Social behaviour and activity patterns of the African ice rat *Otomys sloggetti robertsi*

by

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

(Signature of candidate)

ABSTRACT

I studied the sociality and activity patterns of free-living ice rats O*tomys sloggetti robertsi*. The ice rat is a medium-sized, diurnal, herbivorous rodent, endemic to the alpine habitats of the southern Drakensberg and Maluti Mountains in southern Africa. These environments are characterized by sub-zero temperatures in winter and high levels of solar radiation in summer, and snow can be expected at any time of the year. Previous research by other scientists indicated that the physiology of ice rats is more similar to congeners living at lower altitudes, and, instead the taxon has morphological and behavioural adaptations for coping with the temperature extremes in its environment. Predator pressure on ice rats was negligible in my study site, making the ice rat an ideal model for testing how environmental factors influence sociality and activity patterns.

Sociality was investigated by using direct observations and through experimental manipulations. Colonies comprised 4-17 individuals with several reproductively active males and females. Colony members had a high degree of home range overlap, whereas interactions between colony members were rare and usually resulted in agonistic behaviour. Ice rats responded aggressively to experimentally-caged colony members positioned in different parts of their own colony and these were treated with the same level of aggression as were strangers. Moreover, colony members competed aggressively for better-quality introduced food, particularly in winter.

From direct observations of male-female interactions, it appeared that ice rats mate promiscuously, which is most likely a consequence of the multi-male and multi-female colonies. Females spent long periods of time belowground with unweaned young which emerged aboveground independently at four weeks of age. The first litter born in a season dispersed at sexual maturity (males±14 weeks; females±9 weeks), but, since I did not observe the behaviour of litters born later in the breeding season, I was not able to tell if these dispersed as well.

I excavated the burrow systems of ice rats and found an intricate interlinking underground tunnel system with sometimes more than 25 entrance holes and 1-2 nesting chambers, which would provide a thermoneutral refuge for the ice rats at night as well as during adverse weather conditions. Because the ratio of the number of animals in the colony to the number of nest chambers exceeded one, I predicted that huddling occurs belowground, which was confirmed by video recordings of nest chambers.

Diurnal aboveground activity patterns of ice rats were influenced by prevailing environmental conditions, which resulted in synchronous aboveground appearance of members in a colony. The summer activity pattern was bimodal, dominated by foraging and sun basking behaviour aboveground, with animals retreating belowground to escape high temperatures and radiation levels prevalent around midday. Ice rats utilized the warmer temperatures throughout the day in winter for aboveground foraging and basking.

Otomys s. robertsi displays a spatial shift in its social system: colony members huddle belowground but display temporal territoriality aboveground. Such a social system is contrary to predictions previously made for this taxon (i.e. they live as family groups). Ice rat relatives living at lower altitudes mainly occur as non-social aggregations and one relative, the vlei rat *O. irroratus*, also displays temporal territoriality. Although sociality is common in rodents inhabiting temperate environments in the northern hemisphere, these rodents do not show territoriality at other times. I conclude that the social system of ice rats, in the absence of significant predation pressure, is determined by a combination of 1) environmental factors driving communal thermoregulation and 2) phylogenetic constraints imposed by competition for limited food resources.

DEDICATION

I dedicate this thesis to Hagen Hinze-

without your continuous support and dedication in every way I would not have come this far.

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First and foremost I need to thank my supervisor Neville Pillay for his guidance and support throughout this project.Working together through different aspects of ice rat behaviour has taught me many things. I also want to thank my co-supervisor Stefan Grab for valuable input into my study by assisting me with the data collection of climatological and microhabitat data. Ute Schwaibold and I spent numerous days together at Sani Top, collecting data and trying to understand ice rat biology. Surviving the extremely cold nights in the Maluti Mountains would have been much more difficult to endure on my own! Jonathan Aldous and his staff at Sani Top always provided me with a warm fire and tried to make my stay at Sani Top as comfortable as possible. Many acquaintances were made in the Highest Pub in Africa, where tourists from all over the world always showed a keen interest in my study. I want to thank the numerous field assistances who helped me to collect the data that are presented in this study: Hagen Hinze, Tony Hibbits, Ruben Gutzat, Eben Meets, Claire Knoop, U. Schwaibold, R. Gutztat, Bongi Twala, Graig Marais and Stefan Muritz. My family stood by me throughout this project, providing me with support whenever necessary. Numerous drafts of the chapters were reviewed by Jack Harrington, Liz Wenzel and Hagen Hinze. I also want to thank the National Research Foundation (grant number: 2053514) and the University of the Witwatersrand for the funding of this project. I declare that the experiments comply with the current laws of the Republic of South Africa. Animal ethics clearance numbers: AESC 2000/21/2a, AESC 2002/12/2a.

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1 Introduction

1.1 Small mammals in temperate habitats

Small mammals inhabiting temperate environments experience short summers, with low primary productivity, during which time they need to maximise energy intake for reproduction and survival during harsh winters, which are characterised by limited food availability and low temperatures (Barash, 1974; Arnold, 1990b). Also, due to their small size, small mammals are subject to large convective heat losses (Chappell, 1980), which are exacerbated in winter. In response, small mammals have evolved several characteristics, including physiological, morphological and behavioural adaptations for life in temperate habitats. Physiological adaptations include hibernation and torpor (Ruf & Arnold, 2000; Barnes & Buck, 2000), metabolic and thermogenic acclimatization (Feist, 1984; Zegers & Merritt, 1984), and changes in body tissues, such as an increase in the quantity of brown body fat (Quay, 1984). Seasonal changes in the pelage, such as colour, thickness and length may be thermally beneficial in some rodents during winter, maximising retention of heat, as well as heat gain through solar radiation during the day (Chappell, 1980; Walsberg, 1988). Huddling with conspecifics is one of many behavioural adaptations (Canals *et al.*, 1989). Other adaptations include timing of activity during more favourable times (Türk & Arnold, 1988), selecting suitable microhabitats in heterogeneous environments (Whitney & Feist, 1984) and utilization of burrows to buffer temperature extremes (Chappell, 1980; Madison, 1984).

1.2 Social Systems

For researchers of animal behaviour, the study of differences in social organization has always been a fascinating topic (Lott, 1991). There are many reasons why animals live in groups and many why they do not. Understanding these reasons has been an ongoing challenge for behavioural biologists.

Social systems are determined by inter-individual social behaviour of conspecifics (Crook, 1965; Happold, 1976; Barash, 1989), which in turn influences the spatio-temporal distribution of individuals in animal societies. Social systems are subject to intrinsic (genetic) and extrinsic (environmental) influences, and may vary in time and space (Crook, 1965; Happold, 1976; Crook *et al.*, 1976; Standen & Foley, 1989). Social systems are therefore capable of evolutionary change and are adaptive (Barash, 1989), despite the fact that individuals of a society usually act to maximise their personal and/or inclusive fitness (Hamilton, 1964; Wilson, 1975). Social systems tend towards being either dispersed or communal (Eisenberg, 1967; Happold, 1976), depending upon whether individuals favour interactions that cause mutual attraction (e.g. amicable behaviour) or mutual repulsion (e.g. agonistic behaviour; Happold, 1976).

Asocial (territorial) systems are maintained by high levels of aggression between conspecifics, with amicable interaction restricted only to those periods when males and females meet for mating and to periods when females share a territory with unweaned young. Solitary social systems are often associated with a territory, an area inhabited by an individual from which it excludes conspecifics (Davies & Houston, 1984). In small mammals, territoriality occurs in response to spatial distribution, abundance and/or renewal rate of one or more resources (Ostfeld, 1990). If any resource is abundant and distributed evenly in the environment, the cost of defending it is too high relative to the fitness gained from the resource, so that territoriality will evolve if a resource is clumped and can be economically defended (Ostfeld, 1985, 1990). The availability of a resource may change seasonally and with this, the dispersion of a population (Ostfeld, 1990). There are costs associated with defending a territory (e.g. fitness may be lost due to an injury as a result of territory defence; Alcock, 1975).

In contrast, communal systems arise when interactions between conspecifics are predominantly amicable. Sociality can result from one or more of several selection pressures. A major motivation for animals to live in a group may be to minimise predation risk (Alexander, 1974; Hoogland, 1995; Armitage, 1998), for example through the dilution effect (Hoogland & Sherman, 1976). Therefore, group living often results in the development of a predator awareness system, where sentries and/or alarm calling may reduce the risk of predation (Alexander, 1974; Hoogland, 1995). Group living may also increase exploitation of a food resource (Alexander, 1974); for example, looking for a food resource in a group will sometimes yield faster results with less energy expenditure than hunting for food alone (Hoogland & Sherman, 1976). Social living can be promoted if resources are difficult to localise, such as sleeping places, mates or nesting sites (Alexander, 1974).

Although living in a group ultimately leads to an increase in fitness in individuals of many species, there are always costs associated with sharing the environment with other individuals. The major costs are usually associated with the sharing of resources (Alexander, 1974; Rubenstein, 1978; Ostfeld, 1990). Larger groups of animals are also more conspicuous to predators so that group living may in some cases increase the risk of predation. Other detrimental aspects of group living include misdirected parental care and a higher probability of parasite transmission (Alexander, 1974; Barash, 1974; Rubenstein, 1978; Hoogland, 1995).

Many types of social system exist between the two extremes, so that social systems are commonly viewed along a continuum, ranging from solitary animals to those that are eusocial (Wilson, 1975). Moreover, even within one species, social structure may vary spatially or seasonally (Ginsburg, 1978; Ostfeld, 1990; Lott, 1991; Salvioni & Lidicker, 1995) – the latter illustrating the dynamic nature of social organisation.

1.2.1 Sociality in temperate environments

The marmots (*Marmota* spp.) are ideal models for studying how small mammals cope with temperate climates and numerous studies have been conducted on this taxon (see Barash, 1989; Armitage, 1999). The 14 marmot species occur in the northern hemisphere at high altitude or latitude (Ferron, 1996), and all hibernate in winter (Arnold, 1990a, b). Because of the similarity in habitat type between marmots and my study animal, I review the social systems of marmots below to facilitate comparisons of social systems later.

The woodchuck *Marmota monax* is widely distributed at low altitudes in North America (Barash, 1974; Ferron, 1996). In the more southerly part of its distribution, it remains active throughout the winter season (Ferron, 1996). It is solitary throughout its range (Barash, 1974, 1989), even in the northern latitudes, and hibernates singly in well insulated hibernacula (Ferron, 1996). At higher elevations, where the growing season is shorter, the yellow-bellied marmot *M. flaviventris* lives in recognizable groups consisting of numerous adults, but individually distinct home ranges are maintained aggressively within the group, although occasional tolerance interactions occur, where individuals of a group meet without exhibiting agonistic behaviours toward each other (Barash, 1974; Armitage, 1999). During winter, yellow-bellied marmots hibernate in groups, increasing the chances of survival of all individuals in a group, especially the juveniles (Arnold, 1990a), which subsequently disperse as yearlings (Barash, 1974). The olympic marmot *M. olympus* inhabits high elevation alpine meadows, where the growing season is only 40 to 60 days long (Barash, 1974). Because of the shorter growing season coupled with more severe winters, offspring require comparatively more time to attain a body mass sufficient for successful dispersal and reproduction (Barash, 1974). As offspring accumulate body mass comparatively slowly, juvenile mortality rates are very high in winter, although communal hibernation with mature individuals improves survival rates (Arnold, 1990a, b). Therefore, the breeding pair tolerates its mature non-reproducing offspring in the hibernaculum for up to three seasons, resulting in highly amicable social systems (Barash, 1974; Arnold, 1990a, b; Armitage, 1999).

1.3 General biology of *O. s. robertsi*

In this section, I provide some aspects of the general biology of *Otomys sloggetti robertsi* which are essential for the aims of the study and interpretation of results presented in this thesis. Very little is known of this taxon, so, for comparison, I have also provided information on its closest relatives for which published information is available.

1.3.1 Phylogeny

The murid subfamily Otomyinae comprises two genera, the whistling rats *Parotomys* and the vlei rats *Otomys* (Meester *et al.*, 1986). The genus *Parotomys* is represented in southern Africa by two species, namely Brants' whistling rat *P. brantsii* and Littledale's whistling rat *P. littledalei*, both of which are endemic to the south-west arid zone of southern Africa (Skinner & Smithers, 1990). The genus *Otomys* includes species that are mainly adapted to mesic environments, such as the vlei rats *O. irroratus* and *O. angoniensis* which inhabit the eastern parts of the subregion (Skinner & Smithers, 1990). However, the bush karoo rat *O. unisulcatus* inhabits the drier parts of southern Africa, occurring syntopically with the whistling rats in parts of its range (Jackson & Spinks, 1998). Compared to the other otomyines, Slogget's rat *O. sloggetti* Thomas, 1902 is found at high altitudes, and comprises five subspecies (Meester *et* *al.*, 1986), of which the ice rat *O. s. robertsi* Hewitt, 1927 occurs at the highest altitudes (up to 3200m) and is endemic to the southern African Drakensberg and Maluti mountains (Roberts, 1951; Davis, 1974; De Graaff, 1981, Meester *et al.*, 1992). The ice rat is the only *O. sloggetti* that has been karyotyped (2n=42; Contrafatto *et al.*, 1992).

In terms of the phylogenetic relationships within the subfamily, evidence from allozyme electrophoresis (Taylor *et al*., 1989), immunoblot (Meester *et al*., 1992) and sperm morphology (Bernard *et al*., 1990, 1991) analyses shows a dichotomy between the arid species occurring in the western parts of southern Africa (e.g. *P. brantsii*, *P. littledalei*, *O. unisulcatus*) and the mesic species in the eastern parts (*O. angoniensis* and *O. irroratus*). Interestingly, *O. s. robertsi* groups with arid-living species despite living in eastern parts of southern Africa. However, recent mtDNA studies indicate that the position of *O. s. robertsi* within the arid group is equivocal, indicating that the phylogeny is as yet unresolved (Maree, 2002).

1.3.2 Description

The thick pelage of *O. s. robertsi* is predominantly reddish-brown, although the fur at the sides of the snout and behind the ear pinnae is a rusty-yellow colouring. Adults weigh 120-140g and grow up to 150-170mm in body length; males are 10% larger than females (Roberts, 1951; Willan, 1990). Compared to *O. irroratus* which is of similar size to *O. s. robertsi* but occurs at lower warmer altitudes, *O. s. robertsi* has a short tail (60-70mm vs 101-122mm) and small ears (16-17mm vs 19-25mm). However, the kidney of *O. s. robertsi* has a low medulla/cortex ratio and other characteristics indicating mesic physiological adaptation (Pillay *et al.*, 1994; see below).

1.3.3 Distribution and habitat

Otomys s. robertsi is confined to the cold subalpine (1830-2895m) and alpine (2860-3484m) phytogeographic belts (as defined by Killick, 1978). Richter *et al.* (1997) suggested that competitive exclusion between *O. irroratus* and *O. s. robertsi* has resulted in the allopatric distribution of these taxa along an altitudinal gradient, resulting in *O. s. robertsi* being restricted to altitudes higher than 2000m and *O. irroratus* below this altitude.

Otomys s. robertsi is abundant in suitable habitats, such as gently sloping ground and surface rocks, and they apparently avoid steep slopes, deep valleys and boggy areas (Willan, 1990). Colonies of ice rats construct underground burrows with several entrance tunnels, although they are also reported to nest in rock crevices (Willan, 1990).

1.3.4 Habits and diet

The name “ice rat” reflects the habit of sun basking during cold winter days when snow is on the ground (Skinner & Smithers, 1990). The ice rat is strictly diurnal, but aboveground activity appears to be influenced by ambient temperatures; during periods of extremely cold weather, ice rats do not emerge from their burrows, foregoing basking and foraging (Willan, 1990).

All otomyines studied are specialised herbivores, feeding almost exclusively on fresh green plant material, although some species eat fruit and flowers (Roberts, 1951; Nel & Rautenbach, 1974; Curtis & Perrin, 1979; Jackson, 1998). Field observations indicate that ice rats feed mainly on the floral parts, leaves and stems of grasses and herbaceous plants (Schwaibold, unpublished data).

1.3.5 Reproduction and sociality

Based mostly on anecdotal information, Willan (1990) maintained that the breeding season of *O. s. robertsi* occurs between March and October, and that population densities peak in autumn. Reproductive information is available only from a captive study by Willan (1990): the gestation period of ice rats was approximately 38 days; the mean litter size was 1.44 young (range 1-2); and young were born semi-precocial (weighing 10.6-12.2g) and nipple-clung from one of two pairs of inguinal nipples during the first few weeks of their life. Weaning occurred at 16 days of age and sexual maturity at 16 weeks in males and 11 weeks in females (Willan, 1990), which is delayed in comparison to *O. irroratus*, which achieves sexual maturity at eight weeks in males and four weeks in females (Davis & Meester, 1981).

Members of the Otomyinae display different forms of social organization. *Otomys irroratus* (Davis & Meester, 1981), *P. brantsii* and *P. littledalei* (Jackson, 1999, 2000) are solitary species. Three taxa are reported to live in small family groups, including *O. angoniensis*, *O. unisulcatus* (Skinner & Smithers, 1990) and *O. s. robertsi* (Willan, 1990).

1.3.6 Physiology

Richter *et al.* (1997) studied the effects of different ambient temperatures on the metabolism of *O. s. robertsi*. The metabolic rate of small mammals living under cold conditions is expected to be higher when compared to that of rodents of similar mass inhabiting a more hospitable climate (Koteja & Weiner, 1993). This is not the case for the ice rat, however, and its thermal conductance is higher than that predicted for a rodent living under such conditions. The resultant F-ratio (metabolic rate: thermal conductance) is 0.87, which is similar to many arid/warm adapted mammals. Oxygen consumption of *O. s. robertsi* decreases linearly with an increase in temperature between 0.7 and 26.0°C. Between 26.0 and 28.0°C the zone of thermoneutrality is reached, which again is unusually high for a rodent inhabiting a climate where it very seldom experiences such high temperatures. Experiments with injecting noradrenaline yielded results that were very similar to the oxygen consumption of *O. irroratus* (Richter *et al.*, 1997). The metabolic rate of the ice rat is too low to counteract the huge heat loss in its cold environment, particularly in winter. Therefore, the ice rat appears to be physiologically adapted to the warm mesic conditions such as those inhabited by *O. irroratus* (Pillay *et al.*, 1994).

Despite its physiological shortcomings, *O. s. robertsi* has evolved several behavioural and morphological adaptations to cope with the demanding conditions in its alpine habitats. Although sun-basking has been reported as being the main form of behavioural thermoregulation (Willan, 1990; Lynch & Watson, 1992), social huddling belowground has also been suspected to occur (Pillay, personal communication). Morphological adaptations include small appendages (tail, ear pinnae) and thick fur (Richter, 1997). Moreover, Schwaibold and Pillay (2003) reported that the gut morphology of *O. s. robertsi* shows broad similarities compared with other mesic- and arid-living otomyines, but that *O. s. robertsi* has a larger small intestine, caecum and stomach, adaptations which may facilitate increased energy uptake and/or ability to absorb nutrients and energy from the low quality foods available in their cold alpine environments. In addition, female ice rats increase the size of their small intestine in summer compared to winter, which apparently corresponds to times of greater energy need during the breeding season; male gut dimensions do not change seasonally (Schwaibold & Pillay, 2003).

1.4 Motivation and aims of the study

Erosion processes in the Maluti Mountains in the Kingdom of Lesotho, southern Africa, have been the focus of numerous geomorphological and climatological studies (Van Zinderen Bakker, 1984; Grab, 1999; Grab & Deschamps, 2004). Recently, researchers in the School of Geography, Archeology and Environmental Studies of the University of the Witwatersrand noticed a concerning increase in the rate of erosion, which coincided with atypically mild winters (S. Grab personal communication). Historically, overgrazing by domestic livestock, especially on the north-facing slopes and along stream banks, was suspected to be the main contributing factor for the erosion (Jacot-Guillarmod, 1963), but Grab (personal communication) hypothesised that the burrowing habits of *O. s. robertsi*, could also contribute to the erosion processes in the Lesotho highlands. This hypothesis was based on the increasing number of ice rats observed in recent times in suitable habitats.

Although predation is an important regulator of population numbers in many small mammals (Dickman, 1992; Lima & Dill, 1990), from my observations and those of Willan (1990), as well as anecdotal reports by Basotho shepherds at my study site, predation pressure on ice rats is minimal in summer and absent in winter. Instead, Willan (1990) and later Lynch and Watson (1992) maintained that the population numbers appeared to be regulated by density dependent mortality due to resource-limitation during the cold winters and prolonged periods of snowfall. Minimum temperatures in the Sani region have increased by as much as 3°C in the last 13 years (Lesotho Weather Service; Figure 1.1); maximum temperatures have remained more or less constant. Although snowfall data are not available, visitor reports at the Sani Top Chalet (5km from my study site) indicate a marked drop in the number of days with snow over the past decade. It is most likely that the greater numbers of ice rats in recent years

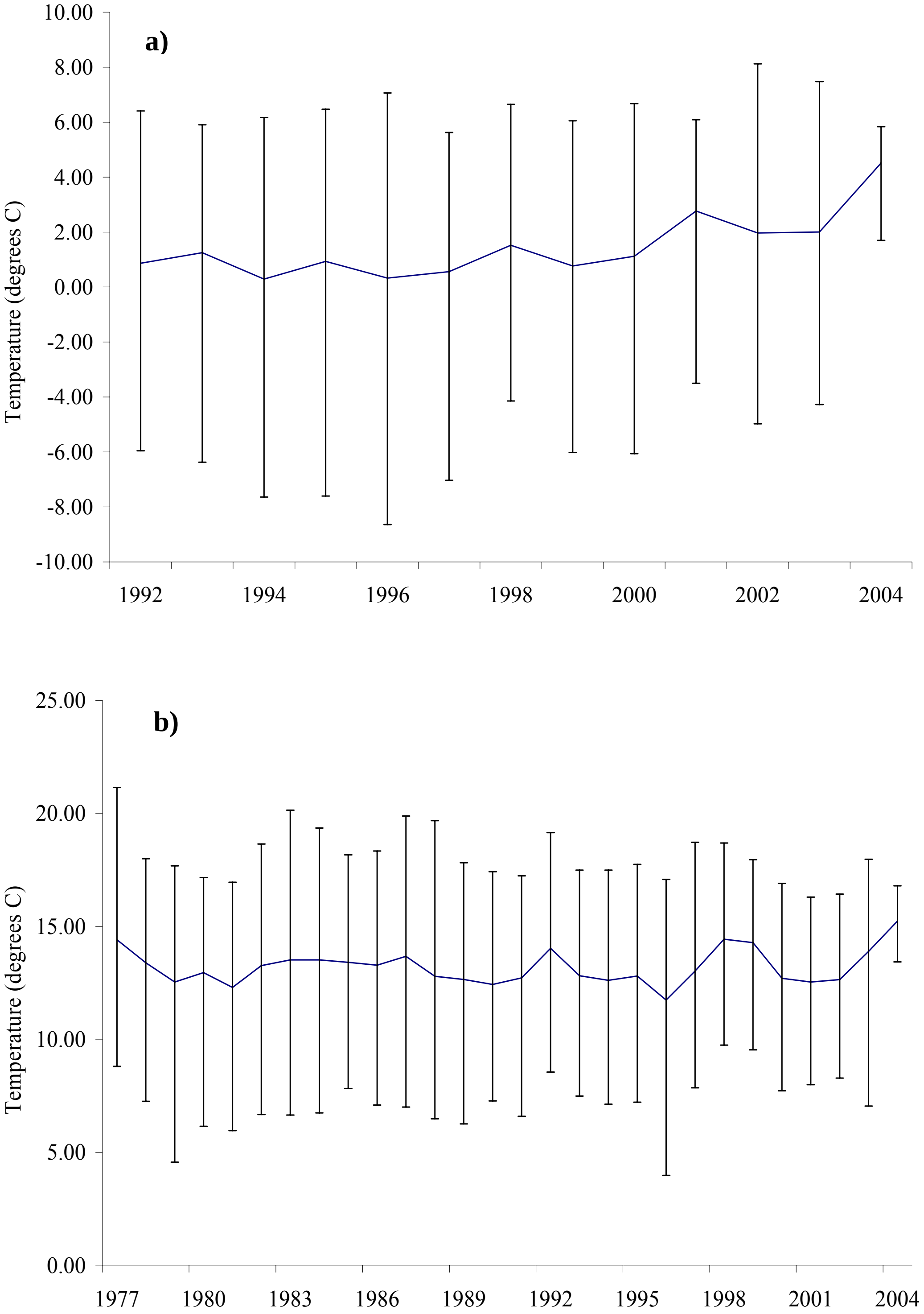

Figure 1.1 Mean ± (SD) of a) minimum and b) maximum ambient temperatures measured at Sani Top, Lesotho.

are related directly or indirectly to increasing temperatures and lower levels of snowfall. Unfortunately, no long term data are available for ice rat populations.

A joint project was initiated by the Schools of Animal, Plant & Environmental Sciences and Geography, Archaeology and Environmental Studies at the University of the Witwatersrand to investigate whether the ice rat contributed to erosion processes. At the outset, I realised that although *O. s. robertsi* is diurnal and easily observed in the field, very little is known about the subspecies. This in part may reflect the remote locations it inhabits. Therefore, there was a need to study the biology of *O. s. robertsi*, including its social biology, particularly given the apparent increase in population size (see Macdonald, 1979).

In the absence of high predation levels, which influence the social behaviour of many small mammals (Ostfeld, 1985, 1990), the ice rat is an ideal model for studying how environmental factors such as seasonal climatic change and resultant differences in physiological demands in summer and winter, influence the social behaviour of an alpine rodent. Some information regarding its physiology and metabolism (Richter *et al.*, 1997) and reproduction (Willan, 1990) is available from captive studies. Based on the social behaviour of ice rats in captivity, as well as personal observations, Willan (1990) predicted that *O. s. robertsi* is colonial with a clumped dispersion.

Because of their cryptic habits, it is often challenging to conduct detailed behavioural studies on small mammals in nature. Therefore, much of my knowledge about the social organization of small mammals has been reported from indirect trapping techniques (Wallen, 1982; McGuire & Getz, 1995; Salvioni & Lidicker, 1995). However, there is always a danger that the results of such studies are artefacts of the trapping protocol or the laboratory conditions. Nonetheless, extensive field studies have been conducted on three diurnal African small rodents: *P. brantsi, P. littledalei* (Jackson, 1999, 2000) and the striped mice *Rhabdomys* *pumilio* (Schradin, 2004; Schradin & Pillay 2004, 2005). The social organization and behaviour of these species was investigated by directly observing known (i.e. marked) individuals in nature. All studies revealed distinct differences in their social organization from previously published descriptive studies. For example, *P. brantsii* was thought to be gregarious due to their clumped distribution, but Jackson (1999) revealed that they are solitary. Also, *R. pumilio* was originally described as a solitary species (Schradin & Pillay, 2004), although their social organization is flexible and changes from social to solitary depending on food availability (Schradin & Pillay, unpublished data).

The primary aim of my study was to investigate the social organisation of *O. s. robertsi* in its natural habitat. I therefore conducted field observations of the behaviour of ice rats, resulting in four chapters. In Chapter 2, I conducted several experiments to investigate the social organization of ice rats. The emphasis here was how ice rats use space, interact with colony members and strangers and compete for experimentally introduced food. This is the first time that the social organization of ice rats has been studied in any detail and my study attempted to understand how the behaviour of ice rats is influenced by seasonal variations in environmental conditions. Chapter 3 provides information about the demography and reproduction in ice rats, and considers some of the important social biology that would influence colony formation and persistence. Comparisons are also made with other members of the Otomyinae to examine the influences of both environmental conditions and phylogeny on demography, reproduction and social behaviour of ice rats. In Chapter 4, I provide a quantitative analysis of the burrow structure of ice rats, which differs from previous studies which only described the burrow system (see Willan, 1990). The aim here was to document whether ice rats dig complex burrows like their desert-living relatives *P. brantsii* and *P. littledalei* (Jackson, 2000) and whether there was any evidence of communal nesting belowground. I again include a comparison with some of the other members of the family to understand environmental and phylogenetic influences of the burrow systems and the social behaviour of the ice rat. Chapter 5 examines the aboveground activity patterns of ice rats and the aims here were to establish the main aboveground activity patterns, and to ascertain how prevailing environmental conditions in addition to social phenomena such as social facilitation or alarm calling influence ice rat behaviour

1.5 Study Area

The kingdom of Lesotho is located in the highlands of the Maluti/Drakensberg massif, which gives rise to the highest mountain peaks in southern Africa and is the source of the Senqu River system. The Maluti Mountains comprises an ancient basaltic plateau with intermittent deep valleys, resulting in soil depth that is inversely proportional to the gradient (Killick, 1978). The vegetation comprises mainly *Helichrysum* species on the mountain slopes, while several flowering plants, such as *Haplocarpa nervosa, Trifolium burchellianum, Saniella verna, Limosella vesiculosa, Cotula paludosa* and *Ranunculus multifidus* are found within the wetlands. My study area was located in the Sani Valley within the Maluti Mountains, which is relatively easily accessible through the Sani Pass. The ice rat colonies selected for study were located in and around a wetland (29°33’ S, 29°14’ E) in one of the Sani tributary valleys, 5km west of the Sani Top border post between South Africa and Lesotho at an altitude of about 2800m. Mean air temperatures in the Sani Valley range from 0°C in winter to 10°C in summer, with a mean annual temperature of approximately 6°C. Ambient air temperatures regularly drop to below 0°C in winter and in summer often plunge to around 0°C between sunset and sunrise (Grab, 1997). The mean annual precipitation is over 1200mm, occurring mainly as snow (Killick, 1963). The growing season is relatively short (October to April) compared to lower lying regions (September to May) and primary productivity is low (Willan, 1990).

1.6 Arrangement of the thesis

This thesis is divided into the present, introductory chapter, a general discussion and conclusion chapter (chapter 6) and the main body, comprising four experimental chapters (chapters 2-5). The experimental chapters are written as manuscripts for publication, of which chapters 4 and 5 have been submitted for publication in their current form to Mammalian Biology and Arctic Antarctic and Alpine Research respectively. Because of the format used, there is some repetition of introductory material and methodological detail. The figures and tables are numbered in sequence for each chapter and not for the complete thesis. Each chapter has its own reference section, and the pages of the thesis are numbered sequentially.

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2 Is the African ice rat *Otomys sloggetti robertsi* truly social?

2.1 Introduction

Group living and the associated levels of agonistic and amicable behaviours within a group have been documented in numerous small mammals (Barash, 1974; Ostfeld, 1990; McGuire *et al.*, 2002; Asher *et al.*, 2004; Schradin & Pillay, 2004). For group living small mammals, recognition of familiar conspecifics, i.e. members of the group, is a common characteristic (Johnston & Jernigan, 1994) and as the level of recognition decreases, levels of agonistic behaviour increase (Wallen, 1982). Therefore, the frequency and intensity of agonistic interactions within a group of individuals provide a good indication of the degree of sociality found within that group (Ostfeld, 1985a, b).

Generally, living in a group has been associated with high levels of amicability and low levels of agonistic interactions (Barash, 1974), although this may depend on whether the group is despotic (e.g. house mouse *Mus musculus domesticus*; Gerlach, 1998) or egalitarian (African striped mouse *Rhabdomys pumilio*; Schradin, 2004; Schradin & Pillay, 2004); amicability is common in egalitarian societies. There are usually fitness costs associated with group living, such as increased parasite transmission, infanticide, conspicuousness to predators and competition for resources, such as food and mates. The benefits gained through living in a group can be increased protection against predators, shared care of young and defense or exploitation of food resources (Madison, 1984; Ostfeld, 1990; McGuire *et al.*, 2002).

Another reason for group living is communal thermoregulation (e.g. huddling). The social organization of rodents inhabiting temperate environments is often seasonally labile. For example, meadow voles *Microtus pennsylvanicus* (Madison *et al.*, 1984) and taiga voles *M. xanthognathus* (Wolff & Lidicker, 1981) aggregate into groups during winter, but these disband, with individuals maintaining separate territories during the breeding season in order to monopolize resources. Such social flexibility is an adaptive response to thermoregulatory stress caused by harsh winter conditions. However, not all temperate rodents show such flexibility, for example, alpine marmots *Marmota marmota* (Arnold, 1990a) and golden marmots *M. caudate aurea* (Blumstein & Arnold, 1998) hibernate as a group in winter and maintain their groups in summer through complex social behaviour (Barash, 1974).

One reason for solitary living is competition for limiting resources, especially food (Ostfeld, 1985b, 1990). Resource requirements may vary between males and females and thereby influence the degree of sex-specific territoriality. During the breeding season, the main resource for females is food due to the high energy demands of pregnancy and lactation (Ostfeld, 1985b; Ims, 1987). Females also maintain territories to protect their offspring from infanticide (Wolff & Cicirello, 1989). The reproductive success of males is usually limited by the availability of sexually active females, so males either compete for females directly or defend resources critical to females (Ostfeld, 1985b, 1990).

The ice rat, *Otomys sloggetti robertsi*, is a medium-sized (121-143g), diurnal herbivorous rodent, endemic to the harsh alpine and subalpine phytogeographic belts, exceeding 2000m altitude in the southern Drakensberg and Maluti Mountains in southern Africa (Killick, 1978; Willan, 1990). Unlike rodents inhabiting similar temperate environments in the northern hemisphere, such as the alpine marmot, *M. marmota* (Ruf & Arnold, 2000), *O. s. robertsi* is poorly adapted physiologically to its alpine habitats; they do not hibernate or go into bouts of torpor during cold conditions, and its physiology resembles that of its congeners that inhabit the warmer climates at lower altitudes in southern Africa (Richter *et al.*, 1997). To cope with these demanding conditions, ice rats have several morphological adaptations, such as small ear pinnae, a short tail and thick fur. Behavioural adaptations include sun basking and timing of aboveground appearances during the warmest (winter) and cooler (summer) times of the day (Willan, 1990; Richter, 1997; Schwaibold & Pillay, 2003; Hinze & Pillay, in review, Chapter 5). Another behavioural adaptation may be social huddling belowground, which was first alluded to by Willan (1990), based largely on the social nature (i.e. aggregations of ice rats in colonies) in nature and in laboratory observations, as well as recent observations in the field (Pillay, personal communication). *Otomys s. robertsi* colonies contain up to 17 individuals that inhabit an area of approximately 1200m^2. Importantly, intricate interlinking underground tunnel system with sometimes more than 25 entrance holes and 1-2 nesting chambers, located 280–357mm beneath the surface, provide a thermoneutral refuge for the ice rats at night as well as during adverse weather conditions (Hinze *et al.*, in review; Chapter 4). Because the ratio of the number of animals in the colony and the number of nest chambers exceeds one, it is likely that huddling occurs belowground, and recent video recordings of nest chambers have also provided evidence of huddling in free-living *O. s. robertsi* (Pillay & Hinze, unpublished data).

An important prerequisite for huddling is tolerance among colony members (Barash, 1974), and thus one would expect a high degree of sociality among ice rats in a colony. Indeed, Willan (1990) provided anecdotal information that agonistic behaviour between *O. s. robertsi* colony members is rare in nature. However, in pilot studies, I rarely observed social interactions among free-living ice rats aboveground, and apart from mother and offspring groups, I observed largely agonistic behaviour between individuals regardless of colony affiliation. This suggests that *O. s. robertsi* maintains non-overlapping territories, where individuals within a group defend resources against group members within the home range of the group. Because sociality in the ice rat is unresolved, this study aimed to investigate the aboveground social behaviour and organisation of free-living ice rats through direct observations and by using experimental manipulations to observe the reactions of colony members to strangers or introduced food. I investigated sociality in summer and winter to establish whether social behaviour and social organisation vary seasonally.

2.2 Methods and Materials

2.2.1 Study area

This study was conducted in the Sani Valley in the Maluti Mountains, Lesotho (29°33’ S, 29°14’ E). Ice rats were studied for approximately 400 hours from 2000 to 2003, in summer and in winter; approximately 200 hours per season. All groups of *O. s. robertsi* studied were located within or on the edges of a 4ha wetland surrounded by gentle slopes. The study site was situated at an elevation of 2800m and received a mean annual precipitation of 1200mm, often occurring in the form of snow (Killick, 1963). The mean annual temperature in the Sani Valley is 6°C, with mean ambient temperatures ranging from 0°C in winter to 10°C in summer (Grab, 1997). In summer, flowering plants are abundant in the wetland, and comprise mainly *Haplocarpa nervosa*, *Trifolium burchellianum*, *Saniella verna*, *Limosella vesiculosa*, *Cotula paludosa* and *Ranunculus multifidus*. The surrounding slopes support several types of *Helichrysum* bushes. Much of the vegetation dries out in winter due to the colder and drier conditions prevalent in the Maluti Mountains.

2.2.2 Trapping and marking

Ice rats were trapped in metal live-traps (26 x 9 x 9cm), baited with a mix of fruits and vegetables (e.g. apple, cucumber, lettuce and spinach). Traps were set during early mornings and late afternoons when ice rats are at their most active. The traps were checked every 30 minutes. Trapped animals were weighed to the nearest gram, sexed, and adults were fitted with a uniquely coloured plastic cable tie (length 200mm, width 4.7mm) neck band. Females were fitted with a white neck band and males with a black one. A distinctive colour combination of insulation tape was taped on the neck bands for individual identification. Animals were then released at the point of capture. Collared individuals that were trapped later in my study did not show any signs of distress or injury due to the neck bands, except two animals that presented some chafing around the collar, which were removed subsequently. These trapping and marking procedures were approved by the Animal Ethics Committee of the University of the Witwatersrand (Clearance Number 2000/21/2a).

2.2.3 Behavioural observations

Observations were made of the social interaction of ice rats in eight different colonies with 10 x 50 binoculars. Colonies were defined as a group of individuals occupying a communal burrow system as per Willan (1990). Using continuous sampling, I recorded any instances of social interaction (e.g. agonistic and amicable) within one colony by using a notebook and stopwatch. In addition, group size and composition were also recorded.

Observations were conducted when the ice rats where active (i.e. between 05h00 and 11h00 and between13h30 and 17h30 in summer and during the entire day in winter from 09h00 to 15h00; Hinze & Pillay, in review, Chapter 5) from vantage points approximately 3-5m from a colony. Ice rats are easily observed in nature because the vegetation in their alpine habitats is mostly short (<0.5cm) and they habituate quickly (usually within 5 minutes) to the presence of observers.

2.2.4 Space use and home range determination

I studied the space use of collared individuals in five colonies in summer and winter, by recording their locations within their colony. Each colony was marked off into 4m by 4m grid squares, the corners of which were demarcated with clearly visible coloured pegs (30cm high) to serve as landmarks. Observations of focal animals were made directly, using 10 x 50 binoculars, a notebook and stopwatch for 4-7 hours each season, when the ice rats were most active. I observed 25 females and 15 males in summer and 15 females and 12 males in winter.

To calculate the space use of an animal during observations, I recorded the square in which the individual was located at the start of the session and then all subsequent squares into which the focal ice rat moved. When the focal individual travelled belowground within the burrow system of the colony, I noted the square containing the burrow into which it had disappeared and the square with the burrow from which it reappeared. I determined the home-range size of animals by using the minimum polygon method (Kenward, 1987; Asher *et al.,* 2004), because it is widely used in establishing the home range of rodents (Madison *et al.*, 1984; Tew & Macdonald, 1994) and therefore provides a number of comparative studies (Sterling *et al.*, 2000). In addition, the minimum polygon methods was used in a study of another rodent (i.e. *Rhabdomys pumilio*) which has a fixed nest site (Schradin & Pillay, 2005). The number of squares (4 x 4m) and half grids within this convex polygon was summed to calculate the home-range size in square metres. For my calculations, I excluded obvious excursions (i. e. rare visits of greater than 20m from the cluster of other recordings for a focal rat). The percentage home range overlap among individuals of a colony was also calculated, as well as incidences of temporal overlap.

2.2.5 Reaction to colony members and strangers

The responses of colony members to a single familiar or strange ice rat were investigated in summer and winter. Stimulus subjects were sexually mature (>100g). Immediately after capture, the ice rat was placed in a closed wire cage (w=30cm; l=45cm; h=30cm; mesh: 3 x 1cm) and subsequently positioned into a colony (i.e. either its own or a different one). Cages were thoroughly cleaned with 70% alcohol and air-dried after each trial to remove odours from the previous occupants. All stimulus subjects were used only once.

Tests were conducted in one of three different locations, resulting in three treatments: (1) *home* - the cage with the stimulus subject was placed in exactly the same spot where the subject was trapped; (2) *member* - the cage with the stimulus subject was placed in the colony but at least 10m away from where it was captured; and (3) *stranger* - the cage with the stimulus subject was placed in a different colony, located at least 70m away from its home colony.

A total of 145 stimulus individuals were used, comprising at least eight male and eight female subjects in each of the treatments per season, where each individual was only subjected to the same experimental conditions once. Each test lasted 20 minutes and started once one or more ice rats in a colony showed a general movement towards the cage. The duration of agonistic (e.g. boxing, bar biting) and tolerance (sitting in close proximity) behaviours by colony inhabitants directed towards the stimulus subject were recorded (Martin & Bateson, 1993) using a notebook and stopwatch. Tests were conducted when most of the colony was above ground; ice rats in a colony have synchronous above ground appearance (Hinze & Pillay, in review, chapter 5). As a control, the empty cage was placed at 10 random sites within a colony per season and observed as described above.

Since only minimal direct contact was possible through the wire mesh, no injuries were seen in any stimulus subjects after experiments. Stimulus subjects were released at their site of capture.

2.2.6 Competition for food

To induce competition for food sources within an ice rat colony, one fresh medium-sized apple cut into small pieces or an equivalent amount of fresh cucumber were placed in the centre of one of four different colonies selected for the study. Apple and cucumber were used because of their high water and sugar content, and they were highly preferred by ice rats in pilot studies. Like other members of its subfamily, *O. s. robertsi* does not drink free-standing water and instead obtains moisture from the food it consumes (Pillay *et al.*, 1994).

Social interactions were recorded within the focal colony from the moment an individual ice rat showed a general movement towards the introduced food item. Observations were conducted, using a notebook and stopwatch, for one hour on each occasion, and 1/0 sampling with a one-minute time interval was used to record the frequency of all agonistic interactions (e.g. boxing, chasing other colony members away) that occurred within a metre of the introduced food, as well as agonistic interactions more than 1m away from the food source. I also recorded all instances of amicability (e.g. huddling, grooming) within the colony; amicability was never observed at the food source. Three replicates were made per colony per season, with each trial at least 24 hours apart and under similar weather conditions. As a control, I replaced the introduced food with vegetation, which was abundant in the colonies and which ice rats normally consumed; the volume of this vegetation was similar to that of the introduced food source.

2.2.7 Data analysis

I tested the data sets for departure from normality and used parametric or non-parametric analyses when appropriate. Data for the space use and home range overlap were tested for sex and seasonal differences using the Mann-Whitney U analyses, and significant values were adjusted using Bonferroni analyses. Kruskall-Wallis and Dunn's *post-hoc* tests were used to analyse the data for the reactions to colony members and strangers. Data for the competition for food manipulation experiments were arcsine transformed and subsequently analysed with a general linear model. Tukey *post hoc* tests were used to test for specific differences. All tests were two-tailed and α was set at 0.05.

2.3 Results

2.3.1 Behavioural observations

Observed colonies (N=8) ranged in size from 4 to 17 adult individuals, with a mean±SE of 8.36±1.45. The number of adults in colonies varied from one male and one female to multiples of both sexes. Ice rats are very difficult to trap and therefore the number of collared individuals within a colony varied from 20% to 80% between field trips. Social interactions were rare within an ice rat colony. In approximately 400 hours of behavioural observations in summer and winter, interactions between colony members were observed on about 30 occasions. Of these, 4 comprised interactions where two individuals sun basked alongside each other, and usually comprised a mother and her offspring. Allogrooming was only observed once. Agonistic interactions were observed 25 times (3% of the total time observed) and mainly consisted of two individuals boxing briefly and ending in one individual chasing the other for some distance (up to 12m); no damaging fights were observed. Agonistic interactions were observed significantly more often than tolerance between individuals

(Z=3.47, N=30, p<0.001; Sign Test). Individuals of a colony always foraged alone (N=8 colonies, p<0.05; Sign Test).

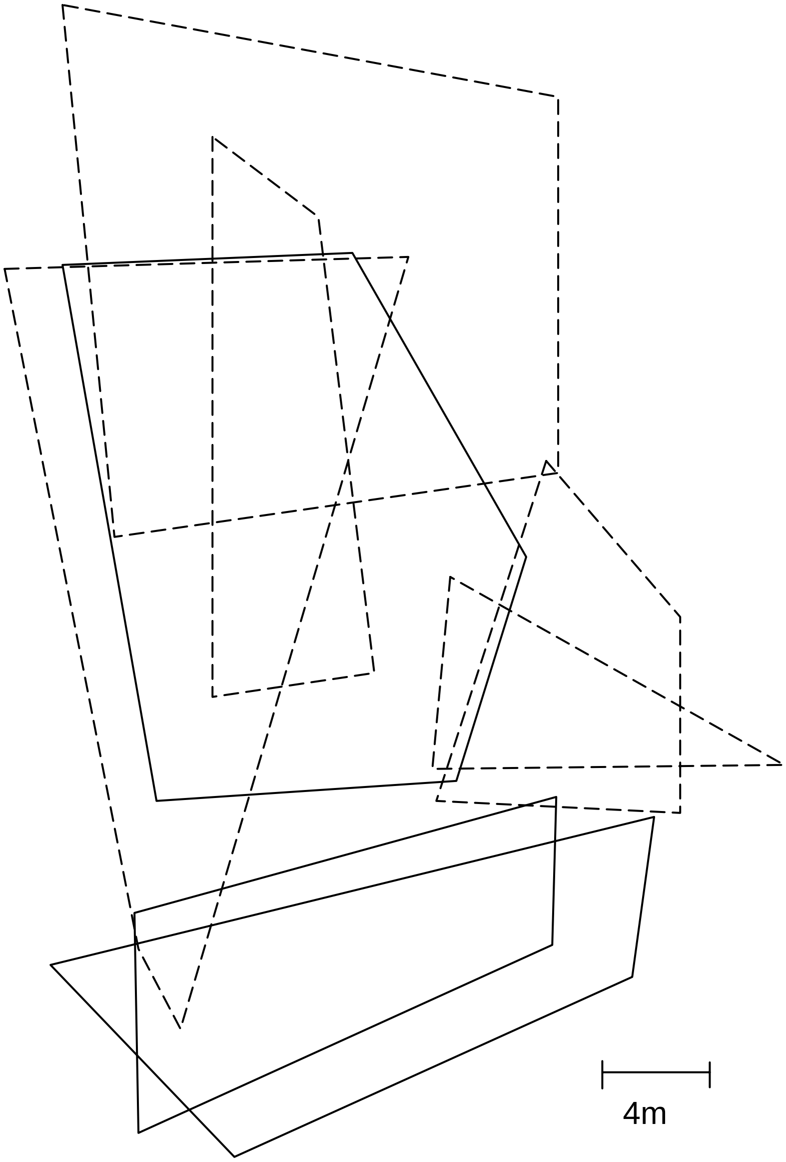
2.3.2 Space use

Home range size was significantly larger in summer than winter for both males (mean±SE: summer=280.94±47.68m^2, winter=135.28±20.85m^2; $U_{15, 12}$=144.5, p=0.015) and females (453.18±50.29m^2, winter=197.65±52.67m^2 $U_{25, 15}$=302, p=0.001). It was not significantly different between the sexes in winter ($U_{12, 15}$=126, p=0.110), but females had significantly larger home ranges in summer than males ($U_{15, 25}$=227 p=0.021). Home ranges of ice rats in a colony overlapped to large degree (Figure 2.1), but there were no significant seasonal differences in the percentage for males (summer=48.48±13.33%, winter=58.37±14.78%; $U_{13, 10}$=54, p=0.629) and females (summer=56.59±10.12%, winter=49.71±14.95%; $U_{18, 12}$=122, p=0.163). There were also no differences in the overlap between the sexes in summer ($U_{13, 18}$=145 p=0.217) and winter ($U_{10, 12}$=68, p=0.417). Although there was a high degree of spatial overlap within a colony, there was very little temporal overlap, and in 302 hours of observation, only four instances of temporal overlap were noted in both seasons, all leading to agonistic behaviour (see also behavioural observations above).

2.3.3 Reaction to colony members and strangers

The empty cage was largely ignored in summer (Figure 2.2a) and only one incidence of cage biting was observed in winter (Figure 2.2b). Tolerance behaviour towards stimulus individuals occurred at low levels and was directed only at stimulus females at the site where they were captured (Figure 2.2); I did not include data for tolerance behaviour in further statistical analyses. Agonistic behaviour was common, directed mainly at stimulus subjects placed elsewhere in their own colony or in another colony. Neither the sex of the stimulus subject nor the season of sampling influenced aggression levels in any of the three treatments ($p>0.05$; Kruskall-Wallis tests). However, there were marked treatment effects in both summer ($H_{3, 74}=8.34$, $p=0.039$) and winter ($H_{3, 71}=11.56$, $p=0.009$). *Post hoc* tests revealed two groupings in respect to aggression levels: equally low when the stimulus subject was placed at the site of capture (one incidence) and when the cage was empty; and equally high when the stimulus

a)



b)

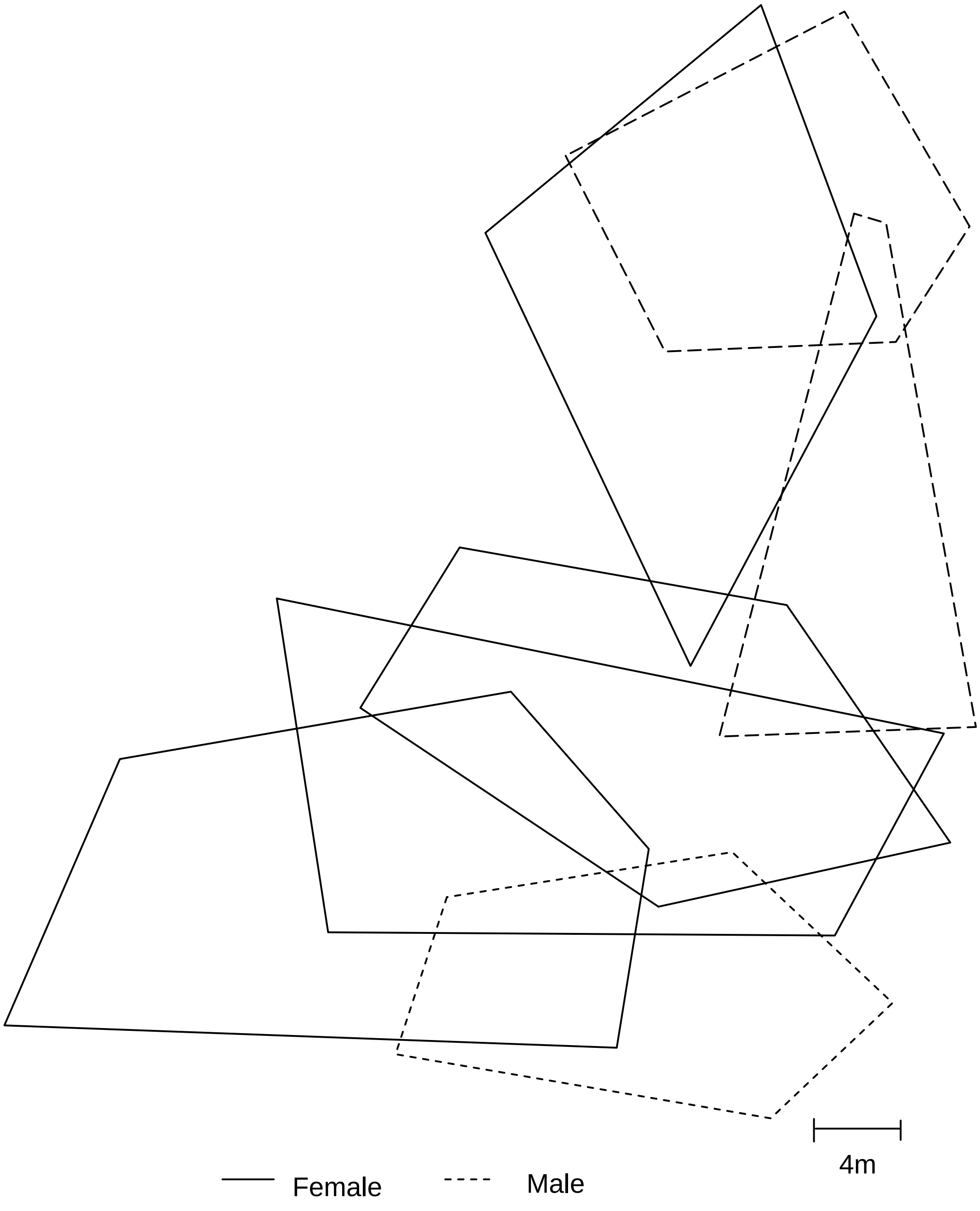


Figure 2.1 Space use and home range overlap of individuals within an *O. s. robertsi* colony in a) winter (3 females, 5 males) and the same colony in b) summer (4 females, 3 males). Females are indicated by solid lines, males by dashed lines.

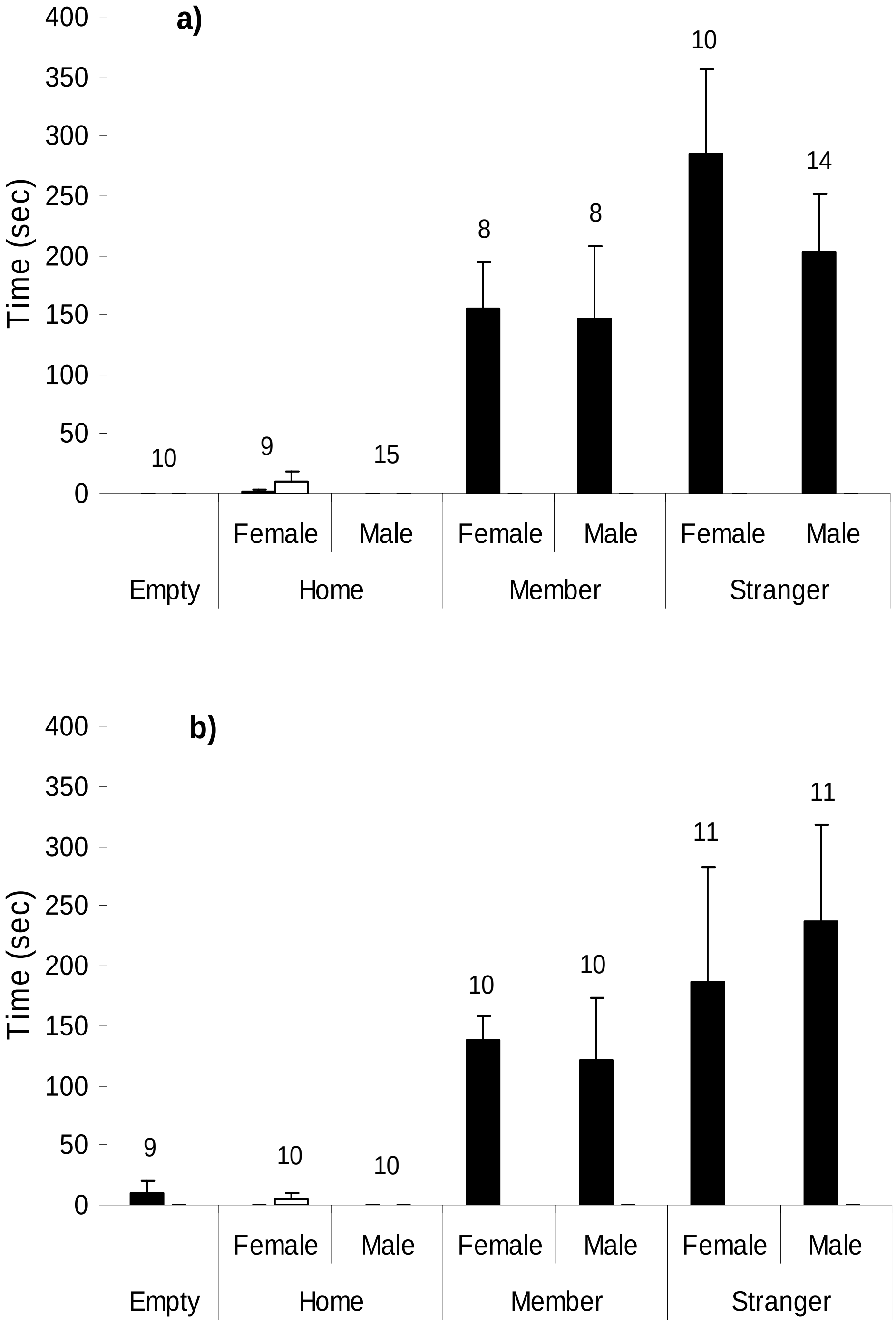
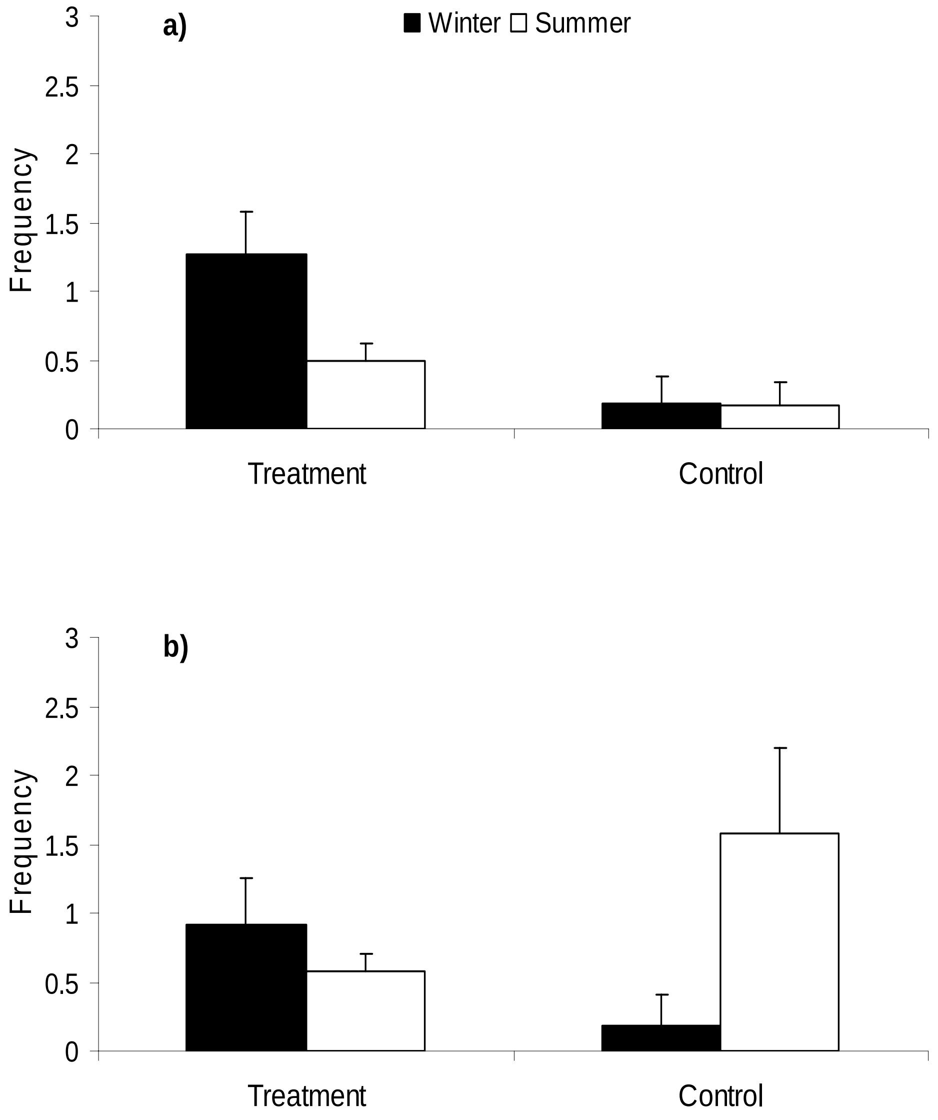


Figure 2.2 Mean (±SE) duration of agonistic interactions by colony members towards stimulus subjects (home, member and stranger) at the wire cage in summer a) and winter b). Sample sizes are given above the bars. Black bars represent agonistic behaviour and the white ones tolerance behaviour.

subject was a stranger or placed elsewhere in its own colony. No analyses regarding sex specific reactivity towards caged stimulus animals were done, and I could not tell with certainty the sex of the colony member/s interacting with the stimulus subject.

2.3.4 Competition for food

I found no difference in the levels of aggression at the introduced food between the seasons ($F_{1, 42}$=3.34, p=0.75), but significantly more aggressive interactions were observed when apple and cucumber treatments were introduced than during controls ($F_{1, 42}$=12.91, p<0.001; Figure 2.3a). Such agonistic interactions consisted mainly of one individual chasing another colony member away from the introduced food. The treatment appeared to influence the behaviour of the individuals only in the immediate vicinity of the introduced food, as the levels of agonistic behaviour beyond a radius of 1m of the introduced food remained unaffected ($F_{1, 42}$=0.13, p=0.72; Figure 2.3b). Although tolerance behaviours between members of a colony were rare (see above), they were recorded more often in winter than in summer ($F_{1, 42}$=14.24, p<0.001; Figure 2.3c). Ice rats appeared to be more tolerant during the treatments ($F_{1, 42}$=4.08, p=0.050) than during the controls (Figure 2.3c), but instances of tolerance behaviour were never observed in the immediate vicinity of the introduced food. The probability that the introduced food sources was approached by an ice rat was higher than an ice rat approaching the control of vegetation ($F_{1, 42}$=48.48, p<0.001) and more so in winter than in summer ($F_{1, 42}$=12.70, p<0.001; Figure 2.3d). During winter, approximately 10% of the introduced food was consumed aboveground, and the rest was carried belowground. In summer, when abundant fresh vegetation was available in the wetlands and surrounding areas, the ice rats consumed and hoarded only about 40% of the introduced food.


a)
■ Winter ☐ Summer
Frequency
3
2.5
2
1.5
1
0.5
0
Treatment
Control
b)
Frequency
3
2.5
2
1.5
1
0.5
0
Treatment
Control

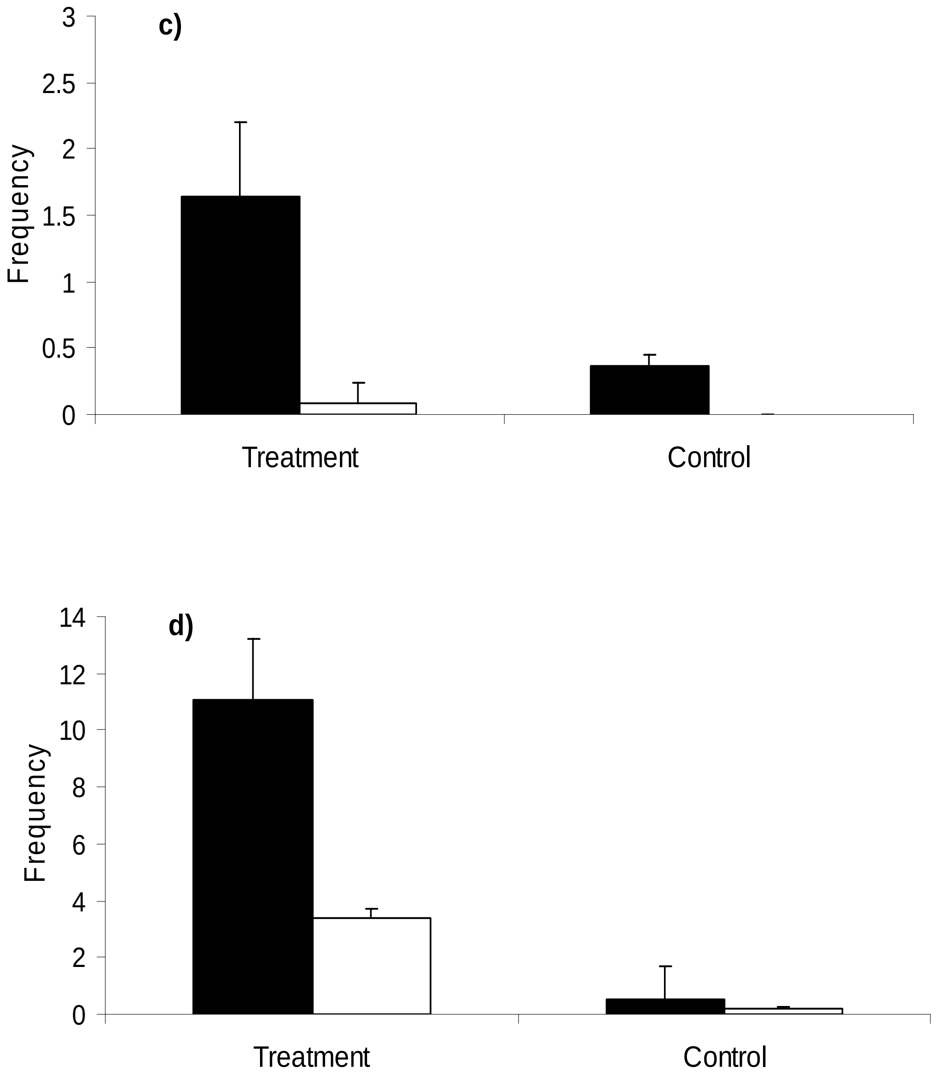


Figure 2.3 Mean (±SE) frequency of four behaviours displayed by *O. s. robertsi* when a food source (treatment) and surrounding vegetation (control) were introduced into colonies in winter (black bars) and summer (white bars). a) agonistic interactions at the food source, b) agonistic interactions beyond a 1m radius of the food source, c) tolerance behaviour in the colony, and d) approaching food source. Sample sizes: N=11 for winter and N=12 for summer.

2.4 Discussion

Our results indicate that while the dispersion of *O. s. robertsi* was typically clumped (see also Willan, 1990) and members in a colony had overlapping home ranges, they rarely interacted with one another aboveground and most interactions were agonistic. Ice rats were as aggressive to colony members as they were to strangers from other colonies, and colony members competed aggressively for introduced food.

Ice rat colonies comprised several adult males and females with sex ratios varying between colonies and seasons. Based on the social behaviour of captive *O. s. robertsi*, Willan (1990) predicted that individuals sharing a burrow system are family groups comprising a founding pair and their non-reproductive offspring. Although I did not know the relationships between colony members, all members were reproductively active during the summer, suggesting that the social system was multi-male and multi-female. A similar social system was observed in the prairie vole (*Microtus ochrogaster*) which forms communal groups during times of high population density, and, during the breeding season, two or more adults of each sex of a group were reproductively active (Getz *et al*., 1993; Lowell & McGuire, 1997).

The home ranges of ice rats from one colony overlapped to a large extent but colony members rarely met aboveground. Such a system is typical of animals that display temporal territoriality, as defined by Leyhausen (1965), and is also observed in a close relative of *O. s. robertsi*, the vlei rat *O. irroratus* (Davis, 1972), which occurs in the same geographical region but at lower, warmer altitudes. Temporal territoriality occurs in *O. irroratus* when conspecifics use the same home range but at different times, and is a behaviour that reduces the possibility of damaging conflict between neighbours (Willan, 1982)

I used artificial procedures (caged animals) to increase the probability of observing interactions between colony members and between strangers (see also Schradin, 2004 for similar procedures), as interactions under natural conditions were very rare. Ice rats mainly ignored or were sometimes tolerant to colony members caged at the site of capture, but those displaced within the colony were attacked and treated in the same way as strangers from other colonies. These reactions resemble the territorial behaviour of the whistling rat *Parotomys brantsii*, where each individual defends a territory within the warren of a group (Jackson, 1999). The potential for aggression is likely to cause mutual avoidance (Manning & Dawkins, 1998) and may explain why I observed so little social interaction and temporal overlap during 400 hours of observation.

Since an important determinant of territoriality in small mammals is the defence of limiting resources (Ostfeld, 1985b, 1990), territoriality in *O. s. robertsi* in winter may be related to poor food quantity and quality. Indeed, ice rats in a colony competed aggressively for the experimentally introduced, better quality food. While there was little interest or competition for the introduced food in summer when there was sufficient natural vegetation available, ice rats nevertheless maintained territories. There may be two mutually non-exclusive reasons for territoriality in summer. Firstly, the alpine habitats inhabited by ice rats are characterised by short growing seasons (Willan, 1990) and it is possible that ice rats need to defend territories during summer to obtain sufficient energy for reproduction. Secondly, reproductively active females defend territories to avoid infanticide of unweaned offspring by strangers (Wolff, 1993), and reproductive males might defend territories from other males in order to gain access to receptive females (Ostfeld, 1985b, 1990); the importance of these factors should be investigated further.

Otomys s. robertsi foraged alone which may also be a reflection of avoidance behaviour. In addition to the house mouse *Mus musculus* (Gerlach, 1998), communal nesting and solitary foraging has been reported in the African striped mouse *Rhabdomys pumilio* in arid environments and is thought to be an adaptation to foraging for patchily distributed food, and to minimize predation risk (Schradin & Pillay, 2004). Similarly, despite having a wide diet of green food plants, ice rats feed selectively from particular food patches, preferring wetland sedges to grasses (Schwaibold, unpublished data), which may also explain why they forage alone.

Ice rats display territoriality aboveground although they live in distinct colonies (see also Willan, 1990). Whereas temporal (usually seasonal) variation in social organisation has been reported for some other rodents (see West & Dublin, 1984), *O. s. robertsi* is unusual since its social organisation changes spatially from below to aboveground. The dusky-footed woodrat *Neotoma fuscipes* displays a similar spatial variation in sociality, but, contrary to ice rats, nests alone and seeks direct contact with conspecifics outside its own nest to maintain social knowledge of individuals in the group (Wallen, 1982). The yellow-bellied marmot *M. flaviventris* inhabiting temperate environments also lives in recognizable groups, consisting of numerous adults, but individuals maintain distinct home ranges within the group aggressively, although occasional amicable interactions occur (Barash, 1974; Armitage, 1999).

I suggest that the main driving force for group living in *O. s. robertsi* is communal thermoregulation through social huddling. Because *O. s. robertsi* is poorly adapted physiologically to its cold environment, huddling belowground is likely to lead to thermoregulatory benefits, particularly in winter (Hinze & Pillay, in review, Chapter 5). Likewise, the evolution of sociality in alpine marmots (*Marmota marmota*) is thought to be a result of group hibernation and social thermoregulation; adaptations to the long, cold winters (Arnold, 1990a, 1990b; Armitage, 1999). One cost of group living in *O. s. robertsi* is that colony members compete for food within the colony and, unlike the marmots, they maintain territories aboveground.

Predation risk, which promotes group living in many small mammals (Ostfeld, 1990; McGuire *et al.*, 2002) may not influence group living in *O. s. robertsi*. From my observations and those of Willan (1990), as well as anecdotal reports by Basotho shepherds at my study site, predation pressure on ice rats is minimal in summer and virtually absent in winter, and I have never observed ice rats displaying the behaviours typical of small mammals prone to high predation risk, such as sentries (black-tailed prairie dogs, C*ynomys leucurus*; Loughry, 1993) and alarm calls (marmots, e.g. *Marmota olympus* - Barash, 1975). I also rule out limited space availability as a cause of group living, which influences group living in two close relatives of ice rats, the desert-living Brants' *P. brantsii* and Littledale's *P. littledalei* whistling rats (Jackson, 1999). In spite of the presence of numerous abandoned burrows, ice rats never occurred in groups of less than four individuals throughout my study.

Under particular environmental conditions, group living may be viewed as a behavioural adaptation that increases the fitness of the individuals sharing the environment with other group members (Barash, 1974; Armitage, 1981, 1999). For *O. s. robertsi*, fitness may be a compromise between thermoregulatory benefits through communal huddling and competition for resources, mainly food. Temporal territoriality in *O. s. robertsi* could be a phylogenetic constraint, since it also occurs in the vlei rat *O. irroratus* (Willan, 1990), a species resembling *Prototomys* the Pliocene ancestor of the modern Otomyinae (Pocock, 1976). Like *Prototomys, O. irroratus* is adapted to warm mesic habitats (Willan, 1990). Therefore, group living in *O. s. robertsi* may be a more recent adaptation for life in the harsh alpine regions which it inhabitats.

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3 Demography and reproduction in the African ice rat *Otomys sloggetti robertsi*

3.1 Introduction

Studying social systems has always fascinated animal behaviourists, particularly due to their adaptive nature in response to particular environmental stimuli (Happold, 1976; Barash, 1989; Manning & Dawkins, 1998). However, social systems are not static but can vary spatio-temporally (Lott, 1991) and, even within species, they can vary along a continuum from solitary on the one extreme to social on the other (McGuire & Getz, 1998). Therefore, one of the challenges of studying social systems has been to document most of the components that contribute to a system over a period of time (Happold, 1976). These components include mating systems, population demography, population dispersion and spacing behaviour, and intragroup social behaviour (Deag, 1980).

Documenting the social systems of rodents is difficult because of their cryptic habits. Therefore, most studies have been done in captivity or by the use of indirect techniques in the field, such as trapping and radio-telemetry (Wallen, 1982; McGuire & Getz, 1995; Salvioni & Lidicker, 1995; Eccard *et al*. 2004). However, the results of captive studies of social behaviour (and inferred social organisation) could be artefacts of the optimal environmental conditions in the laboratory, and while they may provide an indication of a potential social system (i.e. along a continuum; Lott, 1991), they may represent an extreme condition. Likewise, indirect methods in the field may underrepresent population size estimates and thus social systems (Schradin & Pillay, 2003). Nonetheless, there have been some studies that have investigated social systems of rodents directly in the field (see Barash, 1974; Jackson, 1999; Schradin & Pillay, 2005), all of which have involved diurnal rodents living in comparatively open habitats.

The ice rat *Otomys sloggetti robertsi* is also a diurnal murid rodent inhabiting open habitats (vegetation < 50cm) in the southern Drakensberg and Maluti Mountains. It is restricted to the cold, harsh sub-alpine and alpine environments exceeding an altitude of 2000m (Willan, 1990). Ice rats have a low metabolic rate and high thermal conductance, very similar to its mesic congeners (e.g. vlei rat *O. irroratus*) inhabiting warmer climates at lower altitudes, suggesting that the ice rats are poorly adapted physiologically to the extreme environment it inhabits (Richter *et al*., 1997). Unlike other alpine rodents, ice rats do not hibernate or display bouts of torpor (Ruf & Arnold, 2000, Barnes & Buck, 2000). Instead, they have some morphological (e.g. small ear pinnae and a short tail), as well as behavioural adaptations (e.g. huddling and sun basking; Hinze *et al*., in review, Chapter 4; Hinze & Pillay, in review, Chapter 5). *Otomys s. robertsi* is a strict herbivore, feeding on a variety of green plants (Schwaibold & Pillay, 2003). Ice rats live in colonies which construct complex burrow systems that buffer temperature extremes externally (Hinze & Pillay, in review, Chapter 4).

Based on the results of captive studies, Willan (1990) proposed that a colony of ice rats consists of a breeding pair and their offspring, which overwinter in a non-reproductive state with their parents, thereby investing in somatic development and improving the probability of survival. Such a social system seemed plausible since it is also found in another alpine rodent, the alpine marmot *Marmota marmota* (Arnold, 1990; Ruf & Arnold, 2000). However, I questioned the validity of Willan's (1990) prediction based on the findings of an earlier study of space use and social interactions of free-living ice rats (Chapter 2). I reported that ice rats live in colonies of up to 17 individuals, comprising several reproductively active males and females. Although members of an ice rat colony huddled belowground and their home ranges overlapped spatially aboveground, colony members avoided one another aboveground (i.e. their territories did not overlap temporally). Moreover, individuals responded aggressively to experimentally-caged colony members positioned in different parts of their own colony and these were treated in a similar way as strangers, and colony members competed aggressively for better quality introduced food, particularly in winter. I concluded that ice rats exhibit a spatial variation in social structure and are social belowground because of a thermoregulatory need for social huddling and solitary aboveground possibly due to competition for limiting food resources.

In this study,Iinvestigated three components of the social system of *O. s. robertsi* that were previously unknown and which would facilitate testing of Willan’s prediction. These included population demography, female-male interactions to establish the mating system, and female reproductive behaviour, postnatal development and dispersal.

3.2 Materials and Methods

3.2.1 Study site

The study was conducted on a 4ha study site in the Sani Valley (29°33’ S, 29°14’ E) in the southern Drakensberg, Lesotho, at an altitude of 2800m. Mean temperatures range from 0°C in winter (May to August) to 10°C in summer (September to April, which is the primary plant growing season) and the mean annual precipitation is approximately 1200mm (Killick, 1963; Grab, 1997). Although most of the precipitation falls during summer, snow can fall during any time of the year. The study area was located in and around a wetland, containing numerous flowering plants, such as *Haplocarpa nervosa, Trifolium burchellianum, Saniella verna, Limosella vesiculosa, Cotula paludosa* and *Ranunculus multifidus*, whereas the vegetation on the slopes was predominantly composed of *Helichrysum* sp.

3.2.2 Demography

Ice rats were trapped using metal live traps (26 x 9 x 9cm), baited with a mixture of fresh apples and vegetables (cucumber, spinach, lettuce) and salt. Data were collected during monthly trapping sessions from January 2000 to December 2002. Each session lasted between 10-14 days.

I trapped in 10 colonies situated in the wetland as well as on the slopes surrounding the wetland. It is usually customary to place traps in a grid formation or along traplines (Mabry *et al.*, 2003; Yamaguchi & MacDonald, 2003; Smith & Nichols, 2004), but these methods are inappropriate for ice rats because of the irregular distribution of colonies. Instead, I randomly placed traps near burrow entrances to improve the chances of capturing ice rats. Traps were set mainly in the mornings and evenings (i.e. when aboveground activity was greatest) and were monitored to reduce the time that animals spent in a trap.

Ice rats were removed immediately after they had entered the traps and weighed (to the nearest 0.1g) and measured (head-body, tail, ear and hind foot measurements to the nearest 1mm). Reproductive activity was indicated by scrotal testes in males and by a perforate vagina or lactation (prominent nipples from which milk could be expressed) in females. All adults were fitted with a unique colour-coded cable tie (length 20cm, width 4.7mm) neck band. Males were fitted with black neck bands and females with white ones, on to which I taped combinations of different coloured insulation tape for individual recognition. Excess cable tie was cut off and the ice rats were released at the point of capture. During subsequent recaptures, the collars of two individuals had to be removed due to chafing. While collared individuals were easily recognised in the field (see Chapter 2), I was concerned that if animals lost their collars in-between trapping sessions (once in pilot studies), I would overestimate population sizes. Therefore, ice rats were also toe-clipped using standard protocols (see Wood

& Slade, 1990; Braude & Ciszek, 1998; McGuire *et al.*, 2002). All these procedures took less than 5 minutes and individuals were released at the point of capture.

To assess changes in population size within a colony over time, the maximum number of colony members in four similar sized colonies (1450-1643m^2) was recorded during every field trip over two years (January 2000 to December 2001); the three colonies were situated no less than 100m apart. For these data, I recorded the number of individuals in a colony regardless of whether or not they had collars. To avoid overestimating the number of individuals I counted individuals only during early mornings and late evenings when ice rats are most active aboveground and the synchrony of appearance within ice rat colonies resulted in most members of a colony being aboveground at those times (Chapter 5). I then calculated the number of individuals in a colony by averaging the counts at three different times during each trip.

3.2.3 Female-male interaction

Our previous studies indicated that ice rat colonies comprise multi-male, multi-female groupings and that aboveground interactions between colony members are rare (Chapter 2). Five colonies were selected for study, located at least 50m apart; these colonies were not part of the demography study (above). Radio tracking technology was not available and therefore to improve the probability of observing mating behaviour the activity of 3 collared females and 2 collared males per colony at the start of the breeding season in August 2000 and again in August 2001 were recorded.

The behaviour of colony members of the five colonies was noted directly on data sheets using 10 x 50 binoculars for more than 500 hours. Initially, I sampled behaviour using scan sampling with a 5 minute interscan interval during the main activity periods (see Chapter

5) of ice rats from a raised vantage point about a metre away from the colonies; ice rats habituate very quickly to human presence. When intersexual interactions were observed between collared females and males (either collared or not; adult males are bigger than adult females and have a more distinct ruff), I initiated focal sampling of the focal female for the rest of the entire day and sometimes on the next day. For focal males, scan sampling was considered adequate for the aims of the study.

The number of males visiting focal females and the number of females which focal males visited were recorded, as well as the frequency of aggressive (i.e. upright sparring, chasing, fighting), tolerance (sitting in close proximity, mutual grooming) or mating behaviour.

3.2.4 Female reproductive behaviour, postnatal development and dispersal

When I observed mating or potential mating (see results) by focal females, focal sampling of the behaviour of these females was continued weekly for four weeks (i.e. a week before parturition; gestation is 38 days; Willan, 1990). The duration of the samples was limited to between one to four hours per day, depending on the time the focal female spent aboveground. Behavioural observations were made only during the active periods of the ice rats (see above). Pregnancy was confirmed visually by the greatly distended abdomen of focal females. In the week preceding parturition, daily focal recordings were made of the percentage of time the focal females spent aboveground and the percentage of time when plant material was taken belowground. I intended to continue with the daily recordings after parturition (which was estimated from the day that females had an obviously more slender profile) until the pups emerged aboveground. Since ice rat pups nipple-cling for the first weeks of life and the young are weaned at 16 days of age in captivity (Willan, 1990), I expected to see females with nipple-clinging young soon after parturition and weaned young approximately three weeks after birth. However, juveniles were first observed aboveground 4-5 weeks after birth, well after weaning, so for logistical reasons I used scan sampling to record behaviour in the second week after parturition until the young were observed aboveground, at which time I recorded litter size for the first time. Thereafter, I monitored all the juveniles for four hours spread over one week for the next three months, and recorded all instances of social interactions between litter mates, as well as between juveniles and the mother. Within that period each juvenile was observed between approximately 20 minutes to one hour depending on how long the juvenile remained aboveground. In particular, I calculated the percentage of amicable and aggressive social interactions. The distances juveniles moved beyond their natal burrow in relation to their age were also recorded as an approximate measure of natal dispersal. Juveniles were generally trap-shy, but when some entered traps, they were toe-clipped and their body mass and reproductive condition were recorded. Juveniles were not fitted with neckbands until they reached sexual maturity, but were recognised because of their association with focal females. The observation of litters and juveniles in this study were limited to the beginning of the breeding season.

3.2.5 Data analysis

Data sets were tested for departure from normality. The following non-parametric analyses were used: Friedman Anova (Fr); Mann-Whitney U test (U), and Wilcoxon matched pairs sign test (W). Students t-test was the only parametric test used. All tests were two-tailed and α was set at 0.05. Unless otherwise stated, the data are presented as mean±SE.

3.3 Results

3.3.1 Demography

Population size - A total of 298 different individuals (143 males and 155 males) were trapped from January 2000 to December 2000. The distribution of captures by sex and age is provided in Figure 3.1. Juveniles were trapped during the summer season only. The number of individuals in four colonies over two years was also recorded to investigate changes in colony sizes. These changed significantly over two years in all four colonies ($Fr_{4,23}=50.18$; $p<0.001$; Figure 3.2), and were highest in summer (September to April) and lowest in winter (May to August). Interestingly, the number of individuals in the colonies I monitored never exceeded 17 individuals and never dropped below four individuals. Overall, the highest population density was 101.92±6.50 animals/ha (January 2001) and lowest population density was 52.30±2.25 animals/ha (July 2000).

Breeding season - Most adult females (individuals weighing > 100g; Willan 1990) were reproductively active during summer, whereas the majority of females trapped in winter were non-perforate ($\chi^2_{11}=37.37$, $p<0.001$; Figure 3.3). Not all males trapped in summer where reproductively active, although significantly more males were reproductively active in the summer than in the winter months ($\chi^2_{11}=19.67$, $p=0.05$; Figure 3.3).

Changes in body mass - Figure 3.4 provides the monthly mass of adult females and males trapped during my study. Females were heavier during the breeding season in summer (143.47±4.34g) than in winter (123.22±3.64g; $t_{154}=2.03$, $p=0.025$; Figure 3.4). In contrast,

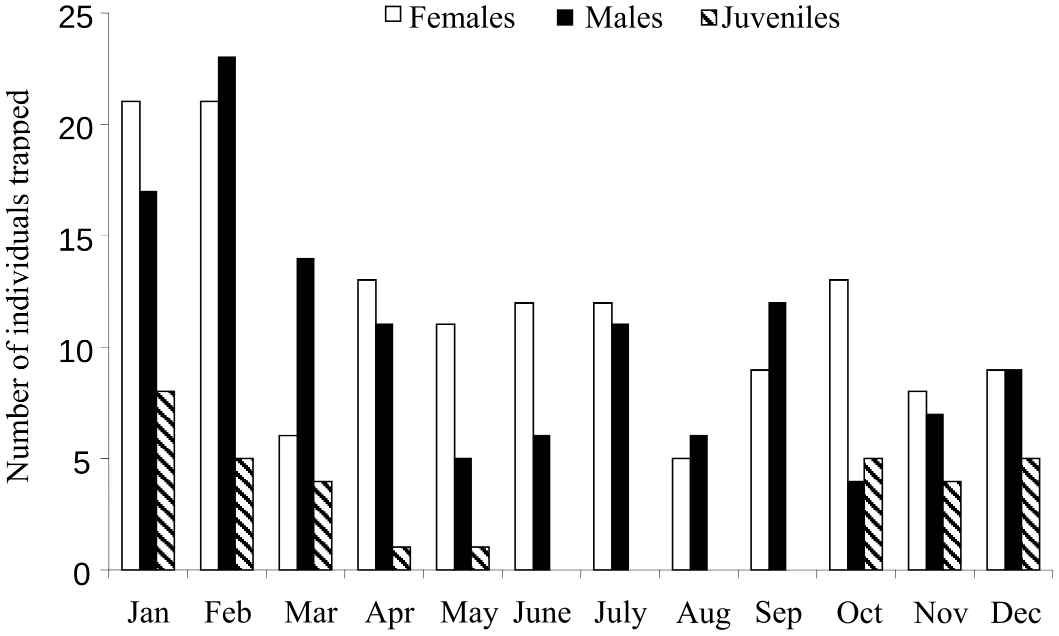

Figure 3.1 The number of female, male and juvenile *O. s. robertsi* trapped during each month of January 2000 to December 2000.

males maintained their weight throughout the year (summer vs winter – 144.65±4.35g vs 145.19±4.48g; t_{142}=-0.23, p=0.59).

Sexual dimorphism - The body mass and body measurements of females and males during the non-breeding season (winter) were compared to avoid the confounding effects of pregnancy. Males were significantly heavier than females in winter (145.19±4.48g vs (123.22±3.64g; t_{91}=3.88, p<0.001; Figure 3.4). In addition, males had longer hindfeet (25.21±0.26 vs 24.87±0.31 mm; t_{91}=2.69, p=0.003) and tails (53.54±1.24 vs 50.56±1.26 mm, t_{91}=3.05;

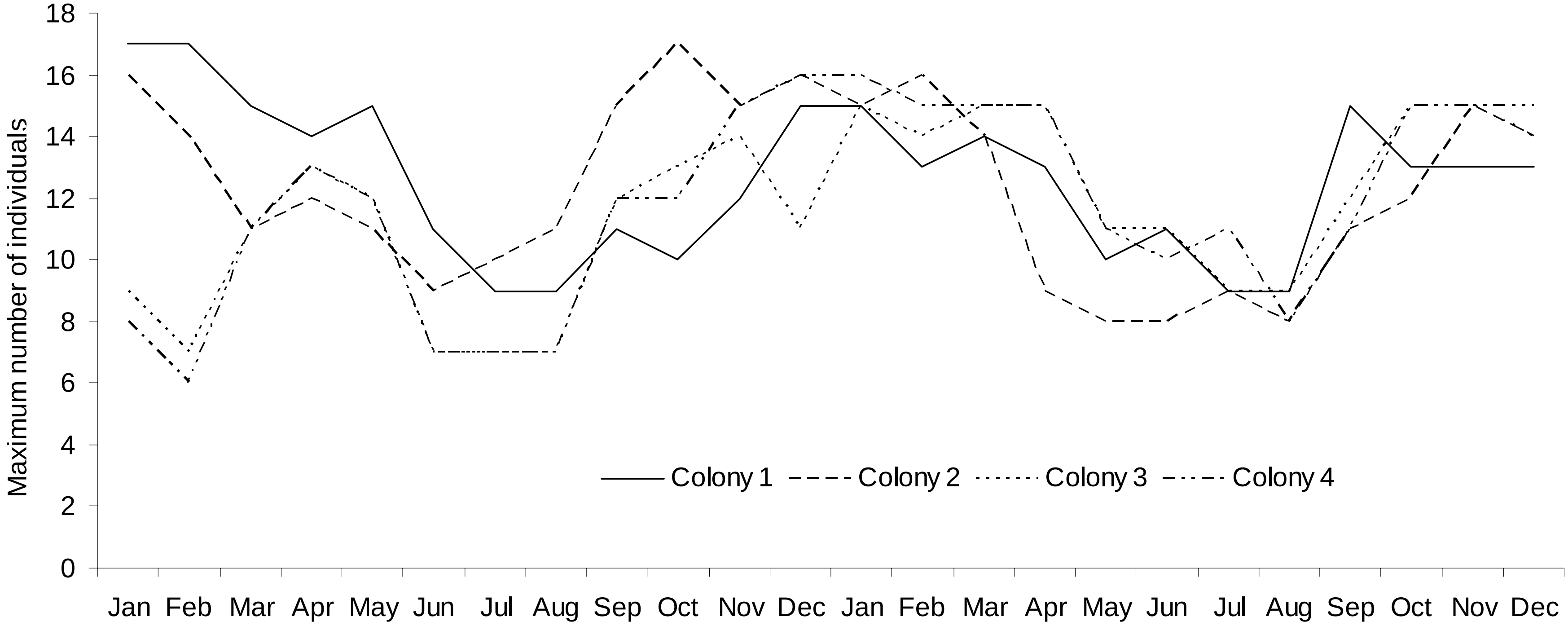

Figure 3.2 Changes in population numbers over two years (January 2000 to December 2001) in four different *O. s. robertsi* colonies.

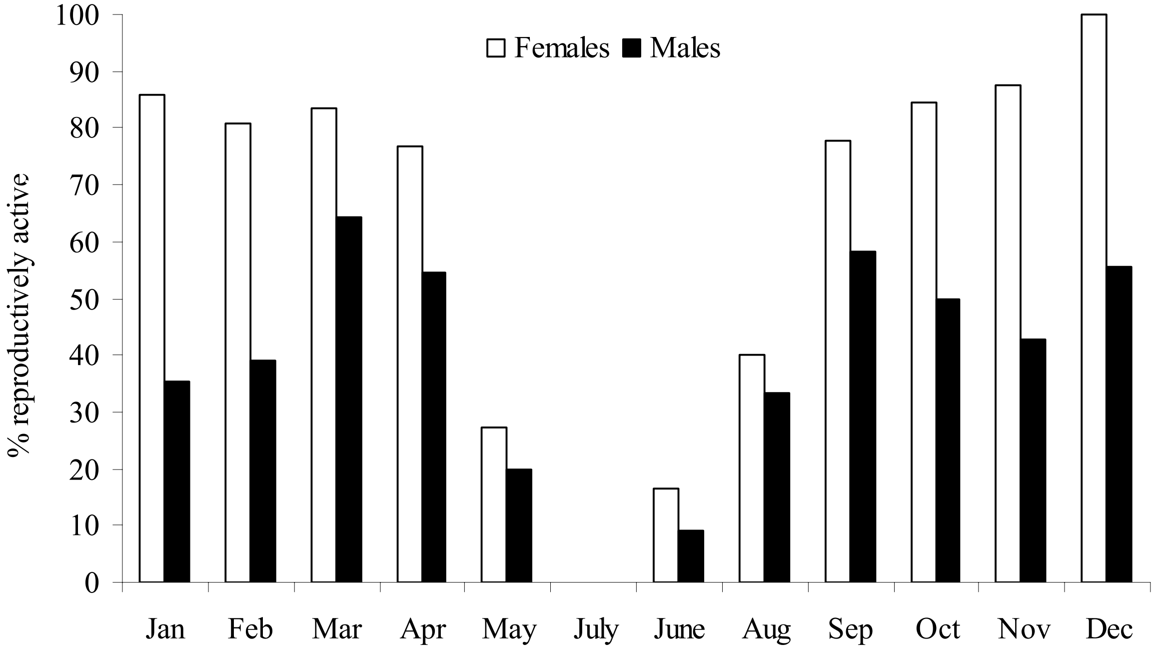

Figure 3.3 Percentage *O. s. robertsi* adults (>100g) that were reproductively active in 2000. Sample sizes as in Figure 3.1.

p=0.002) than females. The sexes had similar head-body (males vs females: 153.84±3.13mm vs 153.17±2.92mm, t_{91}=-0.33, p=0.632) and ear lengths (15.11±0.32mm vs 13.55±0.49, t_{91}=-1.13, p=0.131).

Survival - Most of the collared ice rats (83%) survived for more than one year but I found only one individual which had survived for three years

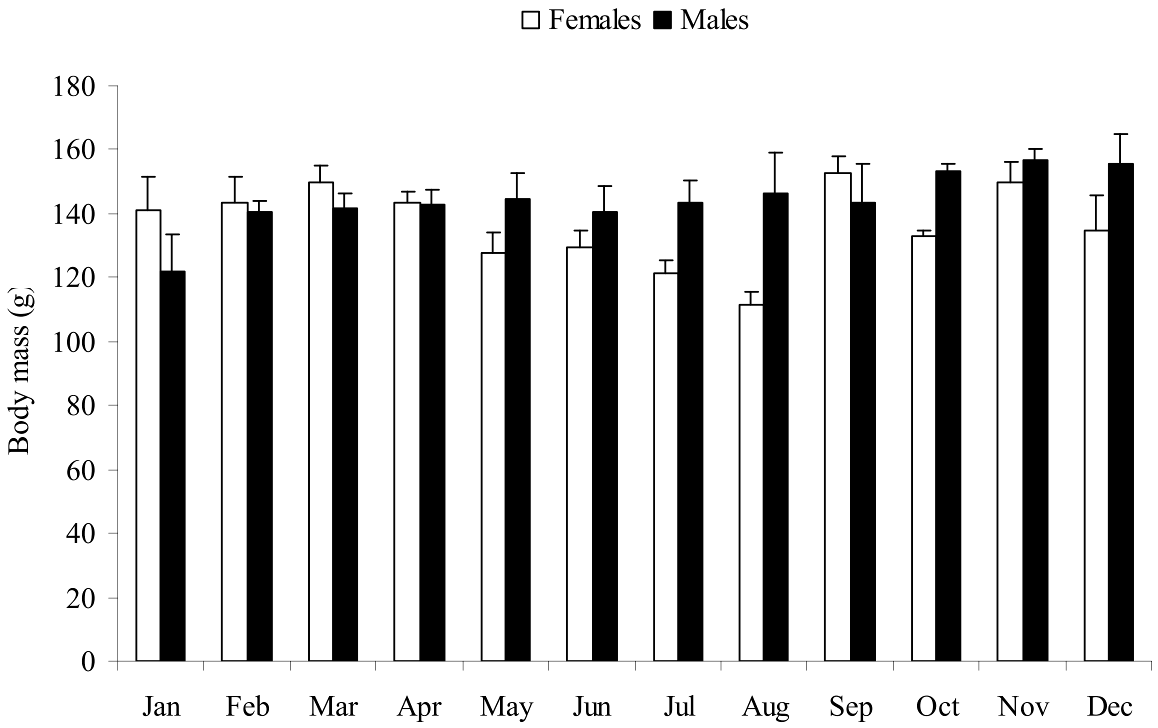

Figure 3.4 Mean±SE body mass of female and male *O. s. robertsi* from January 2000 to December 2000. Sample sizes as in Figure 1.

3.3.2 Female-male interaction

Social interactions were noted in eight of the 15 focal females and five of the 10 focal males. On the one or two days of focal observations, the eight focal females were approached by an average of 3.57 (range 1-5) males and the five focal males visited an average of 4.6 females (range 3-6), which was not significantly different (U=25, p=0.252). Interestingly, focal females were visited by males from neighbouring colonies and focal males visited females in other colonies. Focal females initially responded aggressively to males (81% of observations) but males never reciprocated. Although all the focal females were approached by at least one male, on 12 occasions, females were approached by 2-3 males at the same time. On all these occasions, the males engaged in direct physical aggression with one another and on three occasions males with visible wounds were observed.

Mating was observed in five of the focal females, where the females did not differentiate between males from their own colony or from a different colony. This was followed by a period of mutual grooming and some chasing of the female by the male. I regarded these behaviours as a part of a courtship sequence, and during these times, the pair periodically disappeared belowground. In the remaining three focal females, tolerance and chasing behaviours were noted and although mating was not seen, I suspected that they had mated because of the similarity of these behaviours to the courtship observed in other pairs.

Two focal females were found mating with two different males over the two days of focal observations. On four occasions, females and males interacted for an extended period of time for up to four hours within the females' territory. These associations appeared to be a form of mate guarding, since males usually interacted with females for 15-30 minutes at other times. Also, females were tolerant of these males, which did not feed for long periods (<30% of the interaction vs >50% usually) and instead spent their time grooming the female or resting.

3.3.3 Female reproductive behaviour, postnatal development and dispersal

The pre- and post-partum behaviour of seven of the eight females which I observed mating or suspected to have mated (see above) was recorded; the eighth female had disappeared from the study site. One female was observed mating a week after parturition, suggesting the occurrence of post-partum oestrus. Based on the time from observed or potential matings to the estimated time of birth, the gestation period was estimated at 37 days

(Mean±SE=37.14±0.70, range 33-40). The average litter size of the seven focal females and seven other females in my study site was 2.14±0.19 (range 1-3, mode 2).

Focal females spent significantly more time aboveground a week before parturition than the week after (68.63±6.59% vs 45.01±6.54%, W=26, p=0.031). In addition, females carried plant material belowground significantly more often in the three weeks after parturition (5.43±1.21% vs 14.14±1.96%, W=-28, p=0.016) than in the preceding week, and it is likely that these plants were used for bedding (see Chapter 2) or eaten by the young pups (i.e. feeding on solid food starts from day 10; Willan, 1990).

Because litters were not trapped and hence weighed regularly, I did not generate growth curves. Juveniles were weighed for the first time when they were four weeks old (i.e. the first time they entered the traps). Mean body mass at this age was 40.68±1.11g (N=5, range 37.9-43.2). Based on the appearance of a perforate vagina, the minimum age at sexual maturity was nine weeks in females (N=2, weighing 73.2g and 88.7g). Most juveniles had dispersed by week 11 (see below) but none of the male offspring were scrotal at this time. Males attained sexual maturity (2cm scrotal testes) at 14 weeks of age (N=3, weighing 91.2g, 96.4g, 100.2g), although I am uncertain whether some males reached sexual maturity earlier, since most offspring had dispersed by week 11.

Initially, the interactions between littermates and between mother and young were mostly amicable (mutual grooming, huddling, playing; Figure 3.5) and mother and offspring remained in close proximity (i.e. <1m) of one another; although the mother started foraging further away from her young from week 5-6, which appeared to coincide with the birth of her next litter. During weeks 4-8, juveniles were tolerated by the female and all used the same burrows, but high levels of aggression (sparring, chasing) between littermates and between mother and offspring were recorded from week 9 (i.e. when the first female offspring attained

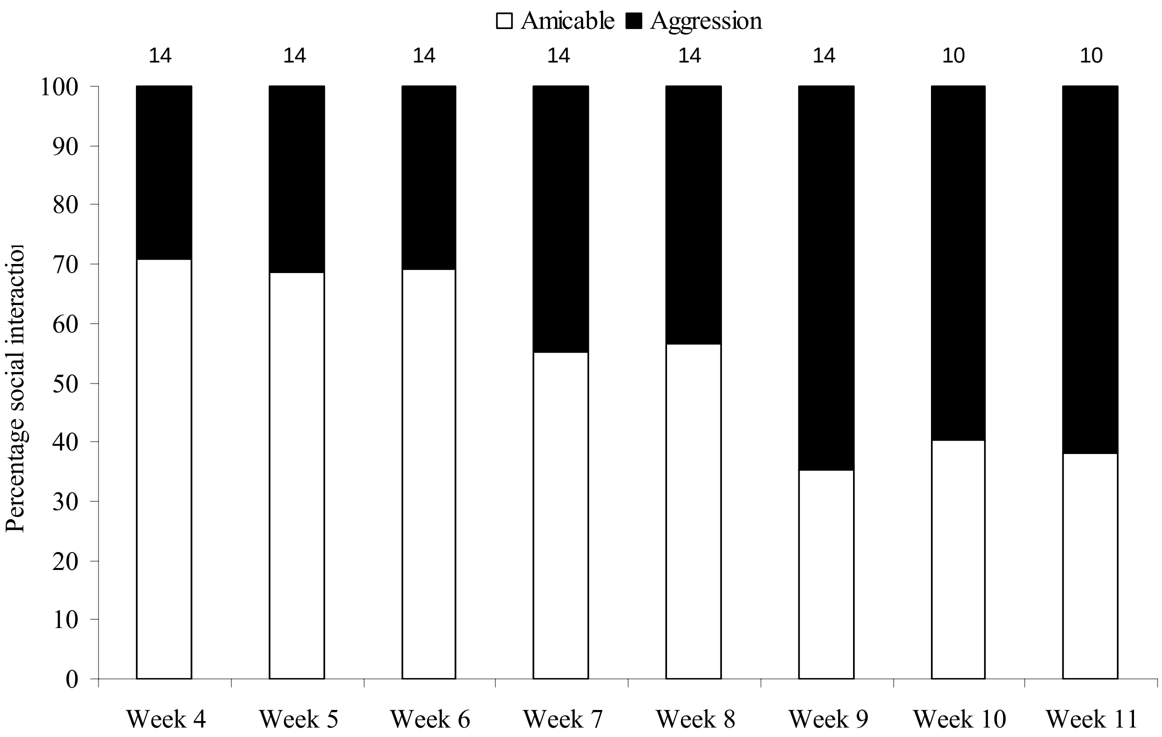

Figure 3.5 Percentage of amicable and aggressive interactions between juvenile siblings and between mother and offspring *O. s. robertsi* from the time juveniles emerged above ground until the onset of dispersal. Sample sizes are given above the individual bars.

sexual maturity), coincidentally, just prior to the next litter appearing above ground. In the seven litters monitored, all the juveniles from five litters had dispersed from their natal colony by week 11, some (~30%) had remained in close proximity to their natal colony, but the locations of the others could not be identified. In the remaining two litters, the offspring remained with their mothers until the end of my observation session (week 16).

3.4 Discussion

3.4.1 Demography

Based on my observations and the appearance of juveniles aboveground, the breeding season starts in August and lasts until about March. This pattern is typical of most rodents living in summer rainfall region of southern Africa (Skinner & Smithers, 1990).

Predictably, females were heavier during the breeding season in summer than in winter. In addition to pregnancy, females also have a longer and heavier gut in summer than in winter (Schwaibold & Pillay, 2003). Surprisingly, males maintained a relatively constant body mass from summer to winter, despite food quality and quantity decreasing dramatically from summer to winter (Killick, 1978; Schwaibold & Pillay, 2003).

The population density decreased by about 50% in winter in four colonies that I monitored, confirming the reports by Willan (1990). Nonetheless, the survival of collared ice rats was very high (83%) compared to other southern African rodents for which such information is available. For example, striped mice *Rhabdomys pumilio* in the summer rainfall region of southern Africa has a 2.3% survival rate (Brooks, 1974), and vlei rats *O. irroratus*, which are close relatives of ice rats, inhabiting mesic habitats, have a survival rate of 13% Davis (1973); although it is not clear whether this is due to mortality or dispersal.

Colony sizes ranged from 4 to 17 individuals which most likely represents the optimal range in group size for ice rats (see Vickery & Millar, 1984; Canals *et al*., 1989; Hayes *et al*., 1992). Based on mathematical models and a review of the literature, Canals *et al*. (1989) postulated that the optimal group size for huddling in small rodents is approximately 4-5 individuals, which coincidentally was the smallest number of animals recorded in colonies throughout this study. Social huddling is apparently an important behavioural thermoregulatory adaptation in ice rats (Willan, 1990) and has previously been observed in free-living ice rats in an ice rat nest chamber within their burrow system, where the rodents seek refuge from the cold temperatures during the night (Pillay, personal communication). The maximum number individuals in a colony (i.e. 17 individuals in my study) may be constrained by a combination of above ground territoriality (see Chapter 2) and by the number of individuals that can huddle in an underground nest chamber. *Otomys s. robertsi* burrow systems contain 1-2 nest chambers, which vary in size from 4080 to 7321cm^3 and theoretically could shelter 11 to 20 individuals respectively, based on an ice rat volume of 370cm^3 (Hinze *et al*. in review, Chapter 4).

Predation is normally a major determinant of group size (e.g. dilution effect) and a regulator of population numbers in many small mammals (Madison *et al*., 1984; Lima, 1985; Lima & Dill, 1990; McGuire *et al*., 2002). However, predators of ice rats were virtually absent at my Sani Valley field site (Chapter 2) and it appears that population numbers are regulated more by density-dependent mortality due to resource limitation during winter (Willan, 1990) or because of low temperatures during periods of severe snowfall (Lynch & Watson, 1992). Similarly, mortality in cotton rats *Sigmodon hispidus* in the more northern parts of its distribution is due to higher mortality rates because of severe winter weather (Sauer, 1985).

3.4.2 Female-male interaction

Based on the occurrence of a single breeding pair in an *O. s. robertsi* colony, Willan (1990) predicted that overwintering offspring do not reproduce because of suppression by the parents, as occurs in some rodents living in temperate environments (Arnold, 1990; McGuire *et al*., 2002). My data indicate that most of the adult males and females in a colony were reproductively active during the breeding season in summer.

At the start of the breeding season, adult females were visited by a number of different males, both from their own colony and from neighbouring colonies, and males visited several different females; females aggressively chased males in most of these interactions. Tolerance between a resident female and a visiting male usually resulted in courtship and subsequent mating. Although the sample size of focal individuals was small in this study, I did not see the pair formation alluded to by Willan (1990). Instead, the mating system of *O. s. robertsi* is mostly likely to be promiscuous, since females mated with more than one male and males solicited several females. Promiscuity has also been observed in the vlei rat *O. irroratus* (Willan, 1982; Brown, 1988; Pillay, 1993).

Promiscuous mating systems occur when females practice simultaneous polyandry and males practice serial polygyny (Boonstra *et al*., 1993) and are characterised by multi-female, multi-male home range overlap (Clutton-Brock, 1989; Eccard *et al*., 2004). However, although it appears that random matings occur between any number of males and females and that mate selection does not occur, field studies of several promiscuous vole species revealed that males compete for mating opportunities, and females usually mate with dominant males (Madison 1980, Heske & Ostfeld, 1990). Similarly, the home ranges of female and male *O. s. robertsi* overlapped with several individuals of the same and opposite sex (Chapter 2), and there were instances of aggressive interactions among males in the vicinity of potentially receptive females. *Otomys s. robertsi* has male-biased sexual dimorphism (i.e. males were 10% on average heavier than females; see also Willan, 1990). Sexual dimorphism usually is the result of male-male competition for access to a resource, in most cases receptive females (Clutton-Brock & Harvey, 1978), but Boonstra *et al*. (1993) report that sexual dimorphism can also occur in promiscuous mating systems.

Another strategy observed occasionally in *O. s. robertsi* males in the present study was mate guarding, which is a behaviour to prevent rival males from mating with females (Sherman, 1989). Mate guarding has also been reported in Brants' whistling rat *Parotomys brantsi* (Jackson, 1999), a relative of ice rats.

3.4.3 Female reproductive behaviour, postnatal development and dispersal

Aboveground appearances of female *O. s. robertsi* decreased after parturition, obviously to attend to pups. On three occasions, mothers with nipple-clinging pups were seen aboveground. Nipple-clinging is a characteristic of all otomyines (Davis & Meester, 1981; Pillay *et al*., 1993) and limits the litter size of these rodents to a maximum of four offspring per litter, as the females have only two pairs of inguinal nipples (Roberts, 1951). A mean litter size of 2.14 in *O. s. robertsi* lies within the range of litter size observed in other otomyine rodents (Roberts, 1951; Jackson, 2000), varying from 2.09 in *O. unisulcatus* (Pillay, 2001) to 3.4 in *P. brantsii* (Jackson, 2000). Surprisingly, mean litter size in this study was higher than the 1.44 reported by Willan (1990) during his laboratory study, where the ice rats reproduced under optimal conditions. The difference in litter size between my study and the captive study by Willan (1990) is not readily explained, since one would expect that conditions in captivity would have been optimal for reproduction. However, gestation was similar in both studies (37 days in this study vs 38 days in Willan, 1990).

Female *O. s. robertsi* displayed post-partum oestrus approximately one week after parturition. Based on the gestation period and post-partum oestrous, females can produce up to five litters and 11 young within a breeding season (August to March). If eight females, the maximum number of females ever trapped in a colony during this study, achieved maximum reproductive output during a single breeding season, they could produce up to 88 offspring.

But the largest colony observed in this study consisted of 17 individuals. Therefore, the survival rate of juveniles is very low, or they disperse when they reach sexual maturity before the end of the breeding season (Stenseth & Lidicker, 1992; Solomon, 2003), or a combination of both.

The independent aboveground appearance of juveniles was delayed, and the minimum age of sexual maturity of females and males was nine and 14 weeks respectively, which is much later than in other otomyines (Pillay, 2001). Willan (1990) maintained that resource limitation in the alpine habitat results in low growth and late maturation. As offspring reached sexual maturity, increased levels of aggression between siblings and between mother and offspring promoted dispersal. *Parotomys brantsii* similarly disperses at sexual maturity from their natal warrens (Jackson, 1999). Willan (1990) predicted that the dispersing juveniles inhabit deserted areas of the natal burrow systems rather than establishing in another colony. Although I observed only the first litter born in the breeding season, I suspect that subsequent litters will reach sexual maturity only as the breeding season ends and the cold winter season commences. These offspring would then not have gained sufficient body mass to survive the winter outside their natal burrows and staying and huddling with the family group may be advantageous (Willan, 1990), where the increased survival of the siblings may result in indirect reproductive benefits for the non-dispersing offspring (Stenseth & Lidicker, 1992). A similar dispersal strategy has been observed in marmots (Arnold, 1990).

In conclusion, the results of this study highlight the colonial nature of *O. s. robertsi* social systems, which is likely to facilitate belowground communal thermoregulation (see Chapter 2 & 4). The promiscuous mating system and the dispersal, at least in the first litter, do not match the predictions made by Willan (1990). My study was conducted in nature which may explain the differences between the two studies. Another consideration is that since social systems are flexible (Lott, 1991), the social system observed here is a response to a particular set of environmental conditions which were not met in the study by Willan (1990).

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4 The burrow system of the African ice rat *Otomys sloggetti robertsi*[1]

4.1 Introduction

Rodents inhabiting temperate environments are subjected to harsh environmental conditions, particularly during the winter when low temperatures may impose severe thermoregulatory stress on the animals. To cope with these conditions, rodents may display one or more of several adaptations. Some hibernate or enter into bouts of torpor, whereas those that do not hibernate or are not physiologically adapted to such extreme conditions usually display behavioural adaptations, such as huddling, selecting appropriate microhabitats and sun basking (West & Dublin, 1984, Drew & Bissonette, 1997; Richter *et al.*, 1997). Another adaptation may be to retreat into refugia which provide relatively stable microclimates and which buffer conditions outside (Du Plessis *et al.*, 1992).

Rodents use several types of refugia, such as nests under rocks, for instance, the Namaqua rock mouse *Aethomys namaquensis* (Skinner & Smithers, 1990) and stick lodges, as in the desert woodrat *Neotoma lepida* (Cameron & Rainey, 1972). By far the most common refuge type is the underground burrow. The architecture of these tunnel systems varies from simple structures to more complex systems. Simple burrows comprise a single nesting chamber connected to one or two tunnels which open aboveground, as is found in the water rat *Dasymys incomtus* (Hanney, 1965) and several gerbil *Gerbillurus* species (Downs & Perrin, 1989). Such burrows may provide easy escape from predators as well as protection against the environment. Complex burrows comprise several aboveground entrance holes joined to many interconnected tunnels below ground (Brett, 1991; Goyal & Ghosh, 1993; Mankin & Getz,

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1994). These complex systems may contain one or more nesting, hoarding and nursery chambers, or a combination of these structures (Hoogland, 1995; Khidas & Hansell, 1995). In addition to providing protection against predators and the environment (Downs & Perrin, 1989) the complex systems may have other functions, such as raising offspring (e.g. black-tailed prairie dog *Cynomys ludovicianus;* Hoogland, 1995) and gaining access to high quality feeding sites through numerous entrance holes (e.g. *Parotomys brantsii*; Jackson, 2001). At the same time, as group size increases, the size of the burrow increases to accommodate all individuals of a group (Mankin & Getz, 1994), whereas simple tunnel structures are usually constructed and occupied by solitary rodent species (Downs and Perrin, 1989); but see Jackson (2000) for an exception to this rule.

The African ice rat *Otomys sloggetti robertsi* is an ideal model for studying the ways in which small rodents cope with extreme environmental conditions. This diurnal murid rodent is confined to altitudes exceeding 2000m and is endemic to the southern African Drakensberg and Maluti Mountains. Such a distribution restricts them to the cold, harsh sub-alpine and alpine phytogeographic belts (Killick, 1978). This rodent (121-143g) does not hibernate and is apparently poorly adapted physiologically to the alpine habitats (Richter *et al*., 1997; Hinze & Pillay, unpublished data). The thermophysiology of the ice rat (e.g. low metabolic rate and high thermal conductance) is more typical of its congeners (e.g. *O. irroratus*) which are found in warmer environments at lower altitudes (Richter *et al*., 1997). Oxygen consumption by *O. s. robertsi* decreases linearly with an increase in ambient temperature of between 0.7°C and 26.0°C. The zone of thermoneutrality is reached between 26°C and 28°C, which is high for a rodent living in a habitat that rarely experiences such high temperatures (Richter *et al*., 1997). To cope with thermal stress, *O. s. robertsi* employs behavioural (sun-basking, huddling) and morphological (thick fur, short tails, small ear pinnae) adaptations (Willan, 1990; Schwaibold

& Pillay, 2003). Moreover, ice rat colonies have numerous burrow holes and previous observations showed that individuals spend long periods on burrow maintenance. The burrow systems of ice rats may also function as thermal buffers against climatic extremes, since ice rats retreat into burrows during the coldest and hottest times of the day (Hinze & Pillay, unpublished data).

The ice rat belongs to the rodent subfamily Otomyinae, a group that is widely distributed across the primarily east-west southern African rainfall gradient (Skinner and Smithers, 1990). All otomyines studied are specialist herbivores (Roberts, 1951; Jackson, 1998). In addition to *O. s. robertsi*, two other members of its subfamily, the whistling rats *Parotomys brantsii* and *P. littledalei*, dig burrows. Both of these species are solitary, inhabit the arid western parts of southern Africa and construct complex burrow systems which apparently buffer environmental temperature extremes and provide protection against predation (Du Plessis *et al.*, 1992; Jackson, 1998; Jackson, 2000). Another member of the subfamily, the bush karoo rat *O. unisulcatus*, which occurs syntopically with both *Parotomys* spp. in parts of its distribution, constructs stick lodges instead of digging burrows (Brown & Willan, 1991; Vermeulen & Nel, 1988). Otomyines in mesic habitats, such as the vlei rats *O. irroratus* and *O. angoniensis*, are mainly surface nesters, making use of shallow grass nests under the cover of dense vegetation (Davis, 1972; Packer, 1980; Phillips *et al.*, 1997).

The aim of the present study was to document the architecture of ice rat burrow systems. In my study site in the Lesotho Drakensberg, I observed that ice rats burrow in two different substrates, organic soil in wetlands and basalt mineral soil on the slopes. Since feeding is the predominant activity in the wetlands and overnight nesting appears to occur in burrows in the mineral soils, I predicted that burrows in organic soil would comprise a few shallow escape burrows and hoarding chambers whereas those in mineral soils would contain nesting and hoarding chambers. Furthermore, I expected the tunnel systems to be simpler in the organic soil than in the mineral soil due to the comparatively compact nature of the organic soils and the high water table in the wetland, making digging in such soils more labour intensive for ice rats.

A further aim of the study was to compare the burrow architecture of *O. s. robertsi* with that of the solitary *P. brantsii* and *P. littledalei*. Although the ice rat occurs in colonies, the degree of sociality is questionable as aboveground interactions between individuals of a colony were very rare and usually resulted in agonistic encounters (Hinze & Pillay, unpublished data). Based on the numerous holes in the ground (up to 910 burrow entrances) and the size of the colonies (up to 17 individuals), I predicted that the complexity of ice rat burrow systems would be similar to those of the *Parotomys* spp. There is a positive association between nesting in exposed areas and the size (surface area and number of entrance holes) of burrow systems of *Parotomys* spp. (Jackson, 2000) and I asked whether the same association would be found for *O. s. robertsi*; the alpine habitats are more densely vegetated than the arid ones of *Parotomys* spp., but low plant cover may not provide adequate protection from predators.

4.2 Methods and Materials

This study was conducted in the Sani Valley of eastern Lesotho (29°33’ S, 29°14’ E). The mean annual temperature is approximately 6°C, with mean air temperatures ranging from 10°C in summer to 0°C in winter (Grab, 1997). Mean annual precipitation is over 1200mm and snow can occur during any month of the year (Killick, 1963). *Otomys s. robertsi* burrows in organic soils in the wetlands and shallow basalt soils on the mountain slopes, hereafter referred to as mineral soil (Grobbelaar & Stegmann, 1987; Grab, 1999). Groups of ice rats inhabiting the fringes of wetlands alternate between their use of burrows in mineral and in organic soils throughout the day (Hinze, personal observation).

The number of entrances to a burrow system was counted before further investigations of the tunnels were conducted. During summer when the ground was frost free, eight entire burrow systems (4 abandoned and 4 occupied) were excavated in organic soil and seven (5 abandoned and 2 occupied) in mineral soil, with a minimum of 250m between burrow systems. These were carefully excavated with a spatula and a small shovel so as to maintain the original organisation of tunnels and associated structures. Before excavations were started, the inhabitants of the occupied burrow systems were counted. When I started the excavations, any occupants within the burrow system most likely moved into neighbouring systems. After opening all the interlinking tunnels, a grid comprising 40cm x 40cm quadrats was placed over an entire burrow system to map the tunnels, including the locations of entrances and nesting and hoarding chambers. In each quadrat, one measurement of tunnel depth (from the soil surface to the bottom of a tunnel), height and width were made in a randomly determined position. I measured the height of nesting and hoarding chambers, and took two width measurements at right angles to each other per chamber. All measurements were conducted with a measuring tape to the nearest millimetre. Based on the assumption that the nesting chamber is ellipsoid, the volume was calculated using the formula V=¾ width 1 x width 2 x height. I identified nesting chambers by the presence of dried, tightly compacted grass material, whereas a hoarding chamber in an occupied burrow system was situated at the dead end of a tunnel and contained fresh vegetation that the rodents had carried below. Hoarding chambers in abandoned burrow systems could not be identified because they could not be distinguished from simple dead ends in the burrow structure. The average of the six deepest and six shallowest readings chosen randomly were used to establish the maximum and minimum depth of each burrow system. I counted the number of entrance holes and bifurcations within a burrow system and calculated the surface area of each system.

After taking the first set of measurements, another lower level of tunnels was found beneath five burrow systems in the organic soil with the two levels interlinked by tunnels. The second burrow system was subsequently excavated and another set of measurements made as described above.

In order to measure temperature changes within a nesting chamber of an occupied burrow system in the organic soil, a temperature probe was inserted into the insulating grass lining of a nesting chamber, without disturbing the nest structure and occupants. A Tinytag^{TM} data logger (manufactured by Gemini data loggers, UK) recorded the temperature within the nest every hour from April (early autumn) to November (early summer) of 2002. Due to the remote location of the study site only one probe was successfully inserted into an active nest chamber. The loggers were calibrated before installation in the field and had a resolution of 0.2°C. Readings were obtained simultaneously from a temperature probe placed into the soil about 20m from the burrow system at the same depth as the nesting chamber. Air temperature readings were also taken at a weather station located 5km from our study site.

Data are presented as mean±SE. Inter-substrate differences in burrow architecture were analysed using the Mann-Whitney U test (Zar, 1999). Since a probe was inserted into only one nesting chamber and one location in the surrounding soil, the temperature data retrieved from the data loggers were not statistically analysed but instead were plotted and the patterns of change in the temperature profile within the nesting chamber were then compared visually to those of the soil and air.

4.3 Results

The number of ice rats inhabiting a burrow system ranged from 4 to 17 individuals. The number of entrance holes in excavated burrows ranged from 4 to 25 per system, although the number of entrance holes exceeded 25 in other parts of my study area. Burrow systems in the organic soil had between 9 and 21 entrance holes and those in the mineral soil between 4 and 20. Well-defined aboveground runways connected some of the entrance holes and extended out into frequently used foraging sites. Belowground, all tunnels were interlinked, with 28 to 43 bifurcations in burrow systems in the organic soil and 8 to 26 bifurcations in burrow systems in the mineral soil (Figure 4.1 and 4.2). Five of the eight systems in the organic soil had a lower level with a much simpler architecture (Figure 4.2b) and which were interlinked with the top tunnels via connecting tunnels. Only one burrow system in the mineral soil showed any evidence of the beginning of a lower level in the form of one tunnel leading into half an excavated chamber situated below the top level of tunnels.

Except for one system located in the mineral soil, which had no distinguishable nesting chamber, burrow systems had 1 or 2 nesting chambers. In the mineral soil, the nest chambers were located deeper (357±33.33mm) than the tunnels (average maximum depth 262.67±77.96mm), whereas nest chambers (280±32.15mm) were located higher than most tunnels (average maximum depth 315.6±48.89mm) in the organic soil. Nest chambers varied in size from 4080cm^3 in the mineral soil to 7321cm^3 in the organic soil and contained a large quantity of compacted dry grass (*Pentaschistis oreodoxa* and *P. galpinii*) at different stages of decomposition. *Otomys s. robertsi* was often observed carrying large quantities of these grasses belowground and if a burrow system was occupied before excavation, the inner layer of the nest chambers consisted of fresh dry grass. Occasionally, decomposing dry grass, similar to that found in unoccupied nest chambers, was seen on a mound in front of an active

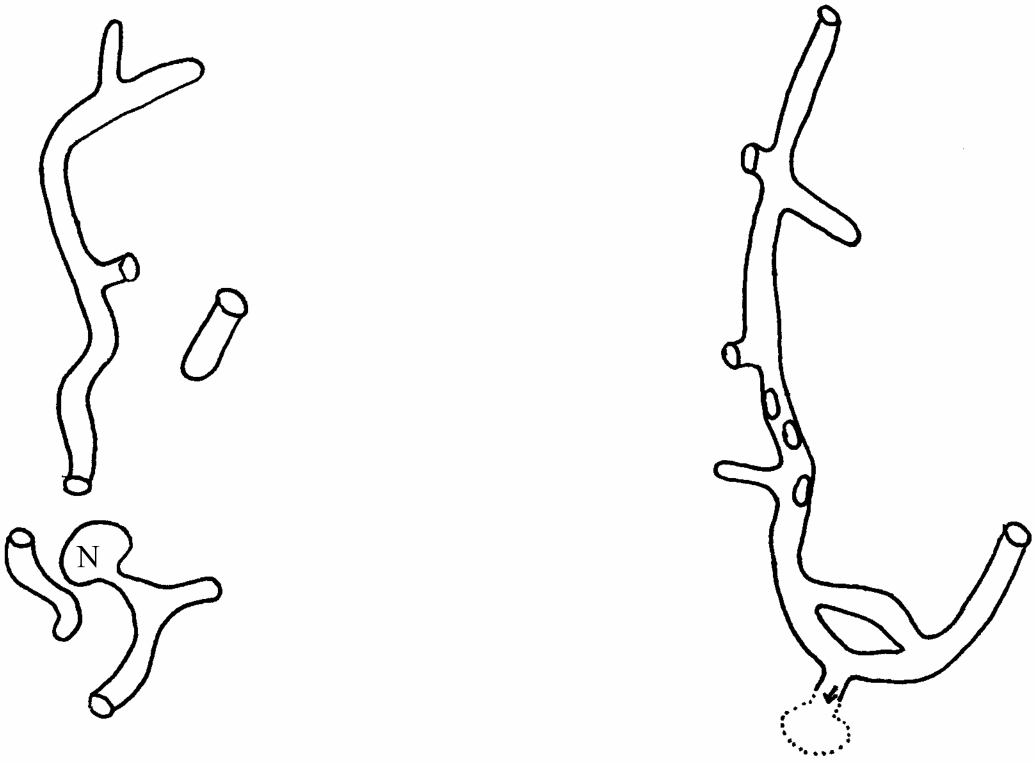

Figure 4.1 Drawing of an ice rat burrow system in mineral soils. N=Nest chamber

burrow entrance, suggesting that the occupants had cleared out decomposing plant material and lined the nest chamber with fresh dry grass. Non-utilised nest chambers contained only dirty and moist grass, indicating that the nest had not been used for some time.

Hoarding chambers were found in four burrow systems only, all of which contained a few fresh branches of the *Helichrysum subglomeratum* shrub. The hoarding chambers did not differ in their dimensions from the tunnels, but were located at the dead ends of some of these and could be identified as possible hoarding chambers only because of the vegetation they contained. Although ice rats were found to carry *H. subglomeratum* belowground, there are no records of them consuming it aboveground. No latrines were located belowground and

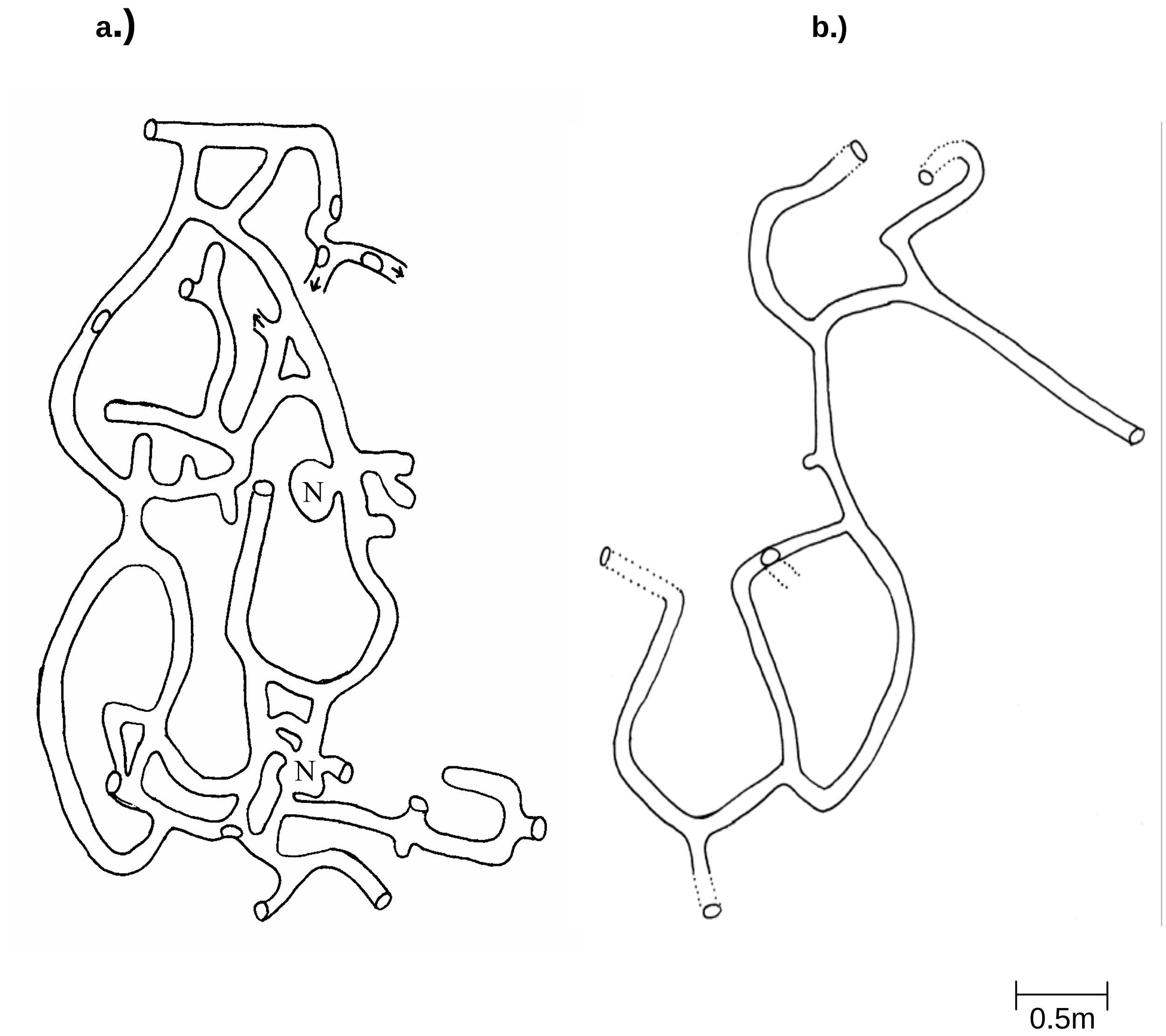

Figure 4.2 Drawing of an ice rat burrow system in organic soil a) and the tunnel system located beneath it b). N=Nest chamber. Dotted lines indicate tunnels linking the two systems.

instead, a faecal mound was present aboveground in each colony. Ice rats maintained their tunnels regularly, keeping the entrances clear of debris. In abandoned burrow systems, most entrance holes had started to cave in and fill up with soil.

Tunnel structure was similar in the burrows of the two substrates although the tunnels were shallower in the organic soil compared to the mineral soil (Table 4.1). Tunnel widths were similar in all burrow systems (range: 30mm - 290mm); the maximum depth was greater in the organic soil compared to the mineral soil, but minimum depths between the tunnels and the surface did not vary across systems (Table 4.1) with some of the tunnels reaching immediately below the vegetation layer. The surface area of burrow systems in the organic soil was much larger (range: 7.80 – 15.75m^2) than in the mineral soils (range: 4.50-8.25m^2).

Table 4.1 Mean (±SE) physical characteristics of six burrow systems of *O. s. robertsi* in organic and mineral soils. U = Mann-Whitney U test.

Characteristics	Organic soil (mm)	Mineral soil (mm)	U	*p*
Tunnel height	82.59 (42.91)	107.5 (68.66)	794	0.029
Tunnel width	60.03 (19.94)	68.14 (35.42)	2634.5	0.102
Maximum tunnel depth	315.60 (48.89)	262.67 (77.96)	77.5	0.0015
Minimum tunnel depth	121.96 (39.78) range:12-190	134.64 (30.66) range: 80-210	148	0.56

In both winter and summer, soil temperature was usually very similar to that in the nest chamber, which in turn was much more stable than the ambient temperatures (Figure 4.3). Coinciding with the coldest times in winter, nest temperatures regularly spiked between 1 and 4°C above the soil temperatures (Figure 4.3a). These spikes occurred mainly at night when the ice rats were belowground (Hinze, personal observation).

Comparisons of the burrow systems of ice rats with published data for the arid-living, burrow-dwelling *P. brantsii* and *P. littledalei* indicate that all three species construct complex burrow systems that contain several interlinking tunnels and nest chambers but no hoarding chambers (Jackson, 2000). *Parotomys littledalei* constructs its burrows in areas with good cover (e.g. under bushes) whereas *P. brantsii* burrows in comparatively open areas (Jackson, 2000) and *O. s. robertsi* burrows in areas with and without vegetative cover. The dimensions

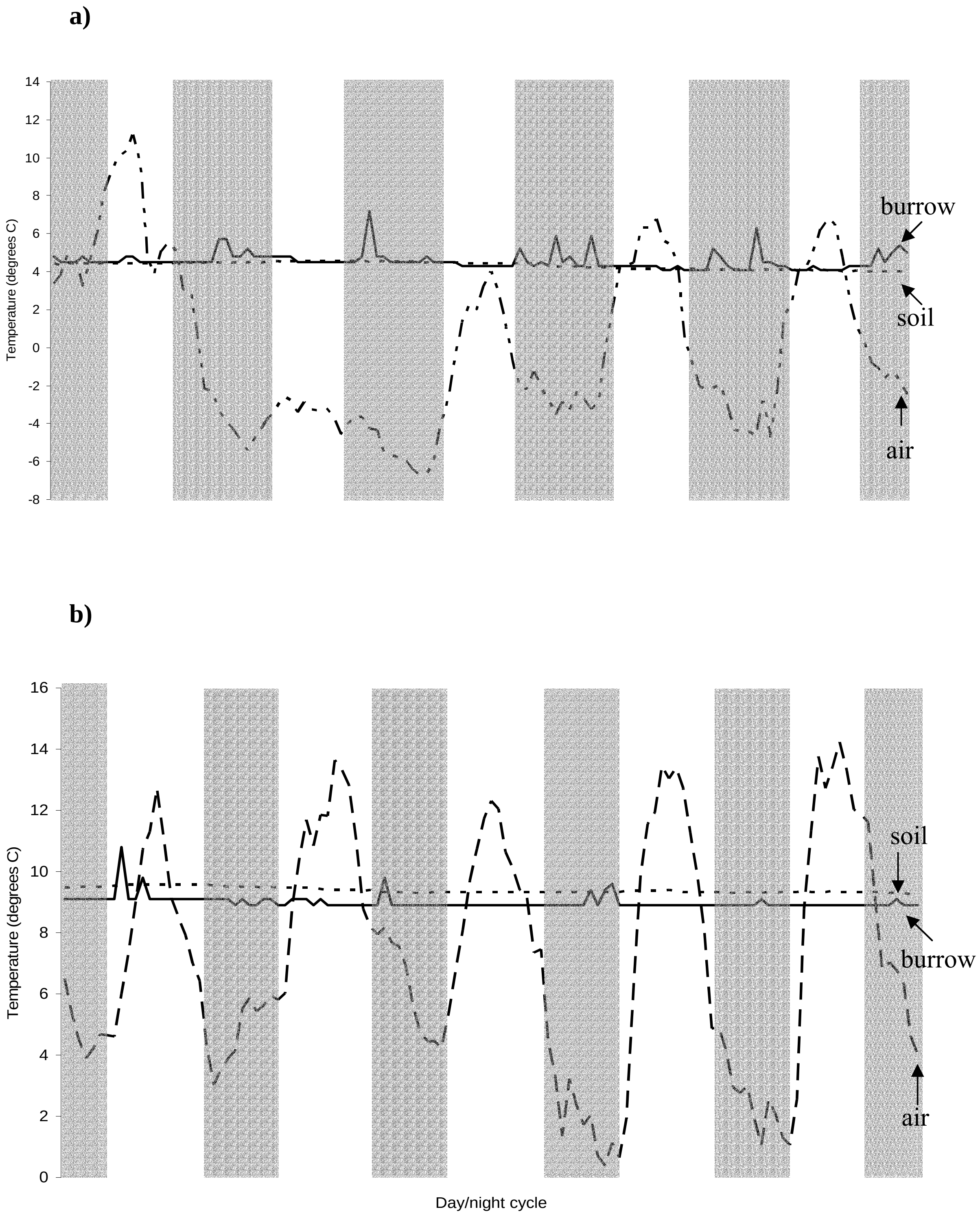

Figure 4.3 Comparison of nest and ambient temperatures during a) a particularly cold spell in early spring (September 2002) and b) typical ambient and nest temperatures measured in summer 2002. Shaded columns indicate night time.

of the burrow systems are similar among the three taxa and only a few differences are evident (Table 4.2). Notably, the burrows of *O. s. robertsi* contain fewer nesting chambers than that of *Parotomys brantsii* that has the greatest upper range in the density of entrance holes. Also, the burrow systems of *P. brantsii* cover a much greater surface area than those of the other two taxa (Table 4.2).

4.4 Discussion

Burrow systems in both organic and mineral soils contained numerous interlinking tunnels, at least one nest chamber and a number of entrance holes. Contrary to the prediction that the compact nature of the organic soils would make digging more difficult in organic than mineral soils (Schwaibold, unpublished data), burrows in organic soils had a larger surface area and were deeper. Five burrow systems in the organic soils contained two levels. This is surprising given the higher water table in wetlands, but the consistency of the organic soils in roots and decaying matter, supports the tunnels' structures, whereas the binding capacity between individual mineral grains in the mineral soils is much lower, thus decreasing the stability of the tunnel system. For these reasons the potential for tunnel collapse is lower in the organic soils which effectively support deeper tunnels and double storeys.

The arid-adapted *Parotomys brantsii* also constructs complex burrow systems (Jackson, 2000), which may be due to the limited availability of suitable habitat, resulting in these solitary animals aggregating into groups. Individual members of *P. brantsii* defend their territories below and aboveground and do not share nest chambers within a warren system (Jackson, 1999). The complex burrow systems of *O. s. robertsi* may also result from many individuals aggregating in one area and so expanding the tunnel system. Supporting evidence for this is

Table 4.2 Comparisons of the burrow systems of three otomyine rodents: *Otomys s. robertsi*, *Parotomys brantsii* and *P. littledalei* (De Graaff & Nel, 1965; Du Plessis *et al.*, 1992; Coetzee & Jackson, 1999; Jackson, 2000).

Parameters	*Otomys sloggetti robertsi*		*Parotomys brantsii*	*Parotomys littledalei*
Habitat	alpine		arid	arid
Burrow location	open/under bushes		open	under bushes
	Organic soil	**Mineral soil**		
Entrance holes	9-21	4-12	13-21 (Kalahari); up to 500 (northern Namaqualand)	8
Density of entrance holes (m^{-2})	0.43-2.84	1.67-4.69	0.5-8.8	0.8-5.3
No. of nest chambers	1	0-2	1-6	3
Tunnels leading to nest chambers	1-3	1	2-6	1-6
Mean depth of nest chambers (cm)	28	35.67	31-34	22-37
Maximum depth of location of nesting chamber (cm)	39	35	39	42
Depth of tunnels (cm)	12.2 – 31.6	13.5 – 26.3	25-27	20-27
Mean surface area of burrow system (m^2)	7.8	3.5	72.9	4.7

provided by a significant positive association between the numbers of entrance holes in a colony and the number of individuals in a colony (n=20; Spearman r=0.69; p=0.0008). Like *P. brantsii*, individual ice rats in a colony defend their territories against group members aboveground (Hinze & Pillay, unpublished data). However, the maximum of two nest chambers per burrow system implies that up to 17 individuals co-inhabit nesting chambers excavated in burrow systems.

Huddling in underground nest chambers is a common behavioural adaptation in small mammals occurring in cold environments (Canals *et al.*, 1989) and is likely to be important in *O. s. robertsi* as well (Willan, 1990). Huddling has been observed in captive ice rats as well as in free-living *O. s. robertsi* (Pillay, personal communication). These observations are supported by the fact that several ice rats share one or two nest chambers. Further evidence for this is provided by temperature recordings. During winter, when ambient air temperatures at night dropped to below freezing in the Maluti Mountains, the soil temperature at the depth of an *O. s. robertsi* nest chamber was slightly above this, whereas the temperature in the grass padded nest chamber always remained higher than the surrounding soil temperature, suggesting that grass padding is a very good insulator. Irregular temperature spikes measured in the nest chamber especially during cold nights suggest that the nest chamber was occupied. An increase of up to 4°C above soil temperature was recorded, and it is likely that on these occasions the nest chambers were occupied by more than one ice rat. Further studies are required to investigate the thermal biology of ice rats. A prerequisite for huddling is a high level of amicability between colony members, which contrasts with the territorial behaviour observed aboveground. This dichotomy of below and aboveground social behaviour is currently being investigated.

The nest chambers of *O. s. robertsi* in the mineral soil were located at similar depths to those of *P. brantsii* and *P. littledalei*, suggesting that all these nest chambers are adequately buffered from aboveground temperature conditions at a depth of about 25cm. Nest chambers in the organic soil were located slightly higher in the soil profile, however, which may be the result of the higher water table in the wetland. Roper *et al*. (2002) reported that *P. brantsii* individuals regularly switch between nest chambers in order to minimise the build up of ectoparasites on the pelage resulting from the prolonged use of a single nest chamber. During my study, I noticed very few ectoparasites on *O. s. robertsi* and it is possible that in this taxon there is no need to implement a nest switching strategy. Alternatively, the thermoregulatory benefits of huddling might outweigh the need to construct and occupy several nest-chambers.

Otomys s. robertsi carried food belowground and then reappeared aboveground too soon to have consumed the food, suggesting that food is stored belowground for later consumption (Hinze, personal observation). Food storage is common in many burrowing small rodents, such as *Microtus ochrogaster* (Mankin & Getz, 1994) and *Apodemus sylvaticus* (Khidas & Hansell, 1995; Kinlaw, 1999). *Otomys s. robertsi* has not been observed aboveground during the night, but it is likely that some activity, particularly the consumption of cached food, takes place in the burrows at night. Moreover, food caches can be used during the middle of the day in summer or during periods of bad weather when surface activity is minimal (Hinze & Pillay, in review). Feeding on caches also extends the length of feeding time available to the rodent, which may be an important adaptation in this non-ruminant herbivore (Schwaibold & Pillay, 2003).

Since *Otomys s. robertsi* constructs crude hoarding chambers at the dead end of tunnels, and no evidence of long term caches was found, it appears that all cached food taken into the burrow system is consumed during the same day or overnight. A diet of primarily fresh green plant material (Schwaibold & Pillay, 2003) precludes individuals from storing plants for long periods of time. Similar temporal patterns of caching behaviour have been reported in *P. brantsii*, where food plants are carried belowground mainly in the afternoon and consumed during the night (Du Plessis, 1989; Jackson, 2001). No food caches were found during the excavation of burrow systems of *P. brantsii* (De Graaff & Nel, 1965).

The ice rat forages in close proximity to its burrow entrance and runs back to the comparative safety of the entrance between foraging bouts (Schwaibold, unpublished data). The burrow system with its extensive network of tunnels extends the foraging range of individuals in a colony with access to food items while remaining close to an entrance hole. Feeding in such close proximity would also provide quick escape from predators (Lima, 1985; Nonacs & Dill, 1990; Eisenberg & Kinlaw, 1999; Kinlaw, 1999) and returning regularly to a nearby entrance hole during feeding bouts would also reduce exposure to extremes of temperature.

Some important interspecific differences in burrow location and architecture exist between *O. s. robertsi* and the two species of *Parotomys*. Whereas *P. littledalei* burrows in areas of good plant cover, the tunnels of *P. brantsii* are found in areas with little plant cover and its burrows cover a larger area and have several entrances (Du Plessis *et al.*, 1992; Jackson, 1998, 2000). Complex burrows buffer environmental temperature extremes in both species but the large multi-entranced burrow system of *P. brantsii* serves as a refuge from predators, so that it is no longer confined to areas with cover, as is the case with *P. littledalei* (Jackson, 2000). In comparison, the burrow systems of *O. s. robertsi* are located in the open but some entrance holes are often shielded by alpine heath, and the size of ice rat burrow systems (i.e. surface area and number of holes) falls between those of the two *Parotomys* species.

In conclusion, three factors may have influenced the burrowing habits of *O. s. robertsi* 1. Its burrow systems provide a suitable microhabitat in which to escape adverse environmental conditions, particularly during winter. 2. The more intricate burrow architecture appears be the product of the collected efforts of several individuals, and the few nesting chambers support previous observations that individuals huddle belowground. 3. The extensive interlinking tunnels may provide underground routes to aboveground feeding sites, thereby reducing exposure to adverse conditions and predation risk. The similarity in burrow architecture between the arid-adapted *Parotomys* species and *O. s. robertsi* alludes to phylogenetic influences but is perhaps moreover a reflection of the similar functions that burrow systems have in the extreme habitats inhabited by these otomyines.

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5 Life in an African alpine habitat: diurnal activity patterns of the ice rat *Otomys sloggetti robertsi* [2]

5.1 Introduction

Temperate climates are characterised by fairly cool summers and extremely low temperatures in winter. To cope with these conditions, rodents may display one or more of several adaptations: some hibernate or enter into bouts of torpor, whereas others, which do not hibernate or are not physiologically adapted to extreme conditions, usually display behavioral adaptations such as huddling, selecting appropriate microhabitats and sun basking (West & Dublin, 1984; Drew & Bissonette, 1997; Richter *et al.*, 1997). Another adaptation for surviving cold temperatures is to retreat into protected refugia. Because they provide a comparatively stable microclimate, underground burrows can buffer temperature extremes outside (Jackson, 1998), which together with restricted space for movement, may reduce energy loss (Eifler & Slade, 1998). However, time spent in the burrow has to be traded-off against time spent foraging during which energy stores could be replenished. Therefore, the timing of activity patterns may reflect how rodents respond to and cope with prevailing environmental conditions.

There is overwhelming evidence that environmental variables have a strong influence on both the daily and seasonal activity patterns of small mammals living in temperate environments (Chappell & Bartholomew, 1981; Türk & Arnold, 1988; Bacigalupe *et al.*, 2003). For example, alpine marmots *Marmota marmota* reduce aboveground activity during

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the hottest times of the day, resulting in a bimodal activity profile and they remain aboveground for most of the day during cool days (Türk & Arnold, 1988). Such bimodal activity appears to be an adaptation for avoiding times when temperature and solar radiation levels are at their highest during the middle of the day (Walsberg, 1988). Alpine rodents hibernate in winter to survive the cold season, but rodents that do not hibernate during the winter months need to maximize the time spent foraging or sun basking to take advantage of the short, comparatively warm daylight hours (Perrin, 1981). The actual time individuals can spend aboveground in winter, however, decreases as the day is much shorter. Subsequently, to minimize their exposure to the cold, especially before sunrise and after sunset, there is less aboveground activity in winter compared to summer (Zielinski *et al.*, 1983).

An interesting model for studying how small mammals cope with temperate climatic conditions is the African ice rat *Otomys sloggetti robertsi*. This medium-sized (121 – 143g) murid rodent is endemic to altitudes exceeding 2000m in the southern African Drakensberg and Maluti mountains (Willan, 1990), a distribution which restricts them to the cold, harsh sub-alpine and alpine phytogeographic belts in Africa (Killick, 1978). Ice rats are herbivorous and diurnal and live in colonies which may cover an area of up to 1200m^2, with 25 or more entrances connecting to an intricate interlinking belowground tunnel system in a colony (Skinner & Smithers, 1990; chapter 4). Importantly, *O. s. robertsi* is not physiologically adapted to the temperate habitats it occupies and its physiology resembles that of its congeners inhabiting warmer climates (Richter *et al.*, 1997). Unlike most small mammals that inhabit similar environments in the northern hemisphere, ice rats do not enter torpor or hibernate during winter. The low temperatures and prolonged snow cover in winter in the Maluti Mountains are suggested to regulate ice rat population numbers (Willan, 1990; Lynch & Watson, 1992).

Ice rats have a few morphological adaptations in response to low temperatures, such as short tails and small ear pinnae (Richter, 1997). The gut morphology of *O. s. robertsi* shows some adaptations to the cold environment, as it promotes longer retention of food for digestion, which may facilitate increased energy uptake (Schwaibold & Pillay, 2003). Apart from these morphological adaptations, ice rats have a range of behavioural adaptations (e.g. sun basking, huddling and retreating into their underground burrows). Grass padded nest chambers, located 280 – 357mm deep in the soil profile, shelter groups of ice rats from extremely cold temperatures during the night (Hinze *et al.*, in review).

Whilst their refugia and feeding habits have previously been studied in some detail (Schwaibold & Pillay, 2003; Hinze *et al.*, in review), little is known about the diurnal activity of ice rats, apart from anecdotal information of their sun-basking behavior (Willan, 1990). The present study examined how ice rats may have adapted their activity patterns to cope with the environmental conditions imposed by the harsh alpine climate. Direct observations were made of the aboveground diurnal activity of free-living *O. s. robertsi* to ascertain seasonal differences in their activity patterns. The influences of seasonal variation in solar radiation and temperatures on activity were also examined, as was the presence of snow on the ground. A bimodal activity profile was expected during summer, with aboveground appearance and activity taking place in the morning and afternoon/evening but decreasing during the middle of the day when solar radiation and ambient temperatures reach high levels. In contrast, a unimodal activity profile in winter would maximize the time the rodents have available for foraging and sun basking (Perrin, 1981; Zielinski *et al.*, 1983). I previously observed that ice rats spend extended periods sitting in the sun and basking when temperatures were below 5°C. If sun basking is a behavioral strategy to decrease energy expenditure during cold periods, I would expect the level of sun basking to increase in winter compared to summer. If so, sun basking, especially in winter, is likely to be traded-off against other behaviors, particularly foraging. *Otomys s. robertsi* feeds on a wide range of fresh green plant food, and rarely hoards food in their burrows during any time of the year (Hinze *et al.*, in review). Therefore, ice rats presumably need to consume sufficient food during the day to meet their energy needs for the night, particularly during the cold winter months, as no nocturnal aboveground activity has been observed.

Another aim of this study was to compare my data on the activity of ice rats with those available for other members of its subfamily Otomyinae. The desert dwelling Brants'whistling rat *Parotomys brantsii* is also diurnal and retreats into its burrows when temperatures become too hot during the middle of the day, leading to a bimodal aboveground activity profile during hot days (Jackson, 2000). The vlei rat *Otomys irroratus*, which inhabits low-lying mesic environments in southern Africa, is diurnal, although foraging also occurs at night probably to meet metabolic requirements (De Graaff, 1981; Perrin, 1981).

5.2 Methods

Fieldwork was conducted in a 4 ha site in the Sani Valley located in the Maluti Mountains, Lesotho (29°33' S, 29°14' E). The study site lies at an elevation of 2800m and comprises a wetland surrounded by gentle slopes. The mean annual temperature in the Sani Valley is approximately 6°C, with mean air temperatures ranging from 0°C in winter to 10°C in summer (Grab, 1997). The mean annual precipitation, often in the form of snow, is over 1200mm (Killick, 1963). The vegetation comprises mainly Helichrysum species on the slopes, while the wetlands contained several flowering plants, such as *Haplocarpa nervosa, Trifolium burchellianum, Saniella verna, Limosella vesiculosa, Cotula paludosa* and *Ranunculus multifidus.*

Observations were conducted in two phases. In phase 1, field work was done during 10 days (140 hours) in summer (October and November) and 10 days (100 hours) in winter (May and August) over 2000 and 2001. In each season, observations were made on days with similar weather conditions. On different days, I observed the activity of ice rats belonging to three colonies with similar environmental conditions, but situated at a minimum of 75m apart. Detailed observations were made from a raised vantage point approximately 3m from the colony under observation only when the visibility was such that the entire colony was clearly visible. This allowed for a full view over a colony where all animals aboveground could be clearly seen.

The activity of colony members was recorded on datasheets using instantaneous scan sampling at one minute intervals (Martin & Bateson, 1993) from first light in the morning until it became too dark in the evening to observe colony members. On the minute mark, I recorded whether the majority of the colony members (>50%) were foraging (searching, handling and ingesting food), basking (sitting motionless in the sun) or had retreated belowground into their burrows. Nothing was known of the belowground activity, although it is possible that the ice rats were consuming stored food or were simply resting. Other activity, such as social behavior, was also recorded but not included in the present analysis since such activity was rare. The maximum number of individuals observed in a particular colony during the observation period was used to calculate the per minute proportion of individuals aboveground.

In phase 2, I studied the relationship between environmental parameters (solar radiation and ambient temperature) and activity of ice rats. Because of the remote location of the study site and because equipment for measuring environmental conditions was available for a limited period only, I studied the relationship between activity and environmental conditions for three days in summer (2002) and three days in winter (2002). Based on the data collected during phase 1, I increased the sampling interval to 5 minutes for the instantaneous scan sampling. Both ambient temperature and solar radiation were measured at five minute intervals, using respectively a Tinytag^{TM} data logger within a radiation shield and Tinytag^{TM} data logger without a shield which were calibrated at the start of the experiment and logged readings in five minute intervals. Both probes were set up alongside one colony under observation and at a similar height (5cm) above the ground at which the rodents were active. Readings taken of solar radiation, temperature and behavior of the colony were synchronized, so that activity could be correlated with the environmental parameters.

Ice rat activity was also recorded on three separate occasions (eight days in total) when the habitat was covered in a thick layer of snow using the same recording techniques as described in phase 1. Snow was rare during my study, and I used the opportunity to study how snow on the ground influenced ice rat behavior. For comparison, I also recorded ice rat activity a week after the snow had melted. For comparison of activity in the presence and absence of snow, I recorded activity from 10h00 to 16h00.

5.3 Data analysis

For the sake of simplicity, the data for each hour of observation per day for all three colonies were pooled and used in general linear model (GLM) with a repeated measures multivariate design to compare the behaviors between seasons for phase 1 and to compare behaviors when snow was present and absent, with time of day in hours being the repeated measures variable. Tukey *post hoc* tests were used to reveal specific differences (Zar, 1999). The influence of environmental parameters on activity was analyzed using a general linear model (GLM) with a nested design: location above or belowground (fixed effects variable) was nested in time of day (random effects variable) and both of these were nested in season (fixed effects variable); and temperature and radiation were the response variables. All data were analyzed for normality, significance was accepted at $P<0.05$ and all tests were two-tailed.

5.4 Results

As soon as the sun reached a colony, approximately 05h00 in summer and 07h00 in winter, the first ice rats emerged from their burrows to bask briefly at the burrow entrance before starting the first foraging session of the day. Within approximately 10 minutes, about 80% of the individuals of a colony appeared aboveground and similarly, around 80% of the individuals retired into their burrows in the evenings within a few minutes of one another (Figure 5.1). Throughout the day, ice rats alternated between foraging and basking, although there were occasional social interactions (<1% of active period) and burrow maintenance (approximately 4% of active period). In summer, there was a decrease in aboveground activity during the middle of the day, leading to a bimodal diurnal activity profile whereas ice rats spent almost all their time aboveground in winter. In the evenings, before sunset, at approximately 17h00 in winter and 19h00 in summer, foraging levels increased again before the colony retreated into their burrows for the night. Some aboveground activity was observed for approximately 30 minutes after sunset in winter (Figure 5.2).

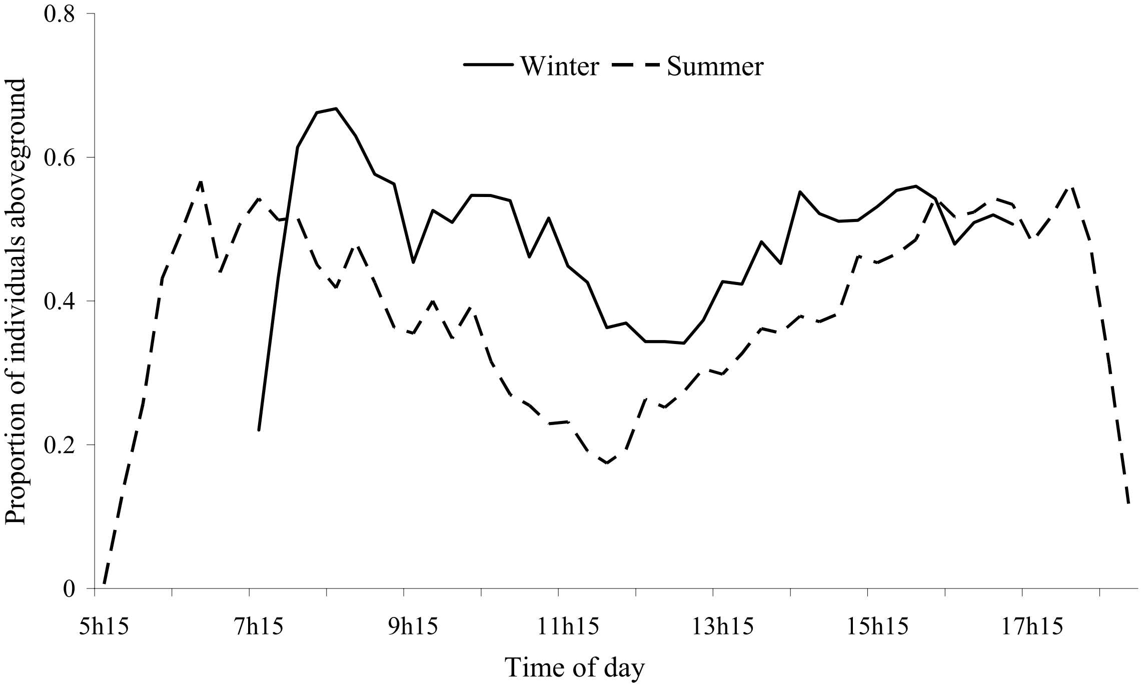
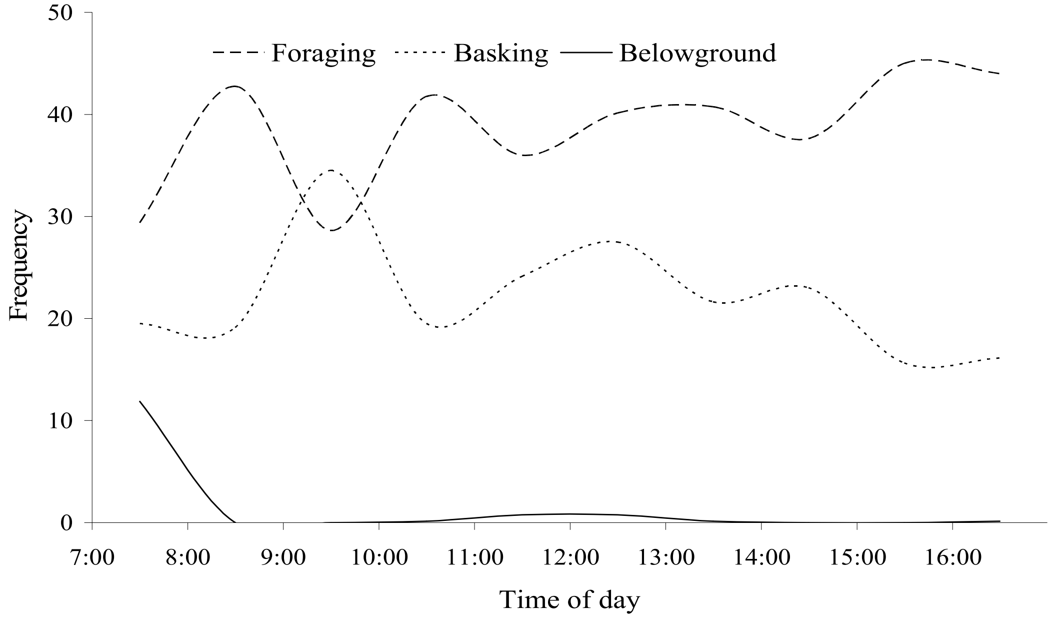


Figure 5.1 Proportion of *O. s. robertsi* aboveground in summer and winter during different times of the day.

Ice rats significantly altered their activity between seasons ($F_{3,13}$=5.04, p=0.016). More time was spent foraging in winter than in summer, whereas more basking behavior was displayed in summer than in winter (*post hoc* tests; Figure 5.2), Moreover, *O. s. robertsi* spent more time belowground during the day in summer compared with winter. Behavior was not influenced by time of day nor by the statistical interaction between time of day and season (p>0.05).

a) Winter



b) Summer

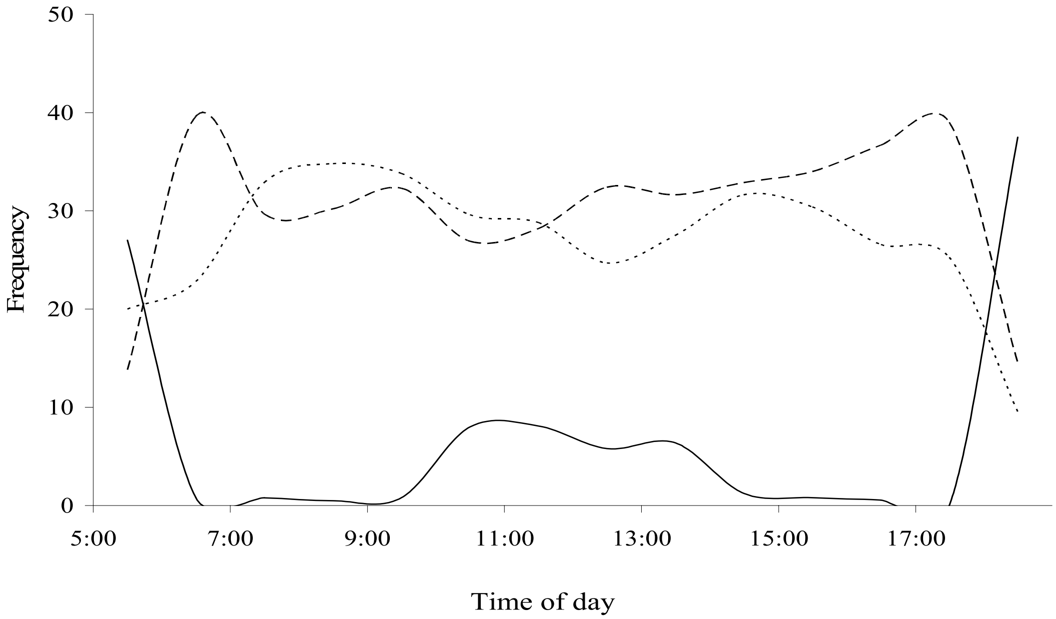
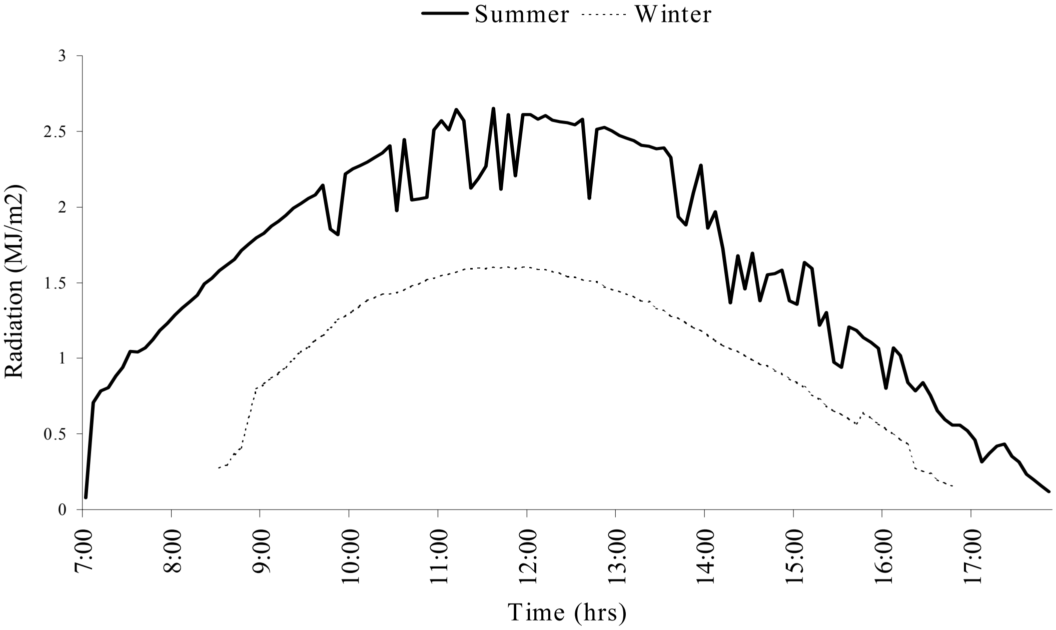


Figure 5.2 Mean frequency per hour spent foraging, basking and belowground by the majority of an *O. s. robertsi* colony from 7h00 to 17h00 during a) winter and from 5h30 to 19h00 during b) summer.

Solar radiation and ambient temperature were much higher in summer than in winter ($F_{1,306}$=78.61; p<0.001). Levels of solar radiation and ambient temperature were significantly associated with time of day in both seasons ($F_{217,306}$=1.73; p=0.014). Although overall solar radiation levels were highest during the middle of the day in summer (*post hoc* tests), they peaked during the middle of day in both seasons (Figure 5.3). Interesting fluctuations in radiation were recorded in summer, apparently coinciding with the presence and absence of cloud cover. There was very little overlap in daily temperatures between seasons (*post hoc* tests), with very low temperatures being measured in winter and higher ones in summer. On the days sampled, temperatures ranged from 7.7 to 20.6°C in summer and -4.9 to 11.7°C in winter. The disappearance of ice rats belowground coincided with periods of high ambient temperatures and high levels of solar radiation ($F_{73,306}$=1.97; p<0.001), this effect being more pronounced in summer than in winter (*post hoc* tests; Figure 5.4).

Heavy snowfall significantly modified the behavior of ice rats ($F_{3,12}$=3.80, p=0.041): levels of basking increased and levels of foraging decreased during days with snow but time spent belowground remained unchanged (*post hoc* tests; Figure 5.5). Behaviours were not influenced by time of day nor by the statistical interaction between time of day and presence or absence of snow. When the snow had melted, numerous runways that had been created beneath the snow cover could be seen and these most likely provided access routes to foraging sites. Generally, only heavy snow and rain prevented aboveground activity, but activity continued during light rain and snowfall, and basking behavior was observed occasionally under heavy cloud cover and light drizzle.

a) Radiation



b)Temperature

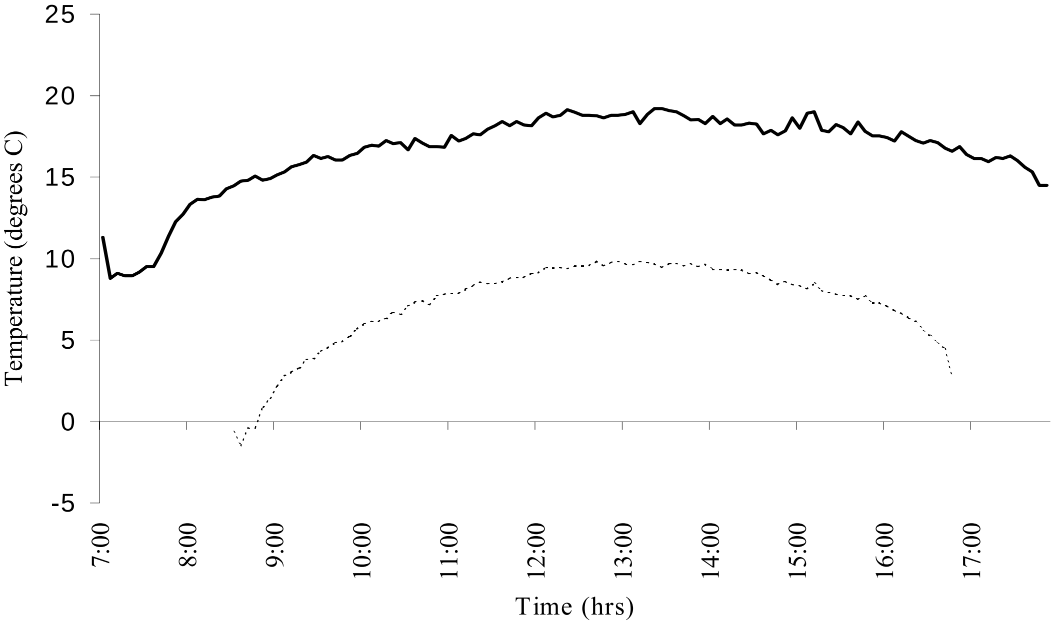
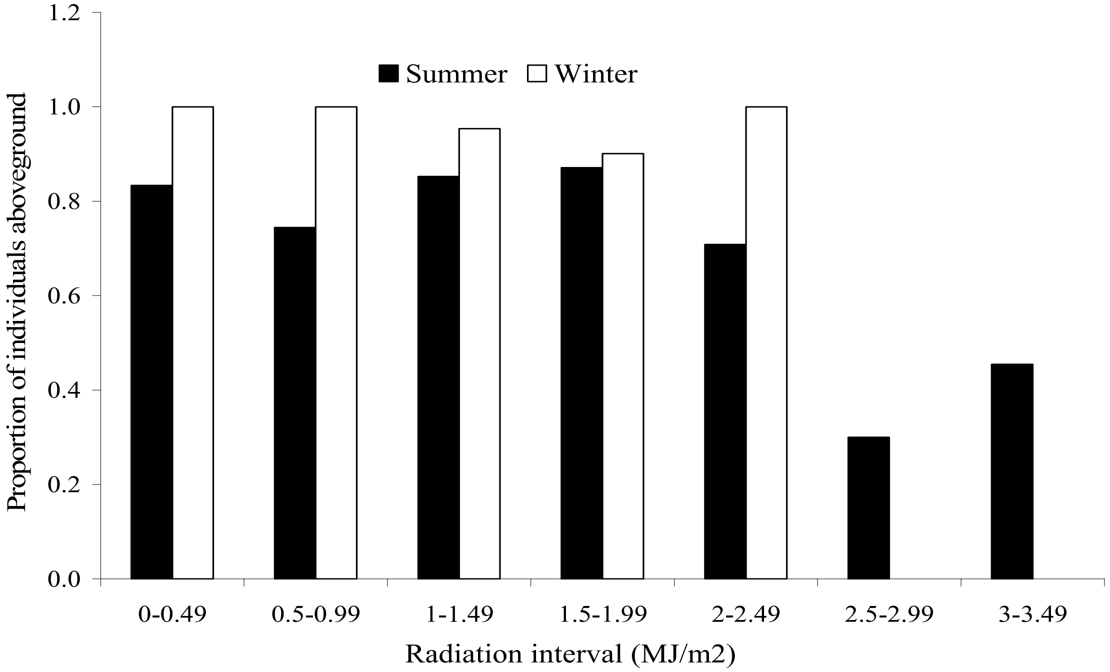


Figure 5.3 Mean a) solar radiation and b) temperature measurements during the day in summer and winter at the study site in the Sani Valley.

a) Solar radiation



b) Ambient temperature

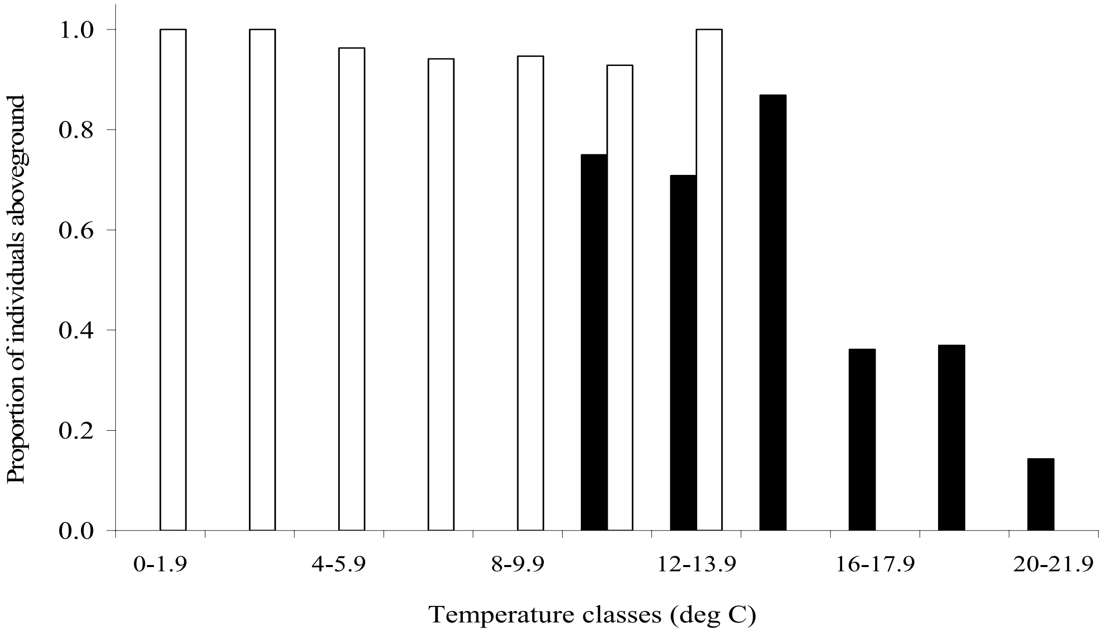


Figure 5.4 The relationship between the proportion of *O. s. robertsi* aboveground and a) solar radiation levels and b) ambient temperature in summer and winter.

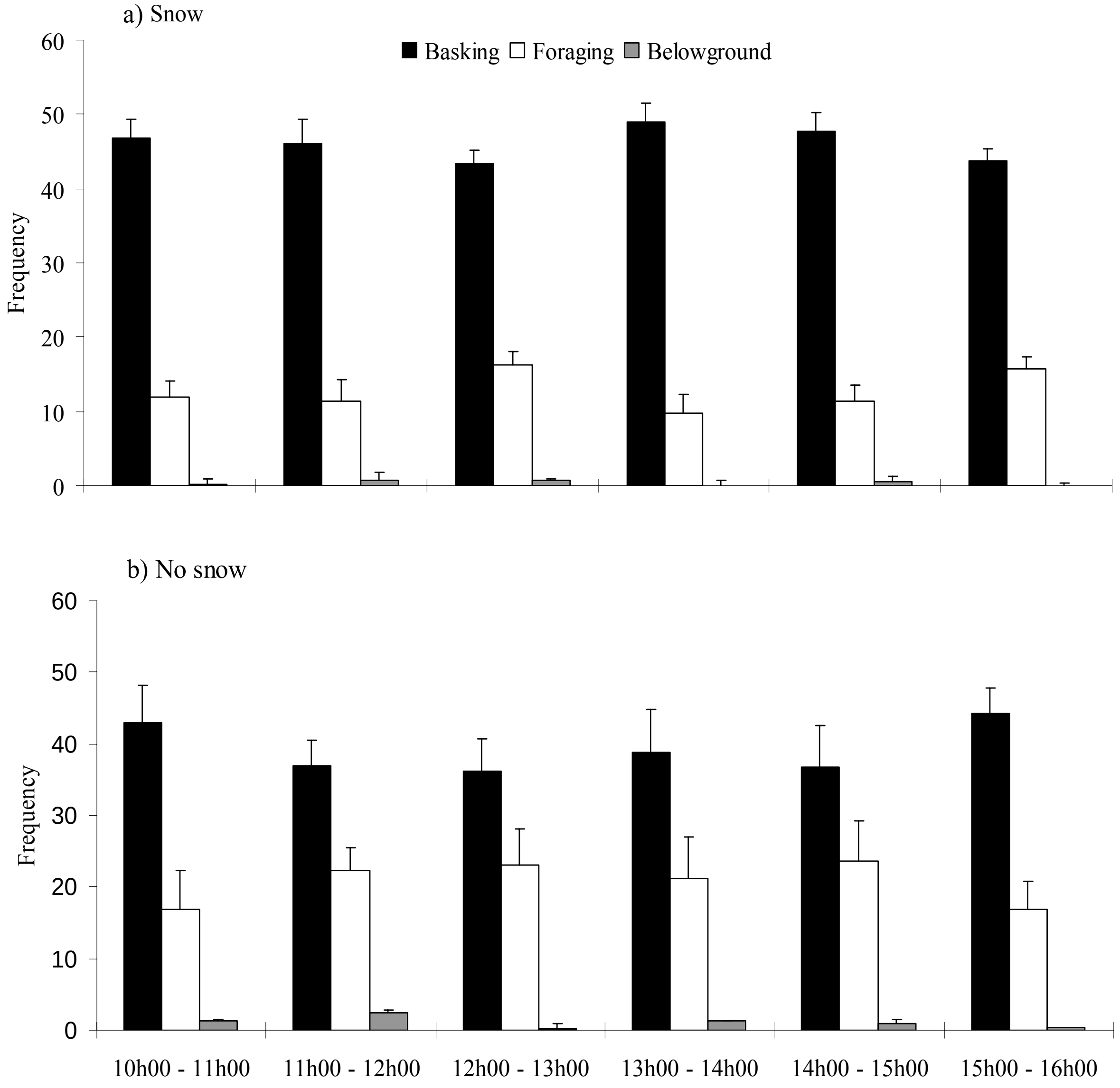


Figure 5.5 Mean (±SE) frequency per one hour spent foraging, basking, and belowground by *O. s. robertsi* during the a) presence and b) absence of snow cover.

5.5 Discussion

The specific thermal microclimate occupied by small rodents has a great influence on their behavior. Due to low thermal inertia, changes in microclimate results in rapid behavioral or physiological responses (Chappell, 1980; Wolf & Walsberg, 1996; Bozinovic *et al.*, 2000). As predicted, *O. s. robertsi* displayed an almost unimodal diurnal activity profile during winter, spending most of their time aboveground foraging or basking before retreating into their burrows after sundown. A bimodal profile was observed in summer, with ice rats disappearing belowground during the middle of the day, a period coinciding with the highest ambient temperatures and levels of solar radiation. These environmental factors did not limit aboveground activity in winter, perhaps because levels of solar radiation and temperature were lower in winter than in summer, but see below.

Ambient temperature is usually the main factor influencing the activity of many rodents (Vispo & Bakken, 1993; Ellison *et al.*, 1994; Eifler & Slade, 1998), including *P. brantsii*, the desert-dwelling relative of the ice rat. *P. brantsii* also spends most of the day aboveground in winter (Nel & Rautenbach, 1974; Jackson, 1998) and displays a bimodal diurnal activity profile in summer, retreating into burrows during the hottest times during the middle of the day (Jackson, 1998). I do not know whether *P. brantsii* is similarly affected by increased solar radiation, since this was not measured. However, solar radiation can also influence activity profiles, as is found in the Harris antelope squirrel *Ammospermophilus harrisi* and the round-tailed ground squirrel *Spermophilus tereticaudus* (Walsberg, 1988).

Although *O. s. robertsi* reaches its zone of thermoneutrality between 26-28°C, ambient temperatures in the Maluti Mountains rarely reach 20°C during most times of the year. Yet high temperatures and solar radiation did influence the activity of ice rats and they even sometimes displayed heat stress. On many occasions (during the day when solar radiation and ambient temperature levels were expected to be high) individuals were observed flattening themselves on a substrate, a behavior associated previously with heat dissipation by increasing the body surface in contact with a cooler substrate (Bustamante *et al.*, 2002).

In both summer and winter, *O. s. robertsi* exhibited a peak in activity early in the morning and late in the afternoon, just before they retreated into their burrows. A similar increase in activity has been observed in *P. brantsii,* as well as in another relative, the mesic-occurring *O. irroratus* (Davis, 1972; Nel & Rautenbach, 1974; Perrin, 1981). These peaks in activity probably result from a combination of factors. In summer, ambient temperatures and solar radiation levels are relatively low in the mornings and evenings and therefore do not constrain aboveground activity (Pritchard & Robbins, 1990). Another reason for high levels of activity observed in the colony during those times may be related to foraging behavior. Since *O. s. robertsi* does not hoard food, at least in the quantities that are likely to sustain them throughout the night (Hinze *et al.*, in review) increased foraging in the mornings may replenish energy stores. In fact, foraging bouts in the mornings were unusually long compared to foraging bouts during the day (personal observation). The peak in activity in the late afternoon may likewise provide the opportunity for feeding before retiring for the night, as no aboveground activity has been observed at night**.** In contrast, *P. brantsii* spends most of its time during afternoon foraging sessions collecting plants for consumption overnight in its burrows (Jackson, 1998). Although *O. s. robertsi* does not hoard food to the same extent as *P. brantsii*, it may compensate for this shortcoming in another way: compared to its relatives living in warmer, low-lying areas, *O. s. robertsi* has a larger gut capacity, particularly its caecum, stomach and small intestine, which may increase the quantity of plant material it can consume per unit time and at the same time increase the retention time of food in the gut (Schwaibold & Pillay, 2003).

Small rodents, such as the thirteen-lined ground squirrel *Spermophilus tridecemlineatusi* (Chappell, 1980; Vispo & Bakken, 1993; Wolf & Walsberg, 1996) which inhabit temperate environments similar to that of *O. s. robertsi* generally limit their activity in the cold by remaining in relatively thermoneutral refugia, by entering into bouts of torpor, or by hibernating in order to conserve energy that otherwise would be spent on thermoregulation. In contrast, ice rats spend most of the daylight hours in winter aboveground, engaged primarily in foraging behavior. Also, *O. s. robertsi* continued to forage for approximately 30 minutes after sunset, exposing it to potentially lethal temperatures. It appears therefore that the energy gained through foraging beyond sunset is traded-off against the energy saved by retiring into the thermoneutral nest chamber (Hinze *et al.*, in review). A major factor limiting the time spent foraging during winter in diurnal vertebrates in temperate areas is the number of daylight hours (Drew & Bissonette, 1997; Eifler & Slade, 1998). For herbivores, another limitation is food quality and quantity, both of which decrease dramatically during winter in the alpine habitats of ice rats, reducing the effective foraging time to approximately ten hours per day. Therefore, foraging by ice rats beyond sunset in winter is likely to increase the quantity of poor-quality food acquired. This could provide the energy requirements for thermoregulation, which is regarded as critical in rodents that do not hoard food for inactive periods (Chappell, 1980; Vispo & Bakken, 1993; Drew & Bissonette, 1997).

Of the 14 hours of daylight in summer, *O. s. robertsi* utilizes only 12 for foraging since activity decreases during the middle of the day. Additional foraging time is apparently not required as ice rats retire belowground at sunset. In summer, the need to avoid high solar radiation and high temperature may limit foraging time, a phenomenon also observed in the degu *Octodon degus*, which inhabits arid habitats in Chile (Bozinovic *et al.*, 2000). However, reduced foraging time in summer is most likely offset by better quality and increased quantity of food in ice rat habitats, and by energy saving behavior such as basking.

The level of aboveground activity observed in ice rat colonies is probably not influenced by predator risk. Although predator avoidance and vigilance behavior were not recorded in this study, these behaviours were rarely observed. Vigilance behavior influences aboveground activity in small rodents, such as *P. brantsii* (Jackson, 1998), but levels of predation in the Sani Valley are virtually non-existent as most of the natural predators of the ice rats have disappeared over the last decade (Willan, 1990). Only two instances of predation on an ice rat by a jackal buzzard *Buteo rufofuscus* were observed throughout the study period. Therefore, aboveground activity is largely influenced by energy acquisition rather than predator avoidance.

In the mornings, most individuals in a colony appeared aboveground within a few minutes of each other to bask briefly before the first foraging session of the day. Similarly, every night around sundown, the members of a colony disappeared belowground within a short period of time. This phenomenon was also observed during the day when individuals in an entire colony retreated belowground, mainly at midday in summer, and later reappeared aboveground, all within a few minutes of one another. Such synchronization of behavior could reflect the social nature of ice rats (Willan, 1990), although the higher than expected incidences of aboveground aggression between colony members (Hinze & Pillay, unpublished data) suggest that the timing may be due to exploitation of favorable environmental conditions (Vispo & Bakken, 1993; Ellison *et al.*, 1994; Eifler & Slade, 1998), particularly following a night spent belowground with little or no food stores. Synchronization of behavior has been also associated with the dilution effect by minimizing the probability of predation risk in large groups (Slater, 1999). Given the low levels of predation in the ice rat I am uncertain as to how the current population in the Sani Valley responds to predation threat, and this needs to be investigated in future.

The presence of snow on the ground, and the persistence of this over a few days, changed the aboveground activity pattern of ice rats. Compared to periods without snow, levels of basking increased and levels of foraging decreased when snow was present. I did observe runways when the snow had melted, which may have provided routes to foraging sites, a phenomenon also observed in voles in the Ural mountain chain (Bolshakov, 1984). Even so, the actual time spent on various activities indicates behavioral priorities change when snow is present. Therefore, prolonged snow cover, apart from lowering ambient temperatures, also decreases foraging opportunities by limiting access to foraging sites, as well as impose thermoregulatory constraints to *O. s. robertsi*. The combination of these factors could therefore be a major cause for mortality observed in winter in *O. s. robertsi* colonies (Willan, 1990; Lynch & Watson, 1992). Similarly, cotton rats (*Sigmodon hispidus*), which suffer population crashes during winter, are negatively affected by the decrease in foraging time available to them in winter (Sauer, 1985; Eifler & Slade, 1998).

The present study revealed that *O. s. robertsi* adjusts its behavior according to prevailing environmental conditions, seasonally, at different times of the day, and during stochastic events like snowfall. Partitioning activity (i.e. trade-offs) into various energy-acquiring (e.g. foraging) and energy-saving (e.g. basking or disappearing underground) behaviors is critical for meeting thermoregulatory requirements in rodents facing extreme environmental conditions (Cabanac & Johnson, 1983; Collier *et al.*, 1989; Schultz *et al.*, 1999). The mechanisms underlying these trade-offs in behaviors need to be investigated further, particularly when snow cover is present and absent. The seasonal variation in behavioral patterns (unimodal in winter and bimodal in summer) is predictable, and occurs also in desert-living *P. brantsii*, probably indicating similar responses to harsh environments. The ice rat is a unique southern African rodent, since it is endemic to alpine habitats to which it is physiologically poorly adapted. My study shows that in addition to several other adaptations, such as its burrow architecture (Hinze *et al.*, in review) and gut structure (Schwailbold & Pillay, 2003), the diurnal activity of ice rats is adapted for life in alpine habitats.

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6 General discussion and conclusion

The ice rat *Otomys sloggetti robertsi* is unique in southern Africa, since it is the only small rodent endemic to the harsh alpine environment of the southern Drakensberg and Maluti Mountains (De Graaff, 1981; Skinner & Smithers, 1990), yet it is poorly-adapted physiologically to conditions in such habitats (Richter *et al*., 1997). My study was concerned with how the environment shapes the sociality and activity patterns of ice rats. I also investigated burrow systems of ice rats to understand their sociality.

6.1 Adaptations for life in alpine environments

Otomys s. robertsi times its aboveground appearances with the warmest times of the day in winter, when a colony of ice rats emerges aboveground in the mornings almost synchronously, as soon as the sun shines onto the colony. Timing aboveground activity with these times of the day reduces thermoregulatory costs and would facilitate sun basking (Cabanac & Johnson, 1983; Collier *et al*., 1989; Schultz *et al*., 1999; Schwaibold & Pillay, unpublished; Chapter 5). Both behaviours most likely maximise energy gain (see Schultz *et al.,* 1999). In contrast, *O. s. robertsi* avoids periods of high temperatures and radiation in summer by retiring belowground around the middle of the day (Chapter 4). Other rodents inhabiting temperate environments also show similar timing of their activity (Vispo & Bakken, 1993; Eifler & Slade, 1998).

Synchronous timing of aboveground appearance could also be a behavioural response, through, for example the dilution effect, to decrease predation risk (Slater, 1999). However, I have argued throughout the thesis that predation risk is minimal in ice rats in the Sani Valley, and that their activity most likely is related to prevailing environmental conditions. Therefore, the activity pattern of *O. s. robertsi* is a result of environmental factors (Chapter 5). Timing aboveground appearances with the most favourable conditions has also been observed in *P. brantsii,* as well as in another ice rat relative, the mesic-occurring *O. irroratus* (Davis, 1972; Nel & Rautenbach, 1974; Perrin, 1981; Jackson, 1998). Similarly, activity patterns are influenced by ambient temperatures in the alpine marmot, which retreat belowground during the hottest times of the day (Türk & Arnold, 1988). In temperate environments, rodents that do not hibernate or go into extended periods of torpor during the winter months need to maximize the time spent foraging or sun basking to take advantage of the short, comparatively warm daylight hours (Perrin, 1981; Drew & Bissonette 1997; Eifler & Slade, 1998).

A colony of ice rats constructs a complex underground burrow system (Chapter 4), which is another strategy to iincrease survival in alpine habitats. The burrow system of *O. s. robertsi* provides an appropriate microclimate by buffering aboveground lethal temperature extremes. In addition, an ice rat burrow system contains only one or two well-insulated nest chambers, which are shared by colony members. This would facilitate communal thermoregulation (Chapter 4), another important behaviour employed by rodents in the temperate northern hemisphere (Madison, 1984; West & Dublin, 1984), and is well developed in the marmots (Armitage, 1990; Arnold, 1990b; Ruf & Arnold, 2000).

Otomys sloggetti robertsi is likely to employ these behavioural strategies to compensate for its physiological shortcomings in relation to low temperatures. Richter *et al.* (1997) hypothesised that *O. s. robertsi* is restricted to high altitudes due to competitive exclusion by *O. irroratus* which occurs at lower altitudes.

6.2 Sociality in the ice rat

My study was concerned primarily with sociality of free-living *O. s. robertsi*. I investigated several components of its social systems, including social interactions through direct observations and experimental manipulations, space use below and aboveground, demography, mating systems and dispersal. All components were not equally represented in the study, mainly because of the difficulties associated with studying ice rats in the field. However, several clear trends emerged. Ice rats live in small colonies, comprising several males and females. I established that ice rats huddle belowground, and although I did not study behaviour belowground directly, there is little doubt that such behaviour was facilitated by tolerance among colony members (see Wolff & Lidicker, 1981; Madison *et al.*, 1984).

In contrast, aboveground contact between individuals was rare, although I measured extensive spatial home range overlap between members of a colony. If individuals met, interactions were usually characterised by high levels of agonistic behaviour and ultimately lead to one individual being chased across the colony by the other individual (Chapter 2). Adding an artificial food source to a colony increased the levels of agonistic interactions within the colony. Intruders from either same or different colonies were aggressively attacked in home ranges of residents. Although sufficient vegetation is available for *O. s. robertsi* in summer, these resources become limited during the dry and cold winter months (Schwaibold & Pillay, 2003), resulting in high levels of aggression observed at the experimentally introduced food source in winter. Ice rats have increased nutrient demands in winter due to the high thermoregulatory costs associated with the extremely cold temperatures (Schwaibold & Pillay, 2003). Ice rats forage in distinct food patches throughout the year (Schwaibold, unpublished data), and limiting food availability therefore probably promotes territoriality in winter. Due to the short growing season in the alpine habitat, food becomes a limiting factor for the herbivorous ice rats in summer as well. Defending a food source in an environment where food is not readily available has been described as an important cue for territoriality in small mammals (Ostfeld, 1985, 1990).

Willan (1990) suggested that an ice rat colony consists of a founder pair and their offspring, and that reproductive inhibition restricts reproduction to that pair only. In contrast, the promiscuous mating system observed in *O. s. robertsi* in this study seems a logical consequence of an aggregated group of individuals, where several males and females maintain temporal non-overlapping home-ranges (Clutton-Brock & Harvey, 1978; Clutton-Brock, 1982; Boonstra *et al.*, 1993). Willan (1990) based his results on a laboratory study and *ad hoc* observations of free-living ice rats, which could have resulted in the differences observed in the sociality of *O. s. robertsi* between my study and that of Willan (1990). Environmental variables, such as changes in the climate or the predator density could have also influenced the sociality of *O. s. robertsi* during the past 15 to 23 years.

Aggression between members of a colony probably lead to dispersal of the offspring once they reached sexual maturity, although Willan (1990) observed some offspring that remained with their parents. Dispersal influences population fluctuations (Cockburn, 1992). There are several types of dispersal, such as breeding dispersal by females, where females abandon their nests to their offspring, or male-biased natal dispersal in which males leave their natal colony in search of mates (Cockburn, 1992), but the details of the dispersal pattern in *O. s. robertsi* is still unresolved. Yellow-bellied marmot *Marmota flaviventris* colonies, for example, consist of matrilines and one resident male, resulting in a harem-polygynous mating system (Armitage, 1998). Daughters are recruited into the colony, whereas males disperse after spending the first hibernation with the family group (Arnold, 1990a). Most of the other marmot species however live in family groups with a monogamous territorial pair, subordinate adults, yearlings and young (Arnold, 1990a). Here, the marmot offspring usually disperse after their second or third hibernation with their natal colony, thereby delaying their own reproduction (Arnold, 1990a). In prairie voles *Microtus ochrogaster*, inhabiting temperate environments, individuals generally remain in their family groups for varying amounts of time and subsequently, individuals disperse in search of a mate (McGuire & Getz, 1995).

I studied only the first litters born in a breeding season, and it is questionable whether litters born later in the breeding season will also disperse, since they will be exposed to harsh conditions. I predict that these litters either form associations with other ice rats after dispersal or more likely that they overwinter in their natal burrow (see Willan, 1990), thereby increasing their chances of survival by communal thermoregulation (huddling) with their family group (Arnold, 1990a).

6.2.1 Sociality in other otomyines

The murid subfamily Otomyinae consists of representatives living in a variety of habitats in sub-Saharan Africa (Kingdon, 1997). Although very little is known about many otomyine species, such as *O. laminatus* (De Graaff, 1981; Skinner & Smithers, 1990), published information is available for several species (reviewed in the introduction), and I compare my results with information for these species in this section (Table 6.1).

Otomys irroratus and *O. angoniensis* inhabit the more mesic eastern parts of southern Africa (Skinner & Smithers, 1990), which are characterised by long growing seasons and abundant food resources (Davis, 1974). However, *O. irroratus* inhabits areas along wetlands (referred to locally as vleis) whereas *O. angoniensis* prefers the drier areas along rivers, swamps and wetlands (Skinners and Smithers, 1990), as well as grasslands and savannah woodlands (De Graaff, 1981). These species are surface-nesters, and nests are usually constructed under overhanging grass or rocks, although they will use abandoned burrows constructed by other animals (Davis, 1972; Packer, 1980; Phillips *et al*., 1997). *Otomys irroratus* displays temporal territoriality and mates promiscuously, where males compete within a hierarchical framework for females (Davis & Meester, 1981; Willan, 1982; Brown, 1988; Pillay, 1993). Offspring disperse due to population pressure, and usually move into previously vacated areas (Davis, 1973; Pillay, 1993) (Table 6.1). Less is known about *O. angoniensis*, but field reports indicate that this species occurs singly, in pairs or as families (De Graaff, 1981; Skinner & Smithers, 1990; Pillay, 1998), and natal philopatry is suspected (Pillay, 1998). Territoriality in *O. irroratus* is apparently related to competition for limiting space availability (Willan, 1982; Pillay, 1993), whereas small families in *O. angoniensis* are probably related to increased predation risk in their comparatively open habitats (Phillips *et al*., 1997)

The arid living species *O. unisulcatus*, *Parotomys brantsii* and *P. littledalei* occur in the harsher (arid to semi-arid) western parts of southern Africa (Skinner & Smithers, 1990). The nests of these otomyines are sheltered from temperature extremes experienced in their habitat, either belowground in burrow systems (*P. brantsii* and *P. littledalei*; Jackson, 2000; Jackson *et al*., 2002) or in stick lodges (*O. unisulcatus*; du Plessis *et al.*, 1992; Jackson *et al.*, 2002). The whistling rat *P. brantsii* is solitary and exhibits scramble competition polygyny (Coetzee & Jackson, 1999). Although similar social and mating systems are predicted for *P. littledalei* and *O. unisulcatus* (Coetzee & Jackson, 1999; Pillay, 2002), this still needs to be confirmed. Dispersing *P. brantsii* utilize unoccupied warrens, or establish a territory within an occupied warren. Territoriality in *P. brantsii* is a result of limited resources, mainly food and mates (Jackson, 1999).

Table 6.1 Variability of the sociality and nesting habits of the genus *Otomys* inhabiting a variety of habitats.

Species	Habitat	Nesting habits	Social system	References
O. irroratus	Mesic	Surface	Territorial/solitary	Davis, 1972; Davis & Meester, 1981; Skinner & Smithers, 1990
O. angoniensis	Mesic	Surface	Territorial/small families	Packer, 1980; Skinner & Smithers, 1990; Phillips *et al.*, 1997
O. unisulcatus	Semi-arid, arid	Stick lodges	Solitary/pairs/families	Skinner & Smithers, 1990; du Plessis *et al.*, 1992; Jackson *et al.*, 2002; Pillay, 2002
P. brantsii	Semi-arid, arid	Underground burrows	Territorial/gregarious	Skinner & Smithers, 1990; Coetzee & Jackson, 1999; Jackson, 2000; Jackson *et al.*, 2002
P. littledalei	Semi-arid, arid	Underground burrows	Territorial/gregarious	Skinner & Smithers, 1990; Coetzee & Jackson, 1999; Jackson, 2000; Jackson *et al.*, 2002
O. s. robertsi	Alpine	Underground burrows	Spatial variation in sociality:social belowground, temporal territoriality aboveground	Willan 1990, this study

6.2.2 Sociality of *O. s. robertsi*: ecological adaptations versus phylogenetic constraints

Social systems are fundamentally determined by inter-individual social interactions (Happold, 1976; Barash, 1989), and the degree of sociality exhibited by a species is ultimately determined by environmental conditions (Happold, 1976; Armitage, 1999). Therefore, group living under particular environmental conditions may be viewed as a life-history tactic that increases the fitness of the individuals sharing the environment with conspecifics (Wilson, 1975; Deag, 1980; Armitage, 1981). In marmots, for example, reaching an ideal body mass for successful hibernation within the relatively short reproductive season provides the basis for the evolution of group living, and high levels of amicability occur between colony members in most marmot species. As a result of the short growing seasons, marmot juveniles need to remain with adults for at least two summers to reach a particular body size to improve their chances of successful dispersal, and therefore delayed dispersal and retention of juveniles in the natal group form the basis of a social group (Barash, 1974; Armitage, 1999).

Communal thermoregulation is common in small mammals inhabiting temperate environments, since conspecifics share refugia in winter to facilitate communal thermoregulation (Madison, 1984; West & Dublin, 1984; McGuire *et al.*, 2002). However, territoriality among individuals is rare in these species, since tolerance of conspecifics is a usually requirement or a consequence of sharing a refuge. Therefore, the spatial change in the social behaviour in ice rats is unusual for an alpine rodent. While temporal variability in social systems has been observed in a number of rodents (Wolff & Lidicker, 1981; Madison *et al.*, 1984), spatial variability is rare in free-living rodents (Wallen, 1982; Schradin & Pillay, 2004). The yellow-bellied marmot *Marmota flaviventris*, for example, lives in distinct colonies, but individuals within a colony maintain separate home ranges aggressively and social interactions are rare occurrences (Barash, 1974; Armitage, 1999).

Ice rats display a number of behavioural adaptations (e.g. timing of aboveground activity, sun basking) that are also occur in rodents inhabiting temperate environments (Türk & Arnold, 1988; Walsberg, 1988; Bacigalupe *et al*., 2003). Environmental conditions also influence the social system of ice rats. Huddling belowground most likely compensates for physiological shortcomings in ice rats, particularly when ambient temperatures are low. In contrast, competition for patchily distributed food resources (Schwaibold & Pillay, unpublished data) aboveground results in high levels of aggression among colony members, leading to temporal territoriality. Territoriality is displayed by most other Otomyinae, including the arid-living whistling rats *P. brantsii* and *P. littledalei* (Davis & Meester, 1981; Coetzee & Jackson, 1999; Jackson, 1999), and temporal territoriality occurs in the vlei rat *O. irroratus* (Willan 1982; Pillay 1993). In these three otomyines, individuals compete for food and suitable nest sites. I therefore suggest that the aboveground temporal territoriality in *O. s. robertsi* is also a phylogenetic constraint imposed by competition for limiting food in its alpine habitat. Temporal territoriality may be an adaptation for colony members, which otherwise huddle belowground, to avoid damaging fights.

The social behaviour of ice rats varies along a sociality continuum, and it appears that the resulting social system of the taxon is a compromise between competing needs below and aboveground. Such compromises are also evident in other aspects of its biology. For example, the combination of a long gestation period, small litter size and fecundity, delayed aboveground emergence, and well developed parental care in ice rats (Willan, 1990; Chapter 3) are usually characteristics of species inhabiting stable environments (Pianka, 1970), and not the harsh and unpredictable alpine habitats. Willan (1990) suggests the life history traits of ice rats represent a compromise between plesiomorphic otomyine characteristics (i.e. phylogenetic constraints) and adaptations to low temperatures, short growing seasons and stable microclimates created by underground burrows.

6.3 Conclusions and future studies

This study has added to the knowledge of a previously poorly studied otomyine, *O. s. robertsi*. The ice rat was the only small mammal in my study site, although distinctive mounds suggested the presence of mole rats in the same habitat. Therefore this study was conducted under almost ideal conditions of limited predator pressure and little or no competition from other small mammals, which are known to influence social systems in other small mammals (Alexander, 1974; Hoogland, 1995; Armitage, 1998). Therefore, my study has shown how environmental factors have influenced the social system of ice rats. Huddling belowground is an important social behaviour but the energetic gains that are achieved through this behaviour are unknown in the ice rat and worth investigating (see Canals *et al.*, 1989).

This study of the social structure of *O. s. robertsi* has shown the value of field based behavioural research. I confirmed information obtained from earlier studies, such as *O. s. robertsi* lives in colonies (Willan, 1990) and displays behavioural adaptations to its alpine habitat (Richter, 1997; Richter *et al.*, 1997). However, my study also revealed new information about the social behaviour and social system of ice rats. It is also important to note that my study was conducted during a time when ice rat population density was high (compared with Willan, 1990). Since population density influences space use and social organisation (Deag, 1980; Jackson, 1999), it would be interesting to investigate the relationship between these variables in ice rats over time, particularly how population densities are influenced by climatic changes and whether erosion reduces the amount of suitable habitat for burrowing and dispersal.

Whereas predator pressure was comparatively low in the Sani Valley, ice rats are hunted by the local herdsman in other areas of the Maluti Mountains, and other populations experience higher predation risk (Schwaibold & Pillay, unpublished data). The relationship between predation pressure and social structure is well established (e.g. Hoogland, 1995).

Although the social behaviour between individuals within a colony has been established in this study, there is no information available about the kinship within the colony. In addition, the reproductive data collected in the field indicate that almost all sexually mature colony members are reproductively active, and I observed a few incidences of promiscuous matings. The application of DNA fingerprinting analysis (Asher *et al.*, 2004; Spritzer *et al.*, 2005) may resolve the relationships between colony members and between adults and offspring. Such genetic markers will give an indication of philopatry and the dispersal pattern of ice rats.

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