the results of a study such as this, using relatively small samples, individuals from a single population and conducted under specific laboratory/field conditions, cannot be regarded as being representative of the species in general, but rather reflect *G. leucogaster* biology under the experimental conditions used. Since so little was known about the social and mating system of bushveld gerbils, my study has only begun to elucidate the details of these systems, and much still remains to be uncovered and confirmed. Large numbers of rodents seen together does not necessarily indicate a stable social structure, but rather may simply reflect spatial overlap owing to high population density (Randall 1994, 2007). Although it appears that bushveld gerbils can display sociality at times, whether they simply tolerate close neighbours at high population density or rather are able to form stable social groups remains to be discovered.

REFERENCE LIST

Ågren, G., Zhou, Q. & Zhong, W. (1989). Ecology and social behaviour of Mongolian gerbils, *Meriones unguiculatus*, at Xilinhot, Inner Mongolia, China. *Animal Behaviour* **37**: 11–27.

Ascaray, C.M. & McLachlan, A. (1991). Postnatal growth and development of the hairy-footed gerbil, *Gerbillurus paeba exilis*. *South African Journal of Zoology* **26**: 70–77.

Boonstra, R. (1978). Effect of adult Townsend voles (*Microtus townsendii*) on survival of young. *Ecology* **59**: 242–248.

Choate, T.S. (1972). Behavioural studies on some Rhodesian rodents. *Zoologica Africana* **7**: 103–118.

Colangelo, P., Granjon, L., Taylor, P.J. & Corti, M. (2007). Evolutionary systematics in African gerbilline rodents of the genus *Gerbilliscus*: inference from mitochondrial genes. *Molecular Phylogenetics and Evolution* **42**: 797–806.

De Graaff, G. (1981). *The Rodents of Southern Africa*. Butterworths: Durban.

Dempster, E.R., Dempster, R. & Perrin, M.R. (1992). A comparative study of the behaviour of six taxa of male and female gerbils (Rodentia) in intra- and interspecific encounters. *Ethology* **91**: 25–45.

Dempster, E.R., Dempster, R. & Perrin, M.R. (1993). Behavioural divergence in allopatric and sympatric gerbil species (Rodentia: Gerbillinae). *Ethology* **93**: 300–314.

Dempster, E.R. & Perrin, M.R. (1989a). A comparative study of agonistic behaviour in hairy-footed gerbils (Genus *Gerbillurus*). *Ethology* **83**: 43–59.

Dempster, E.R. & Perrin, M.R. (1989b). Male-female interactions in hairy-footed gerbils (genus *Gerbillurus*). *Ethology* **83**: 326–334.

Dempster, E.R. & Perrin, M.R. (1989c). Maternal behaviour and neonatal development in three species of Namib Desert rodents. *Journal of Zoology, London* **218**: 407–419.

Dempster, E.R. & Perrin, M.R. (1991). Neonatal development of *Gerbillurus vallinus* and *G. setzeri*. *Madoqua* **18**: 51–53.

Ebensperger, L.A. (1998). Strategies and counterstrategies to infanticide in mammals. *Biological Reviews* **73**: 321–346.

Ebensperger, L.A. (2001). A review of the evolutionary causes of rodent group-living. *Acta Theriologica* **46**: 115–144.

Ebensperger, L.A. & Blumstein, D.T. (2007). Nonparental infanticide. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective.* The University of Chicago Press: Chicago.

Eisenberg, J.F. (1967). A comparative study in rodent ethology with emphasis on evolution of social behaviour, I. *Proceedings of the United States National Museum* **122**: 1–35.

Ferkin, M.H. (1987). Reproductive correlates of aggressive behavior in female *Peromyscus melanophrys*. *Journal of Mammalogy* **68**: 698–701.

Griffin, M. (1990). A review of taxonomy and ecology of gerbilline rodents of the Central Namib Desert, with keys to the species (Rodentia: Muridae). In: Seely, M.K. (ed.). *Namib Ecology: 25 Years of Namib Research*. Transvaal Museum: Pretoria.

Gromov, V.S. (2007). Spatial ethological structure and evolution of sociality in rodents. *Doklady Biological Sciences* **412**: 46–48.

Happold, M. (1976a). The ontogeny of social behaviour in four conilurine rodents (Muridae) of Australia. *Zeitschrift für Tierpsychologie* **40**: 265–278.

Happold, M. (1976b). Social behavior of the conilurine rodents (Muridae) of Australia. *Zeitschrift für Tierpsychologie* **40**: 113–182.

Hinze, A. (2005). Social behaviour and activity patterns of the African ice rat *Otomys sloggetti robertsi*. PhD thesis. University of the Witwatersrand: Johannesburg.

Jacobs, D.S. (2009). Animal personality and biological markets: rise of the individual. *African Zoology* **44**: 271–282.

Lacey, E.A. & Sherman, P.W. (2007). The ecology of sociality in rodents. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

Lancaster, J.L. (2009). Population and life history characteristics of coexisting small mammal species in a grassland habitat. PhD thesis. University of the Witwatersrand: Johannesburg.

Lott, D.F. (1991). *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge University Press: Cambridge.

Lötter, T.K. & Pillay, N. (2008). Reproduction and postnatal development of the bushveld gerbil *Gerbilliscus* (formerly *Tatera*) *leucogaster*. *Mammalian Biology* **73**: 430–437.

Madison, D.M. & McShea, W.J. (1987). Seasonal changes in reproductive tolerance, spacing, and social organization in meadow voles: a microtine model. *American Zoologist* **27**: 899–908.

McGuire, B. & Novak, M. (1984). A comparison of maternal behaviour in the meadow vole (*Microtus pennsylvanicus*), prairie vole (*M. ochrogaster*) and pine vole (*M. pinetorum*). *Animal Behaviour* **32**: 1132–1141.

Monadjem, A. (1999). Geographic distribution patterns of small mammals in Swaziland in relation to abiotic factors and human land-use activity. *Biodiversity and Conservation* **8**: 223–237.

Neal, B.R. (1991). Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae: Rodentia), in Zimbabwe. *Zeitschrift für Säugetierkunde* **56**: 101–111.

Neal, B.R. (1996). Reproductive response of *Tatera leucogaster* (Rodentia) to supplemental food, water, and 6-methoxybenzoxazolinone. *Mammalia* **60**: 651–666.

Neal, B.R. & Alibhai, S.K. (1991). Reproductive response of *Tatera leucogaster* (Rodentia) to supplemental food and 6-methoxybenzoxazolinone in Zimbabwe. *Journal of Zoology, London* **223**: 469–473.

Nel, J.A.J. (1975). Aspects of the social ethology of some Kalahari rodents. *Zeitschrift für Tierpsychologie* **37**: 322–331.

Nel, J.A.J. & Stutterheim, C.J. (1973). Notes on early post-natal development of the Namaqua gerbil *Desmodillus auricularis*. *Koedoe* **16**: 117–125.

Perrin, M.R. & Kotler, B.P. (2005). A test of five mechanisms of species coexistence between rodents in a southern African savanna. *African Zoology* **40**: 55–61.

Pillay, N. (1993). The evolution and socio-ecology of two populations of the vlei rat *Otomys irroratus*. PhD thesis. University of Natal: Durban.

Pillay, N. (2003). Reproductive biology of a rare African rodent, the water rat, *Dasymys incomtus*. *Journal of Mammalogy* **84**: 505–512.

Randall, J.A. (1994). Convergences and divergences in communication and social organisation of desert rodents. *Australian Journal of Zoology* **42**: 405–433.

Randall, J.A. (2007). Environmental constraints and the evolution of sociality in semifossorial desert rodents. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

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

Rautenbach, I.L. (1982). Mammals of the Transvaal. *Ecoplan Monograph* **1**: 1–211.

Sadleir, R.M.F.S. (1965). The relationship between agonistic behaviour and population changes in the deermouse, *Peromyscus maniculatus* (Wagner). *Journal of Animal Ecology* **34**: 331–352.

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

Schradin, C. & Pillay, N. (2003). Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*): laboratory and field evidence. *Journal of Comparative Psychology* **117**: 317–324.

Skinner, J.D. & Chimimba, C.T. (2005). *The Mammals of the Southern African Subregion*. (3rd ed.). Cambridge University Press: Cape Town.

Smithers, R.H.N. (1971). The mammals of Botswana. *Memoirs of the National Museums of Rhodesia* **4**: 1–340.

Smithers, R.H.N. (1975). *Guide to the Rats and Mice of Rhodesia*. Trustees of the National Museums and Monuments of Rhodesia: Salisbury.

Smithers, R.H.N. (1983). *The Mammals of the Southern African Subregion*. University of Pretoria: Pretoria.

Smithers, R.H.N. & Wilson, V.J. (1979). Check list and atlas of the mammals of Zimbabwe Rhodesia. *Museum Memoir of the National Museums and Monuments of Rhodesia* **9**: 1–147.

Solomon, N.G. (2003). A reexamination of factors influencing philopatry in rodents. *Journal of Mammalogy* **84**: 1182–1197.

Tang-Martínez, Z. (2003). Emerging themes and future challenges: forgotten rodents, neglected questions. *Journal of Mammalogy* **84**: 1212–1227.

Tchabovsky, A. & Bazykin, G. (2004). Females delay dispersal and breeding in a solitary gerbil, *Meriones tamariscinus*. *Journal of Mammalogy* **85**: 105–112.

Volodin, I.A. & Goltsman, M.E. (2002). Strategies of aggressive fighting reflect degree of sociality in three species of gerbils. In: Singleton, G.R., Hinds, L.A., Krebs, C.J. & Spratt, D.M. (eds). *Rats, Mice and People: Rodent Biology and Management*. ACIAR: Canberra.

Waser, P.M. & Jones, W.T. (1989). Heritability of dispersal in banner-tailed kangaroo rats, *Dipodomys spectabilis*. *Animal Behaviour* **37**: 987–991.

Waterman, J. (2007). Male mating strategies in rodents. In: Wolff, J.O. & Sherman, P.W. (eds). *Rodent Societies: An Ecological and Evolutionary Perspective*. The University of Chicago Press: Chicago.

Webb, P.I. & Skinner, J.D. (1996). Physiological adaptation to aridity in the bushveld gerbil, *Tatera leucogaster*. *Journal of Zoology, London* **238**: 693–701.

Wilson, V.J. (1975). Mammals of the Wankie National Park, Rhodesia. *Museum Memoir*

of the National Museums and Monuments of Rhodesia **5**: 1–147.

Wolff, J.O. (1985). Maternal aggression as a deterrent to infanticide in *Peromyscus leucopus* and *P. maniculatus*. *Animal Behaviour* **33**: 117–123.

Wolff, J.O. (2002). Density-dependence and the socioecology of space use in rodents. In: Singleton, G.R., Hinds, L.A., Krebs, C.J. & Spratt, D.M. *Rats, Mice and People: Rodent Biology and Management*. ACIAR: Canberra.

Zuri, I. & Rado, R. (2000). Sociality and agonistic behavior in the lesser white-toothed shrew, *Crocidura suaveolens*. *Journal of Mammalogy* **81**: 606–616.

APPENDIX A

GLOSSARY OF MAMMALIAN SCIENTIFIC NAME CHANGES

The following glossary lists the previous (as per the literature cited in the thesis) and new (as per Wilson & Reeder 2005) scientific names for mammal species used in this thesis that have undergone name changes:

Previous name	**New name**
Cricetulus griseus	*Cricetulus barabensis* or *C. migratorius*
Tatera afra	*Gerbilliscus afra*
Tatera brantsii	*Gerbilliscus brantsii*
Tatera inclusa	*Gerbilliscus inclusus*
Tatera leucogaster	*Gerbilliscus leucogaster*
Tatera nigricauda	*Gerbilliscus nigricaudus*
Rhabdomys pumilio (mesic populations)	*Rhabdomys dilectus*
Rhabdomys pumilio (xeric populations)	*Rhabdomys pumilio*
Otomys sloggetti robertsi	*Myotomys sloggetti*