Foraging biology and habitat use of the southern African ice rat *Otomys sloggetti robertsi*

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

Ute H. Schwaibold

___________day of________________________2005

ABSTRACT

Animals living in cold environments show physiological, morphological and behavioural adaptations to low temperatures. The African ice rat, *Otomys sloggetti robertsi*, which is endemic to the southern African Drakensberg and Maluti mountains above 2000m, is an interesting exception since, unlike most alpine small mammals, it does not hibernate or display torpor and is physiologically poorly adapted to low temperatures. It is a strict herbivore, feeding on a low quality diet. Ice rats do show some morphological (e.g. short tails) and behavioural (e.g. communal huddling; constructing underground burrows) adaptations, but little else is known about their biology, particularly how they maximise energy gain to meet thermoregulatory requirements, especially during cold periods. Since feeding represents the primary method of energy gain in endotherms, I studied aspects of the foraging biology of ice rats, including gut structure, foraging patterns and habitat choice. The gut structure of *O. s. robertsi* is well adapted for a high fibre, herbivorous diet and shows broad similarities with those of its mesic- and arid-occurring relatives. However, *O. s. robertsi* showed increased dimensions of several foregut organs which may be adaptations for increased energy uptake and/or poor diet quality in alpine environments. Furthermore, females had a larger stomach as well as a longer caecum, small and large intestine in summer than in winter but the gut of males was unaffected; such sexual asymmetry may be related to increased energy requirements of females during pregnancy and lactation.

Environmental influences on the aboveground behaviour of *O. s. robertsi* were investigated by recording the duration of behaviours as well as sequential transitions among behaviours. Ice rats spent most of their day foraging and basking, and much time was spent in their underground burrows. Seasonal comparisons revealed that ice rats spent significantly more time acquiring energy through foraging in winter, whereas they remained below ground for longer periods of time during the middle of the day in summer to escape extreme heat and solar radiation.

To understand how low temperatures and predation influenced foraging patterns, the behaviour of ice rats was studied in summer and winter in a population where predators were minimal and in another population which experienced higher levels of predation. Ice rats are central place foragers that travel short distances to forage and display significant seasonal variation in their foraging patterns. In the absence of predation risk, ice rats generally returned to a central place with forage, even though returning to a burrow after foraging in winter was energetically costly. However, these costs must be weighed against the benefits of avoiding exposure to low temperatures by feeding under cover as well as the loss of collected food and possible injury associated with aggressive interactions with conspecifics. Under moderate predation pressure in both seasons, ice rats followed a central place foraging strategy to minimise predation risk, always returning to a burrow entrance with forage collected elsewhere. However, when no perceivable threat was observed, ice rats displayed 'optimal' foraging patterns in summer similar to those recorded in the absence of predation pressure and only returned to a burrow with forage as distance from that burrow increased, suggesting that ice rats display facultative foraging decision making in response to multiple environmental cues.

The distribution of occupied ice rat burrows was correlated against several environmental factors to determine microhabitat requirements. Ice rat burrows were situated in close proximity to herbaceous and wetland plants, but away from woody vegetation, suggesting that habitat choice is related to the presence of food plants and reduction of shade, facilitating short travel distances during foraging as well as promoting basking.

Despite the physiological shortcomings of ice rats, the gut structure, foraging behaviour, and habitat choice of the taxon are adapted for life in cold alpine habitats, most likely by maximising energy intake. Similarities in foraging behaviour and habitat use between *O. s. robertsi* with its closely-related arid-occurring relative *Parotomys* spp. suggest phylogenetic influences, but it is possibly more a reflection of similar phenotypic responses to the extreme habitats inhabited by these otomyines.

DEDICATION

In memory of my father
Wolfgang F. Schwaibold (1944-2000)
who supported me throughout my studies.

With thanks to my family:
Marianne and Marc
for believing in me.

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CONTENTS

CHAPTER SIX: Microhabitat selection by the ice rat *Otomys sloggetti robertsi* in Sani Valley, Lesotho........ 105

LIST OF FIGURES

CHAPTER ONE:

CHAPTER THREE:

CHAPTER FOUR:

CHAPTER FIVE:

CHAPTER SIX:

LIST OF TABLES

CHAPTER TWO:

CHAPTER THREE:

CHAPTER SIX:

CHAPTER ONE: Introduction

Small mammals in alpine environments

The survival and reproductive fitness of any animal depends on its ability to allocate sufficient time and energy to a range of competing demands such as foraging, maintenance and reproduction (Schoener, 1971; Schultz *et al.*, 1999). In alpine and subalpine environments this ability becomes even more crucial. Small mammals in these conditions must cope not only with low temperatures in summer and extreme cold and snow in winter, but with unpredictable and changing weather patterns throughout the year (Happold, 1998). In addition, the growing season is restricted to a few months and food availability is limited (Killick, 1978; Barash, 1989), and it is therefore essential that small mammals maximise their energy intake (e.g. through foraging) while at the same time minimising energy loss (e.g. by exposure to low temperatures). However small mammals, due to their small body size, are prone to rapid heat loss and this, combined with their high metabolic rates, reduces their ability to store large energy reserves internally (Schultz *et al.*, 1999).

To cope with the demands of living in cold environments, small mammals display several morphological, physiological and behavioural adaptations. These include thicker pelage (Chappell, 1980), torpor and hibernation (Geiser and Ruf, 1995), elevated metabolic rates (Weiner and Heldmaier, 1987), modified gut structure (Bozinovic *et al.*, 1990), changes in body tissue (Quay, 1984), sun-basking (Geiser *et al.*, 2002), social huddling and nest-building (West and Dublin, 1984; Schultz *et al.*, 1999).

The effects of cold and especially the presence of snow in winter have formed the basis for a range of studies on the biology of small mammals in alpine and subalpine environments (reviewed in Happold, 1998). While an animal’s physiology is undoubtedly important for survival under these extreme conditions, habitat selection and behavioural adaptations have also been found to affect the ability of animals to cope (Johnson and Cabanac, 1982; Happold, 1998; Schultz *et al*., 1999).

Microhabitat selection and use

Generally, habitat selection describes the process by which animals make behavioural decisions about where to live, which is reflected in their use of space (Stapp, 1997). For many animals these behavioural decisions are based on hierarchical responses to multiple habitat cues, although these responses are less obvious in small mammals as, due to their small size and thus based on the size of their home range or dispersal range, they can only sample a small area within an otherwise extensive and possibly diverse habitat (Johnson, 1980).

Most animals are capable of some degree of habitat selection. As the main reason for animal movement within a habitat is finding more rewarding foraging patches (Charnov, 1976), suitable habitats are often chosen based on proximity to these food patches. Other important factors influencing habitat choice are predation pressure, in which case animals tend to select habitats with more vegetation cover, and interspecific competition (Falkenberg and Clarke, 1998) which may result in microhabitat partitioning (Jorgensen, 2004).

In cold environments, other factors such as protection from low ambient temperatures may influence microhabitat selection. Endotherms, for example, will choose microhabitats with temperatures as close to their thermoneutral zone as possible (Johnson and Cabanac, 1982), thereby reducing the need for active thermoregulation. Furthermore, vegetation and topography may affect the microclimate experienced by small mammals and may therefore significantly determine their microhabitat choice within the limits of their distribution (Happold, 1998). Woodchucks *Marmota monax* select suitable hibernating habitats based on sufficient plant cover such as brush or forested areas which provide better insulation against prolonged persistence of snow (Barash, 1989). However, general macroclimatic phenomena do not necessarily correspond with the microclimate that small mammals may be experiencing, since the climate (e.g. temperature, wind factor) close to the ground may differ from that above the shrub layer (Geiger, 1965). For example, the shade from shrubs results in lower temperatures at ground level than air temperatures, whereas at night shrubs act as a form of insulation and buffer the ground against low ambient temperatures (Eurola *et al.*, 1984).

Physiological adaptations

Most small mammals living in cold environments cope with these extreme conditions through physiological adaptations. Torpor and hibernation are common in high altitude species such as marmots (*Marmota* spp.; Barash, 1989; Müller, 1986). Other species generate heat through shivering and non-shivering thermogenesis (e.g. degus *Octodon degus* and the leaf-eared mouse *Phyllotis darwini*; Nespolo *et al.*, 2001) or conserve heat through increased vasoconstriction in appendages (Adolph and Lawrow, 1951) and increased insulation through integumentary changes or added body fat in winter is common in non-hibernating small mammals (e.g. deer mice *Peromyscus* spp. and voles *Microtus* spp.; Quay, 1984). Morphological modifications may also serve a physiological role. Bozinovic *et al*. (1990) found that the South American field mouse *Abrothrix andinus,* a non-hibernating rodent found in the cold and harsh environments of the Andes, showed significant increases in the length and mass of the whole gut, and the lengths of the small and large intestine, which are likely to improve energy uptake during digestion.

Behavioural adaptations

In addition to physiological adaptations to extreme cold conditions, most small mammals also show behavioural adaptations (Türk and Arnold, 1988), including social huddling, nest-building and sun-basking. While communal huddling and nest-building increase thermal insulation and reduce energy loss in rodents (Glaser and Lustick, 1975; Andrews and Belknap, 1986), basking facilitates energy gain during cold periods via absorption of radiant energy (Barash, 1989). Even though the most common behavioural means of acquiring energy in small mammals is through foraging (Schultz *et al.*, 1999), energy gained from radiant heat may compensate for the limited energy intake from lower quality food under cold conditions and allow for metabolic needs to be met. There is growing evidence that mammals employ basking as a means of rewarming after torpor, thus allowing for lost heat to be restored without any thermoregulatory costs (Geiser *et al.*, 2002). Other studies have found mammals to bask for thermal comfort and energy conservation (Bartholomew and Rainy, 1971).

Nevertheless, in cold environments small animals are faced with conflicting demands of gaining energy through foraging and energy conservation through reduced exposure to low temperatures (Johnson and Cabanac, 1982). Also, time spent foraging reduces the time spent in passive energy acquisition (e.g. basking), which in turn affects overall energy gain. Therefore, small mammals usually display behavioural flexibility by partitioning their time and energy spent on foraging, basking, huddling and other maintenance behaviours (Schultz *et al.*, 1999).

Foraging behaviour

Under natural conditions an animal's fitness is directly affected by its ability to allocate time and energy to finding, handling and consuming food, without impacting on the time and energy spent on other behaviours (Schoener, 1971; Bautista *et al.*, 1998), which is the basis for optimal foraging theory. There are many demands on an animal's time such as sleeping or resting, nest maintenance and searching for mates, so that foraging will not occupy all of the day (reviewed by McFarland, 1975). In addition, foraging is also strongly influenced by numerous external factors such as predation risk (Lima and Dill, 1990) and food availability (Bautista *et al.*, 1998), the presence of conspecific competitors (Schröpfer and Klenner-Fringes, 1991; Krebs and Davies, 1993) and prevailing weather conditions (Stouder, 1987; Sergio, 2003). Grey squirrels *Sciurus carolinensis*, for instance, reject more profitable food items if they locate larger items of less profitable food that could be consumed under cover (Lima and Valone, 1986), thus trading off energy gain against predator avoidance when the most profitable areas for foraging are also the most dangerous areas. As environmental conditions vary over time (e.g. from daily variations to seasonal changes), an animal may need to modify its foraging behaviour temporally in response to changing energy needs (Schultz *et al.*, 1999) and increased thermoregulatory challenges will affect foraging patterns and may result in trade-offs between foraging efficiency and reduced exposure to extreme temperatures (Johnson and Cabanac, 1982). For example, desert antelope ground squirrels *Ammospermophilus leucurus* (Hainsworth, 1995) and thirteen-lined ground squirrels *Spermophilus tridecemlineatus* (Vispo and Bakken, 1993) 'shuttle' between hot desert surfaces where they forage and cool burrows where they escape high temperatures. Likewise, the South American degu (*Octodon degus*) adjusts its activity patterns in response to increasing ambient temperatures by increasing time spent in shade cover (vegetation, rocks; Kenagy *et al.* 2004) or underground if shade is absent (Kenagy *et al.* 2002). Further, Bozinovic *et al.* (2000) found that degus reduce time spent foraging when ambient temperatures increased. Similar patterns could apply to rodents in cold environments.

Commonly, animals exposed to cold conditions are found to adjust their behaviour patterns to facilitate increased foraging and thus increasing overall energy intake (see Johnson and Cabanac, 1982; Perrigo and Bronson, 1985). Similarly, seasonal behavioural changes have also been reported in hibernating species such as marmots (see Barash, 1989). In addition, hoarding is a common behavioural strategy displayed by animals in cold environments and occurs when food is abundant in preparation for future limitations as a result of unpredictable food supply associated with a drop in temperatures (Wood and Bartness, 1996).

Of the many theories associated with optimal foraging models, central place foraging refers to animals that repeatedly return to a fixed point with food items gathered elsewhere (Bryant and Turner, 1982). Typical examples of this behaviour are found in animals that hoard food such as in the grey squirrel (Lessels and Stephens, 1983), as well as animals coping with predators, since returning to a central place (e.g. burrow) reduces predation risk (Lima and Dill, 1990)**.**

The ice rat *Otomys sloggetti robertsi*

The ice rat *Otomys sloggetti robertsi* is poorly studied, which may be because of the remote areas it occupies. In this section I provide some information about the aspects of the general biology of *O. s. robertsi* which are essential for the aims of the study and interpretation of results presented in this thesis. For comparison, I also provide information for its closest relatives for which published information is available.

Phylogeny

The murid rodent subfamily Otomyinae is widely distributed in sub-Saharan Africa (Kingdon, 1974). Two genera are recognised within the subfamily - the vlei rats *Otomys* and the whistling rats *Parotomys*. In southern Africa, six *Otomys* and two *Parotomys* species exist (Meester *et al*., 1986). These species are distributed across the primarily east-west southern African rainfall gradient (Davis, 1974; Skinner and Smithers, 1990) with representatives occurring in both the wettest and driest habitats. While Brants' whistling rat *Parotomys brantsii* and Littledale's whistling rat *Parotomys littledalei* are endemic to the arid regions of southern Africa, the genus *Otomys* has representatives in both the mesic and arid regions of the subregion. The vlei rats *Otomys angoniensis* and *Otomys irroratus* are adapted to mesic environments, while the bush Karoo rat *Otomys unisulcatus* is found primarily in arid environments. The ice rat *Otomys sloggetti robertsi* Hewitt, 1927 is one of five subspecies of *O. sloggetti* that occur in the mountain regions of the eastern parts of southern Africa (De Graaff, 1981) and is endemic to the southern African Drakensberg and Maluti mountains (Roberts, 1951). It shares with other members of this family characteristics reflecting adaptation to a mesic environment such as renal morphology (Pillay *et al.,* 1994), yet unlike its close relatives, the subspecies is confined to altitudes exceeding 2000m, restricting it to the subalpine (1830-2895m) and alpine (2860-3484m) phytogeographic belts (defined by Killick, 1978). It is apparently restricted to the microthermal highlands of Lesotho (Willan, 1990) and 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 sperm structure (Bernard *et al*., 1990; 1991), allozyme electrophoresis (Taylor *et al*., 1989) and immunoblot (Meester *et al*., 1992) analyses shows a dichotomy between the arid species restricted to the western parts of southern Africa (*P. brantsii, P. littledalei* and *O. unisulcatus*) and the mesic species found in the eastern parts (*O. angoniensis* and *O. irroratus*). Interestingly, *O. s. robertsi* falls into the arid group despite living in the eastern parts of southern Africa. However, recent mtDNA studies suggest that the position of *O. s. robertsi* within this arid group is equivocal, indicating that the phylogeny is not yet resolved (Maree, 2002).

Description

The pelage of ice rats is reddish-brown, soft and thick with rusty-yellow colouring at the sides of the snout and behind the ears. They have relatively short tails (60-70mm) and reduced ears (16-17mm; Willan, 1990). Adults can reach up to 150-170 mm in length and weigh between 120g and 140g, and males tend to be about 10% larger than females (Willan, 1990).

Habitat

Otomys s. robertsi is abundant in suitable habitats with 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). These burrows may provide suitable warm microhabitats with below-ground temperatures being 1-2° C higher than above-ground ambient temperatures (Hinze, unpublished). The name ‘ice rat’ reflects its habit of emerging from shelter to sun itself during cold weather, particularly in winter when ice or snow are on the ground (Skinner and Smithers, 1990).

Among the arid-adapted otomyines, the microhabitat distribution of *O. unisulcatus* is apparently related to the presence of suitable woody plants for nesting and food (Brown and Willan, 1991), whereas *P. brantsii* prefers areas with deep sandy soils for the construction of its complex underground warrens (du Plessis and Kerley, 1991), and *P. littledalei* is restricted to areas with good soil for burrowing and adequate cover (Jackson, 2000). Among the mesic-adapted species, at least in *O. irroratus* habitat selection appears to be influenced by the presence of adequate plant cover (Willan, 1982; Pillay, 1993).

Foraging behaviour and diet

All otomyines are specialist herbivores that feed more or less exclusively on green plant material (Roberts, 1951), although there is slight directional modification of the diet, depending on the availability of suitable food plants (Jackson and Spinks, 1998). While mesophylic otomyines such as *O. irroratus* feed primarily on green plant material (Perrin, 1980), the ice rat has a varied diet within the constraints of herbivory and has been found to feed on floral parts of grasses and herbaceous plants as well as on leaves and stems (U. Schwaibold, unpublished data). A similar diet breadth has been found in *O. unisulcatus* (Brown and Willan, 1991).

Previous studies on *P. brantsii* have shown that its foraging patterns change from summer to winter (Nel and Rautenbach, 1974). Foraging time, for instance, has been found to change in relation to season, being shorter during the summer season as more time is spent underground during hot days (Jackson, 1998). Furthermore, *P. brantsii* was shown to be a central place forager and its foraging behaviour was strongly determined by predation pressure (Jackson, 2001). This species forages within the limits of its warren systems and ventures out from protection to gather food, while *P. littledalei* hardly ever leaves the protection of bushes to forage (Coetzee and Jackson, 1999). Similarly, solitary foraging by *O. unisulcatus* appears to be restricted to the immediate vicinity of cover, while groups forage further away from a nest (Vermeulen and Nel, 1988).

Sociality and reproduction

Within the otomyine family, *O. irroratus* (Davis and Meester, 1981), *P. brantsii* and *P. littledalei* (Jackson, 1999; 2000) are solitary living, while *O. angoniensis* and *O. unisulcatus* sometimes live in small groups (Skinner and Smithers, 1990). *Otomys s. robertsi* has also been seen to live in groups (Willan, 1990), although previous research by Hinze (unpublished) suggests spatial variation in sociality, with ice rats displaying temporal territoriality aboveground as a result of competition for resources, and social behaviour belowground for huddling.

The breeding season of the ice rat extends from October to March and in captivity ice rats have shown a gestation period of about 38 days and mean litter size of 1.44 young (Willan, 1990). In fact, the litter size of all southern African otomyine species never exceeds five pups; perhaps a consequence of females having only four nipples and the young nipple-clinging (Pillay, 2001). Young ice rats are born semi-precocial (10.6 – 12.2g), weaned at 16 days of age and sexual maturity is reached at 16 weeks in males and 11 weeks in females (Willan, 1990). Despite the harsh environmental conditions in its alpine habitat, the reproductive biology of *O. s. robertsi* is characterised by low reproductive output (i.e. long gestation period, small litter size, low reproductive effort and fecundity and well-developed parental care), apparently due to the stable microclimate created by underground nests, huddling and hoarding (Willan, 1990).

Physiological considerations

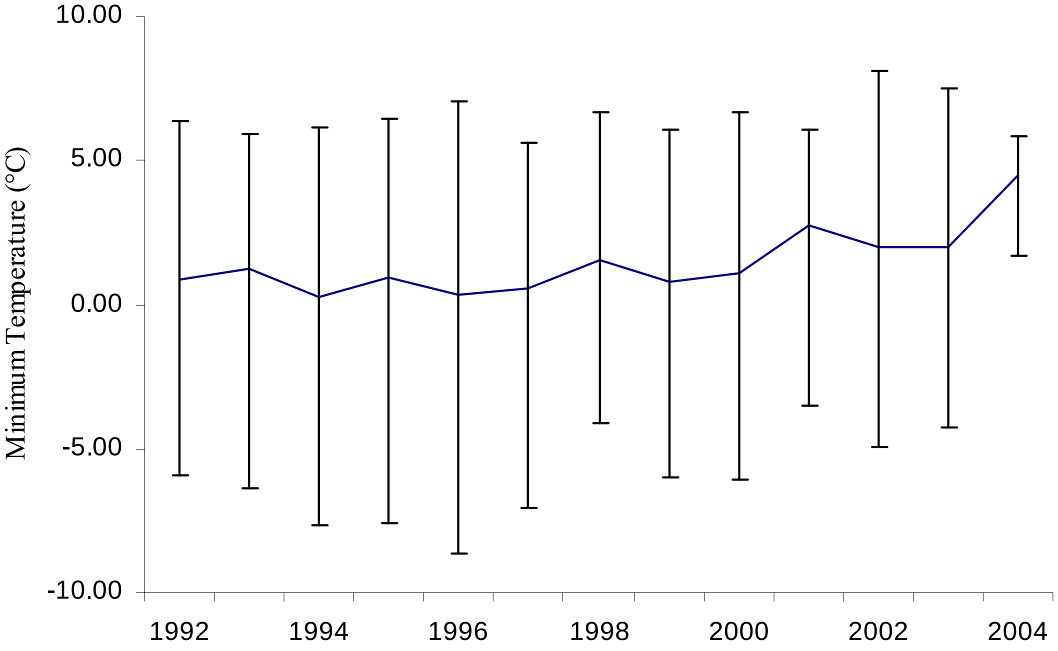
Otomys sloggetti robertsi is not physiologically adapted to the temperature extremes in its habitats. Laboratory experiments done by Richter *et al.* (1997) have shown that oxygen consumption (VO_2) decreases linearly with increasing temperature between 0.7°C and 26.0°C, with little variation between 26-28°C, the range defined as the zone of thermoneutrality. In response to noradrenaline injections, VO_2 was found to be 2.84 ± 0.4 ml g^{-1} h^{-1}, which differs only slightly from the values obtained for *O. irroratus*. The lower critical temperature was determined to be 25.3°C. Further, *O. s. robertsi* can tolerate temperatures higher than those which are experienced in its habitat (e.g. 34°C in contrast to the range of temperatures in its natural environment which is 15-23°C). Its metabolic rate was not found to be higher than predicted, but thermal conductance was greater than expected. The ratio of percentage metabolic rate and percentage thermal conductance was 0.87, which corresponds to values obtained for many arid/warm-adapted mammals. Its metabolic rate is thus not enough to counteract the relatively high rate of heat loss at low temperatures as suggested by the animal's minimal thermal conductance. Body temperature does however appear to remain fairly constant even at low temperatures, which is energetically costly, as metabolic rates are almost twice as high at low temperatures than within the thermoneutral zone (Richter *et al.*, 1997).

Despite these physiological shortcomings to alpine habitats, ice rats do not occur at lower altitudes which Richter *et al.* (1997) suggest may be a result of interspecific competition with *O. irroratus*. Even so, ice rats show behavioural thermoregulation through huddling and sun-basking in response to low temperatures (Skinner and Smithers, 1990; Willan, 1990; Richter *et al.*, 1997). *Otomys. s. robertsi* also shows some morphological adaptation to the cold such as a short tail and ears (De Graaff, 1981; Willan, 1990).

Motivation for the study

Over the past few years, several geomorphological and climatological studies focussing primarily on high levels of erosion have been conducted in the eastern Lesotho Drakensberg (see Grab, 1999; Grab and Deschamps, 2004). Jacot-Guillarmod (1963) originally associated this mass erosion and soil loss with overgrazing by domestic livestock, although little attention has been given to the possible impacts of indigenous fauna on the grazing resource. In particular, the ice rat *O. s. robertsi* is believed to significantly contribute to the erosion process by grazing and burrowing (S. Grab, pers. comm.). Field observations by researchers of the School of Geography, Archaeology and Environmental Studies at the University of the Witwatersrand have indicated that overgrazing and thus mass erosion has occurred in areas where ice rat populations have increased dramatically (S. Grab, pers. comm.).

For many animals, predation pressure plays an important role in regulating population numbers (Lima and Dill, 1990; Wilson *et al*., 1998). However, based on my observations (from 1999 to 2003) and those of Willan (1990), as well as anecdotal reports from local Basotho shepherds, predation pressure on *O. s. robertsi* in my study site in the Sani Valley appears to be negligible in summer and virtually absent in winter. Instead, population numbers are apparently regulated by density-dependent mortality as a result of limited resource availability during cold winters, as well as prolonged periods of snowfall and low winter temperatures (Willan, 1990; Lynch and Watson, 1992). The winters over the past few years have been relatively mild with little snowfall. Moreover, while maximum temperatures have remained constant, minimum temperatures have increased substantially over the last decade (Lesotho Weather Service; Figure 1), which would account for the lower levels of snowfall and better survival of ice rats in the Lesotho Drakensberg.



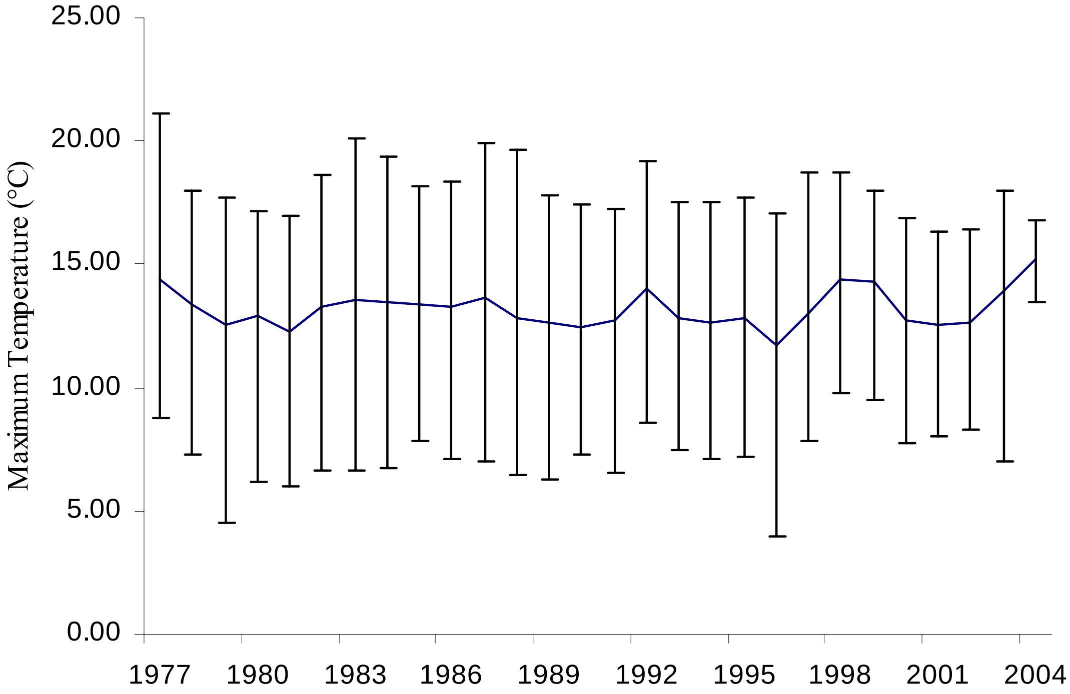


Figure 1. Mean (± SD) annual minimum (1992-2004) and maximum (1977-2004) air temperatures at Sani Top, Lesotho.

Questions were raised by researchers of the School of Geography, Archaeology and Environmental Studies about the biology of the southern African ice rat, and after an extensive literature review it was clear that very little was known about this subspecies, especially under natural conditions. Clearly, there was a need to study the biology of the ice rat, in particular its foraging behaviour, given the concerns about its role in the overgrazing of wetlands.

The ice rat presents a unique study animal since, unlike most alpine small mammals, it does not hibernate or display torpor and is physiologically poorly adapted to low temperatures (Richter *et al.*, 1997). It is a strict herbivore, feeding on a low quality diet. Moreover, in the absence of predation pressure in many parts of its distribution, it is an ideal model for studying changes in foraging activity in response to changing physiological demands from summer to winter. Although ice rats do show some morphological and behavioural (e.g. short tails; communal huddling; constructing underground burrows) adaptations (Willan, 1990; Richter, 1997), little else is known about their biology, in particular how they maximise energy gain to meet thermoregulatory demands, especially during cold periods. As foraging represents the primary method of energy gain in animals (Schultz *et al.*, 1999), I studied aspects of the foraging biology of ice rats, including the gut structure, foraging behaviour and habitat choice, as survival in these harsh conditions is likely to be achieved by behavioural and morphological adaptations to maximise energy gain while minimising energy loss.

The broad aims of my study were to investigate the morphological and behavioural characteristics and foraging decisions of ice rats for life in alpine habitats. This study was driven primarily by the question how an animal that shows only limited physiological adaptation to its environment modifies its foraging biology to compensate for its physiological shortcomings. Chapter 2 provides information on the seasonal and gender variation in gut morphology of *O. s. robertsi* and comparisons are made with its mesic and arid relatives. The aim of this study was to investigate how the gut structure of ice rats is adapted to cold environments. In Chapter 3, I conducted field observations over three years to investigate the behavioural patterns of the ice rat in summer and winter. The emphasis of this study was on how ice rats allocate time to various behaviours and how seasonal climatic changes affect behaviour. Underpinned by the theoretical models of optimal foraging theory, Chapter 4 examines the foraging decisions of *O. s. robertsi* in the absence of predation, and Chapter 5 provides a comparison of the foraging behaviour of ice rats experiencing different levels of predation pressure with the aim of comparing the interplay between predation risk and climatic factors on foraging decisions. The final experimental chapter (Chapter 6) focuses on the environmental factors determining microhabitat selection to explore possible relationships between habitat choice and foraging behaviour.

The study area

Due to the inaccessibility of most of the Drakensberg region in Lesotho, the more easily accessible Sani Valley area was chosen as the primary area of study. My main study site was located south of the Sani River (29° 37’ S; 29°14’ E) about 5km west of Sani Top at an altitude of about 2900m and was situated in one of the Sani tributary valleys. A second site was selected later in my study, situated about 7 km south of Katse Dam along the Sengu River at an altitude of about 2000m (29°21' S; 28°32' E). The Drakensberg/Maluti massive consists of an ancient basaltic plateau marked by deep, steep-sloping valleys. As a result of water seepage to lower ground, extensive bogs are formed in these valleys. Soil depth decreases as gradient increases (Killick, 1978). Mean air temperature in the Lesotho highlands ranges from 0°C in winter to 6°C in summer (Grab, 1997). Rainfall is high (about 1200mm per annum) and snow can be expected at any time of the year (Willan, 1990). Shrubs and herbs (annuals and biennials, woody cushion plants and succulents, aquatics and alien plants) are common and trees are absent.

Arrangement of the thesis

This thesis consists of the present introductory chapter, a general discussion and conclusion chapter (Chapter 7) and the main body comprising five experimental chapters (Chapters 2-6). The experimental chapters are written as manuscripts for publication, with Chapter 2 on gut structure having already been published in the Journal of Comparative Physiology B (Vol. 173, p. 653-659). Because of the format of this publication, which includes substantial background information as well as an abstract and a separate reference list, the subsequent chapters have been formatted in the same manner. The tables and figures have been sequentially numbered for each chapter and the pages of the thesis are numbered in sequence. References are provided in each chapter.

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ORIGINAL PAPER

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The gut morphology of the African ice rat, *Otomys sloggetti robertsi*, shows adaptations to cold environments and sex-specific seasonal variation

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Abstract We studied the gut morphology of the ice rat *Otomys sloggetti robertsi*, a non-hibernating murid rodent endemic to the sub-alpine and alpine regions of the southern African Drakensberg and Maluti mountains. The gut structure of *O. s. robertsi* is well adapted for a high fibre, herbivorous diet, as is the case with other members of its subfamily Otomyinae. Despite the broad similarity in gross gut morphology with mesic- and arid-occurring otomyines, *O. s. robertsi* has a larger small intestine, caecum, stomach volume and parts of the colon, which we suggest are adaptations for increased energy uptake and/or poor diet quality in alpine environments. However, *O. s. robertsi* has a smaller larger intestine than other otomyines, perhaps because it occupies a mesic habitat. Seasonal sexual differences occurred, with females increasing dimensions of the stomach, small intestine length, caecum, and large intestine in summer. Sexual asymmetry in gut morphology may be related to increased energy requirements of females during pregnancy and lactation, indicating phenotypic plasticity in response to poor quality vegetation and a shorter growing season in alpine habitats.

Keywords *Otomys sloggetti robertsi* · Gut morphology · Climate · Diet · Habitat

Introduction

Interspecific comparative studies have shown that rodent digestive tract morphology largely reflects diet (Vorontsov 1962; Perrin and Curtis 1980). Herbivorous rodents, for instance, have a more developed large intestine and caecum than omnivores of the same family, since fibrous plant material is broken down by microbial digestion in the caecum, forming compounds that can then be absorbed by the large intestine (Lange and Staaland 1970). Thus, a larger caecum and large intestine are adaptations for a high fibre diet (Sperber 1968; Perrin and Curtis 1980; Schieck and Millar 1985). Generally, a decrease in food quality results in an increase in gut length and capacity due to an increase in energy demand (Gross et al. 1985; Hammond and Wunder 1991). In addition, the hindgut is important in water re-absorption in small mammals, and there are usually changes in the relative size of the large intestine in animals inhabiting arid regions, reflecting the need for water conservation (Lange and Staaland 1970; Woodall 1987).

Many small herbivores occurring in cold regions will either hibernate or exhibit short periods of torpor, allowing them to conserve energy during the most demanding times (e.g. winter). In contrast, non-hibernating animals, such as arvicoline rodents (lemmings and voles), must maintain a constant body temperature by heat production or conservation, which is achieved through morphological, physiological or behavioural adaptations. The rate of energy acquisition may be limited by seasonal changes in food quality as well as by digestive tract morphology and physiology (Bozinovic et al. 1990). The need for increased energy gain as well as decreased diet quality requires increased food consumption (Green and Millar 1987). Therefore, animals such as the prairie vole (*Microtus ochrogaster*) that face the challenge of cold temperatures as well as a high fibre diet have a larger caecum and small intestine rather than a larger large intestine (Hammond and Wunder 1991). Increases in the length of sections of the gut are necessary for digestion of food of high fibre content, since food is retained for a longer time, enabling digestibility of several components of the diet (Silby 1981). Furthermore, a larger gut may increase the rate of digestion

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and absorption due to an increase in transporters in the gut lining, thus rendering a greater quantity of energy per unit time (Karasov and Diamond 1988). However, a larger gut is probably more important for the processing of a greater quantity of food at a given time.

Digestive tract morphology is sometimes intraspecifically labile. Changes in gut morphology can occur when food quality varies between seasons (Hammond 1993), and reflects changes in energy requirements due to low temperatures in winter (Green and Millar 1987). Increased energy requirements in winter coupled with a poor-quality diet may necessitate the consumption of larger quantities of food. If retention time and digestibility remain constant, an increase in gut dimensions is expected, unless a decline in food quality corresponds with a decrease in activity and thus energy requirements (Green and Millar 1987). Conversely, increases in energy demand because of lactation or increased activity can lead to an increase in gut length in summer (Hammond 1993; Kenagy 1987). For example, female Djungarian hamsters (*Phodopus sungorus sungorus*; Weiner 1987) and wild rabbits *Oryctolagus cuniculus* (Silby et al. 1990) demonstrate an increase in size of several digestive organs (predominantly small intestine and caecum) during reproductive periods, apparently to meet the need for increased energy requirements during pregnancy and lactation.

The murid rodent subfamily Otomyinae is widely distributed across the primarily east-west southern African rainfall gradient (Skinner and Smithers 1990). All otomyines studied are specialist herbivores, feeding more or less exclusively on green plant material including shoots, stems, leaves and grasses, although some species feed on fruit and flowers (Roberts 1951; Nel and Rautenbach 1974; Curtis and Perrin 1979; Jackson 1998). Perrin and Curtis (1980) reported that the gastrointestinal tract of the Otomyinae is the most specialised of any South African herbivorous rodent, and includes a large and complex caecum and a well-developed large intestine.

Data on the gastrointestinal morphology of the Otomyinae are available for two mesic-occurring species, the vlei rat, *Otomys irroratus*, and the Angoni vlei rat, *Otomys angoniensis* (Perrin and Curtis 1980) and three arid-occurring species, the bush Karoo rat, *Otomys unisulcatus*, Brants' whistling rat, *Parotomys brantsii* and Littledale's whistling rat, *Parotomys littledalei* (Jackson and Spinks 1998). There is broad similarity in the gross gastrointestinal anatomy among the species, but the arid-occurring forms have an elongated large intestine and a simultaneous reduction in the small intestine, which may be related to water conservation (Jackson and Spinks 1998).

In contrast to these other otomyine rodents, no comparable data are available for the gut morphology of the ice rat, *Otomys sloggetti robertsi*. The ice rat shares some characteristics (e.g. kidney morphology; Pillay et al. 1994) with mesic-occurring otomyines, yet unlike other otomyines, *O. s. robertsi* is confined to altitudes exceeding 2000 m, and is endemic to the southern African Drakensberg and Maluti mountains. This distribution restricts them to the cold, harsh sub-alpine and alpine phytogeographic belts (Killick 1978). *O. s. robertsi* does not hibernate and apparently is physiologically poorly adapted to the harsh alpine habitats, and instead, its physiology (e.g. low metabolic rate and high thermal conductance) is more typical of its congeners occurring in warmer environments at lower altitudes (Richter et al. 1997). In addition, oxygen consumption of *O. s. robertsi* decreases linearly with an increase in ambient temperature between 0.7 °C and 26.0 °C, and the zone of thermoneutrality is reached between 26 °C and 28 °C, which is unusually high for a rodent living in a habitat that rarely experiences such high temperatures (Richter et al. 1997). To cope with low temperatures, *O. s. robertsi* employs behavioural (e.g. sun-basking, huddling) and morphological (e.g. short tails and small ear pinnae) adaptations (Willan 1990). *O. s. robertsi* has a varied diet within the constraints of herbivory (Rowe-Rowe 1986; U. Schwaibold, personal observation).

In this study, we compared the gastrointestinal morphology of the ice rat with that of two mesic-occurring otomyines and to the published data available for three arid-occurring otomyines. We predicted that the gut morphology of ice rats would be similar to mesic-occurring otomyines. We also asked two questions:

1. Do ice rats show modifications of the gastrointestinal morphology associated with increased energy requirements in the cold, harsh environments they inhabit?
2. Are there seasonal differences in the gut structure between the sexes in response to increased energy demands on females imposed by pregnancy and lactation, and ultimately by the short growing season in alpine environments?

Materials and methods

Eight male and eight female adult *O. s. robertsi* were captured in summer (October 2000, January and February 2001) and eight female and seven male adults were captured in winter (June and August 2000) at Sani Top in the Lesotho Drakensberg (29°37′ S; 29°14′ W). Sixteen adult *O. angoniensis* and *O. irroratus* (eight of each sex) were captured during summer (November 2000 and January 2001), respectively, at Hazelmere (29°34′ S; 31°01′ E) and Karkloof (29°17′ S; 30°11′ E) in KwaZulu-Natal Province, South Africa. Individuals were live-trapped within 4 days of each other during each trapping session. Captured animals were removed from traps within 30 min of entering traps and killed (overdosed with IM Sodium Pentobarbitone 200 mg, Benzyl Alcohol 2%, dosage: 1 ml/kg body weight). Thereafter, mass (to nearest gram measured with a Pescola spring balance) and head-body length (to nearest millimetre) were established for all animals before their digestive tracts from the gastro-oesophageal junction to the anus were removed and preserved in 70% alcohol for no longer than 2 weeks (range 10–14 days) until examination at the University of the Witwatersrand. We assumed that any size and shape changes in the tissue because of fixation would have been similar across all samples. To test this assumption, we took linear measurements from each of three *O. s. robertsi*, *O. angoniensis* and *O. irroratus* digestive tracts immediately after they were killed and again after preservation for 14 days in 70% alcohol. All digestive tracts showed a similar 1–2% reduction in size.

The preserved digestive tract of each individual was cleared of surrounding adipose and connective tissue, blotted to remove excess alcohol, and weighed with its contents to the nearest 0.01 g with a bench top Mettler balance. The digestive tract was straightened but not stretched and, after measuring the total length of the gut on a clean flat surface to the nearest 0.1 mm, the tract was separated into stomach, small intestine, caecum and large intestine. The following mass, linear measurements and counts were then recorded (after Perrin and Curtis 1980; Jackson and Spinks 1998): stomach empty mass (i.e. cleared of contents), length, width and volume; length and mean width of small intestine; length and mean width of large intestine; number of spiral loops in the colon; number of caecal haustra, height and mean width of haustra, caecum volume, mass (empty) and mean width and diameter of caecum. Width in each case was determined as an average of five separate measurements along the length of the organ. The volume of the stomach and caecum were calculated using the formula $\pi r^2 l$, where r is average organ radius (calculated as the mean of five measurements taken along the length of the organ) and l is organ length. The following proportions were also determined: length of hindgut to body length; stomach, small, large intestine and caecal lengths to total gut length.

Statistical analysis

Comparisons among and within taxa were done using an analysis of variance (ANOVA) for single measurements, and a multivariate analysis of variance (MANOVA) was used for several dependent variables (e.g. measurements from the same organ, such as stomach width and length; Zar 1996). A Kruskal-Wallis ANOVA was used for comparisons of ratios (Zar 1996). Tukey HSD and Dunn's post-hoc tests were used to identify specific differences in parametric and non-parametric tests respectively. All tests were two-tailed and α was set at 0.05.

Regression analyses did not show any significant correlation between body mass, length and gut morphometrics. Accordingly, gut morphometrics were not standardised relative to body mass or length.

Results

Interspecific comparisons in summer

Interspecific comparisons were made with animals caught during summer. Body mass varied significantly across the three taxa ($F_{2,42} = 16.59$; $P < 0.0001$), with *O. s. robertsi* (mean ± SE: 130.8 ± 4.6 g) weighing more than *O. angoniensis* (106.8 ± 2.1 g) and *O. irroratus* (106.7 ± 3.0 g); there were no sex ($F_{1,42} = 0.3$; $P > 0.05$) or taxa×sex interactions ($F_{2,42} = 2.8$; $P > 0.05$). In terms of head-body length, *O. s. robertsi* (149.88 ± 2.46 mm) and *O. irroratus* (150.06 ± 4.20 mm) were significantly longer than *O. angoniensis* (131.38 ± 2.02 mm; $F_{2,42} = 20.87$; $P < 0.0001$), and males were significantly longer than females ($F_{1,42} = 10.70$; $P < 0.01$). There was a significant taxa×sex interaction ($F_{2,42} = 11.41$; $P < 0.001$), with *O. irroratus* males having the greatest and *O. angoniensis* females the shortest lengths.

O. s. robertsi had the longest gut compared to *O. angoniensis* and *O. irroratus* (Table 1). The stomach of all three taxa was a simple unilocular sac with very little morphological specialisation. The stomach of *O. s. robertsi* was larger (volume) compared to the other taxa, while stomach length was similar in *O. s. robertsi* and *O. irroratus* but shorter in *O. angoniensis*. In terms of the post-gastric morphology, *O. s. robertsi* had the largest small intestine (length) and caecum (mass, length, volume) but smallest large intestine (length; Table 1). The length of the small intestine was almost double the length of the large intestine in *O. s. robertsi* but was close to parity in *O. angoniensis* and *O. irroratus* (Table 1). While *O. s. robertsi* had the most spiral loops in the large intestine, it also had the shortest hindgut to head-body ratio (Table 1). The hindgut (large intestine and caecum) showed female-biased sexual asymmetry across all three taxa, and there were taxa×sex interactions that mirrored the trends observed in the taxa comparisons, although it is notable that female *O. s. robertsi* had heavier stomachs (empty mass) than their male conspecifics.

Expressed as a percentage of total gut length, the stomach length of *O. s. robertsi* was similar to that of *O. irroratus* and greater than that of *O. angoniensis* (Table 2). The relative contribution of the small intestine and caecum to the length of the gastrointestinal tract was significantly greater in *O. s. robertsi* than in the other two otomyines (Table 2). Conversely, the large intestine was shorter in *O. s. robertsi* than in *O. angoniensis* and *O. irroratus*. The relative length of the caecum was greater in females than in males.

Comparison of the gut structure of the three mesic-occurring otomyines with published data of three arid-occurring otomyines indicated that *O. s. robertsi* had a longer small intestine and caecum than the other otomyines (Table 3). It is also apparent that the large intestine is relatively longer in the arid-occurring taxa (especially in *Parotomys littledalei*) than in the mesic-occurring taxa. In contrast, the caecum is relatively larger in the mesic-occurring taxa. Consequently, the small:large intestine ratio is greater in the mesic-occurring than the arid-occurring otomyines (Table 3). Furthermore, the small:large intestine ratio of *O. s. robertsi*, which is greater than all the other otomyines, is more than double that of *P. littledalei* whose distributional range includes the most arid regions occupied by any of the otomyines.

Seasonal and sexual comparisons in *O. s. robertsi*

There was an increase in the height of the caecal haustra in *O. s. robertsi* caught in summer compared to those trapped in winter (Table 4). The length of the small intestine showed female-biased sexual asymmetry. The statistical interaction between season and sex is important, since it allows us to answer our question about whether there are sex differences in gut morphology between summer and winter. In general, females caught in summer had larger guts than males in both seasons and females in winter (Table 4). From winter to summer,

Table 1 Comparison of gastrointestinal morphology of *Otomys sloggetti robertsi* (*Osr*), *Otomys angoniensis* (*Oa*) and *Otomys irroratus* (*Oi*) caught in summer. Values (mass in grams, linear measurements in millimetres, volume in centimetres squared) given as mean (±SE). (*SI* small intestine, *LI* large intestine, *ns* not significant)

Parameters	*O. s. robertsi*		*O. angoniensis*		*O. irroratus*		Statistics		
	Males	Females	Males	Females	Males	Females	Taxa	Sex	Taxa×Sex
Total length of gut	753.73(33.14)	831.53(33.93)	706.51(10.72)	677.19(9.85)	655.61(7.40)	668.98(7.01)	**Osr > Oa = Oi	ns	ns
Stomach									
Empty mass	1.02(0.36)	1.52(0.17)	1.20(0.10)	1.15(0.12)	1.32(0.08)	1.30(0.08)	ns	ns	***Osr (f) > Osr (m)
Width	23.47(1.41)	23.60(1.40)	23.74(0.31)	23.53(0.36)	24.50(0.63)	24.06(0.40)	ns	ns	ns
Length	35.64(1.65)	32.96(2.34)	25.25(1.19)	28.13(0.77)	31.38(0.26)	31.50(1.52)	***Osr > Oi > Oa	ns	ns
Volume	5.32(0.51)	5.08(0.51)	2.35(0.37)	1.91(0.07)	3.08(0.46)	3.09(0.39)	***Osr > Oi = Oa	ns	ns
Small intestine									
Length	359.56(18.63)	419.41(20.64)	297.93(4.23)	291.85(4.27)	254.86(5.73)	255.91(5.09)	***Osr > Oa > Oi	ns	**Osr (m, f) > others
Width	4.50(0.33)	4.88(0.35)	4.81(0.29)	3.93(0.26)	3.91(0.07)	3.88(0.04)	***Osr = Oa > Oi	ns	ns
Large intestine									
Length	218.33(0.23)	226.67(12.16)	260.33(5.14)	240.10(6.19)	264.30(2.26)	251.96(5.44)	***Oi = Oa > Osr	ns	ns
Width	4.75(0.16)	5.13(0.30)	5.10(0.23)	5.09(0.14)	5.14(0.13)	4.74(0.16)	ns	ns	ns
Number of spiral loops	5.25(0.25)	5.54(0.27)	4.20(0.21)	4.12(0.16)	4.38(0.18)	3.75 (0.25)	***Osr > Oa = Oi	ns	ns
SI:LI	1.65(0.08)	1.86(0.05)	1.15(0.02)	1.22(0.09)	0.96(0.01)	1.02(0.02)	***Osr > Oa > Oi	ns	-[a]
Hindgut:body length	1.49(0.06)	1.48(0.09)	1.91(0.02)	1.91(0.05)	1.63(0.03)	1.84 (0.07)	***Oa > Oi > Osr	*f > m	-[a]
Caecum									
Empty mass	2.96(0.16)	2.84(0.12)	1.83(0.05)	1.76(0.05)	1.83(0.05)	2.05(0.08)	***Osr > Oi = Oa	ns	Osr (m, f) > others
Length	140.19(9.85)	152.49(8.45)	122.99(3.82)	117.12(2.30)	105.08(3.71)	129.62(4.45)	***Osr > Oa = Oi	*f > m	ns
Mean width	16.92(1.52)	22.74(0.61)	22.63(1.35)	25.63(1.02)	21.38(0.68)	20.00(1.74)	ns	*f > m	Osr (m) < others
Number of haustra	28.00(1.67)	30.00(1.00)	28.13(2.15)	27.38 (1.34)	29.13(0.77)	26.88(1.04)	ns	ns	ns
Height of haustra	5.25(0.37)	5.25(0.25)	5.13(0.23)	4.75(0.25)	5.25(0.25)	5.25(0.25)	ns	ns	ns
Width of haustra	4.38(0.26)	4.88(0.23)	4.00(0.00)	5.13(0.30)	4.25(0.16)	4.88(0.13)	ns	ns	ns
Volume	19.96(2.58)	24.10(1.41)	13.79(3.84)	12.38(4.66)	11.15(3.11)	13.73(3.99)	*Osr > Oa = Oi	ns	ns

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$ (2 way ANOVA, 2 way MANOVA and Kruskall Wallis tests). Tukey HSD and Dunn's post-hoc results indicated if significant differences occurred

[a] Kruskall Wallis ANOVA does not perform test

Table 2 Mean (±SE) lengths of divisions of digestive tract as percentages of total gut length in *O. sloggetti robertsi* (Osr), *O. angoniensis* (Oa) and*O. irroratus* (Oi) caught in summer

Parameters	*O. s. robertsi*	*O. angoniensis*	*O. irroratus*	Statistics
Stomach	4.37(0.20)	3.87(0.13)	4.75(0.12)	***Osr = Oi > Oa
Small intestine	49.02(0.80)	42.65(0.31)	38.54(0.35)	***Osr > Oa > Oi
Large intestine	28.11(0.54)	36.14(0.39)	39.00(0.56)	***Oi = Oa > Osr
Caecum	18.50(0.64)	17.34(0.21)	17.70(0.58)	*Osr > Oa = Oi

*$P < 0.05$; ***$P < 0.001$ (Kruskall Wallis tests). Dunn's post-hoc results indicated if significant differences occurred

Table 3 Length of divisions of the hindgut expressed as a percentage of total hindgut length (excluding stomach), and the ratio of large to small intestine length of mesic- and arid-occurring otomyines. Values for mesic-occurring taxa were obtained from this study and for the arid-occurring taxa from Jackson and Spinks (1998)

Parameters	Mesic-occurring			Arid-occurring		
	O. s. robertsi	*O. angoniensis*	*O. irroratus*	*O. unisulcatus*	*P. brantsii*	*P. littledalei*
Small intestine	51.12	43.74	40.59	43.20	41.20	36.70
Large intestine	28.08	38.36	40.26	43.60	45.40	50.90
Caecum	20.80	17.90	19.15	13.20	13.30	12.40
Small: large intestine ratio	1.82	1.14	1.00	0.99	0.90	0.72

Table 4 Comparison of gastrointestinal morphology of male (*m*) and female (*f*) *O. sloggetti robertsi* trapped in summer (*S*) and winter (*W*). Values (mass in grams, linear measurements in millimetres, volume in centimetres squared) given as mean (±SE)

Parameters	Summer		Winter		Statistics		
	Males	Females	Males	Females	Season	Sex	Season×Sex
Total length of gut	753.7(33.14)	831.5(33.92)	816.0(32.15)	820.4(20.27)	ns	ns	ns
Stomach							
Empty mass	1.02(0.07)	1.52(0.17)	1.36(0.06)	1.14(0.03)	ns	ns	***S(f) > S(m)
Width	23.47(1.41)	23.59(1.40)	21.14(1.99)	26.88(1.16)	ns	ns	ns
Length	35.64(1.65)	32.96(2.34)	32.29(1.54)	34.75(1.22)	ns	ns	ns
Volume	5.32(0.51)	5.08(0.51)	4.30(0.43)	5.88(0.37)	ns	ns	ns
Small intestine							
Length	359.56(18.63)	419.41(20.64)	399.71(17.98)	404.50(13.95)	ns	*f > m	S(f) > S(m)
Width	4.50(0.33)	4.88(0.35)	4.93(0.07)	5.00(0.33)	ns	ns	ns
Large intestine							
Length	218.33(10.14)	226.67(12.16)	237.14(12.36)	237.13(8.70)	ns	ns	ns
Width	4.75(0.16)	5.13(0.30)	4.86(0.46)	5.13(0.23)	ns	ns	ns
Number of spiral loops	5.25(0.25)	5.54(0.27)	5.29(0.36)	5.63(0.38)	ns	ns	ns
SI:LI	1.66(0.08)	1.86(0.05)	1.70(0.06)	1.72(0.07)	-	-	**S(f) > others[a]
Hindgut:body length	2.50(0.09)	2.49(0.15)	2.54(0.15)	2.62(0.07)	-	-	ns[a]
Caecum							
Empty mass	2.96(0.16)	2.84(0.12)	2.86(0.16)	2.56(0.12)	ns	ns	ns
Length	140.19(9.85)	158.49(4.45)	146.86(5.68)	141.13(6.57)	ns	ns	*S(f) > others
Mean width	16.92(1.52)	22.74(0.61)	21.57(1.70)	19.50(1.87)	ns	ns	*S(m) < others
Number of haustra	28.00(1.67)	30.00(1.00)	31.00(1.35)	31.88(0.69)	ns	ns	ns
Height of haustra	5.25(0.37)	5.25(0.25)	4.71(0.47)	4.38(0.46)	*S > W	ns	ns
Width of haustra	4.38(0.26)	4.88(0.23)	4.00(0.31)	4.38(0.26)	ns	ns	ns
Volume	19.96(1.09)	24.10(2.58)	22.14(2.58)	25.10(1.41)	ns	ns	ns

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$ (2 way ANOVA, 2 way MANOVA and Kruskall Wallis tests). Tukey HSD and Dunn's post-hoc results indicates if significant differences occurred

[a] Kruskall-Wallis ANOVA applied to ratio data by regarding each season and sex as separate entities

females increased their gut dimensions as follows: stomach empty mass (25%), small intestine length (9%), and caecum length (11%) and width (14%). Seasonal differences in these dimensions ranged from < 1–5% in males. Within-season intersexual comparisons revealed a largely female-biased size and mass difference in summer, which was not as pronounced or reversed in winter, as follows (summer, winter): stomach empty mass (26%, 2%; winter favoured males), small intestine length (18%, 8%), and caecum length (7%, < 1%) and width (13%, 3%; winter favoured males).

Discussion

Like the other otomyines (both mesic-occurring and arid-occurring), the gut morphology of *O. s. robertsi* is adapted for herbivory and for a diet of high fibre foods. A relatively large caecum and large intestine are considered the best indicators of herbivory, since these structures allow for longer retention of ingesta (Vorontsov 1962; Green and Millar 1987) and a greater surface area for microbial activity to break down cellulose (Schieck and Millar 1985). Field observations confirm our findings since the diet of ice rats consists almost exclusively of floral parts of grasses and herbaceous plants, as well as leaves and stems (U. Schwaibold, unpublished data).

O. s. robertsi has a longer gastrointestinal tract than the two other mesic-occurring taxa (*O. angoniensis* and *O. irroratus*), and a longer and larger small intestine and caecum than the other otomyines, including the three arid-occurring taxa (*O. unisulcatus*, *P. brantsii*, *P. littledalei*). These differences indicate modification of the digestive tract morphology of *O. s. robertsi*, and it is apparent that the small intestine and the caecum are important features. Increased dimensions of these organs are characteristic of both hibernating and non-hibernating small mammals in cold environments (Silby 1981; Karasov and Diamond 1988; Hammond and Wunder 1991), and appear to be the case also in *O. s. robertsi*.

A larger small intestine allows for increased retention time of ingesta (Silby et al. 1990) and provides a larger surface area for absorption of digested food, which can be considered an adaptation to cold temperatures, since it would improve the uptake of high-energy components in the diet. An increase in the capacity of the caecum appears to maximise digestibility of a high-fibre diet (Hammond and Wunder 1991; Lee and Houston 1993). Green and Millar (1987) reported that deer mice (*Peromyscus maniculatus*) responded to a decrease in diet quality and temperature between seasons by increasing the length of the small intestine and caecum and showing only slight changes in large intestine morphology.

Although the large intestine is an important feature in the gut of herbivores, it is relatively short in *O. s. robertsi* compared to the other otomyines. The large intestine is important in water absorption, nutrient absorption and possibly enhancing digestive efficiency (Woodall 1987). An increase in large intestine size is expected when there is a high-fibre diet, although the main function of the large intestine is water resorption (Lange and Staaland 1970). Because of the similarity in the diets of the otomyines, Jackson and Spinks (1998) attributed the relatively longer large intestine in the arid-occurring otomyines to a need to improve water retention in arid areas. The *O. s. robertsi* used in this study inhabit wetland habitats where it feeds primarily on wetland plants with high water contents. Much of its water is obtained from plants it consumes (Willan 1990), so that water may not be a limiting resource, thereby obviating the need for a longer large intestine.

The increased number of loops and folds of the colon in *O. s. robertsi* compared to the mesic-occurring *O. angoniensis* and *O. irroratus* may facilitate increased nutrient absorption (Schieck and Millar 1985). The large intestine is important for nutrient absorption from fibrous material broken down in the caecum (Sperber 1968). The transverse muscular folds and loops possibly aid in slowing down passage through the large intestine, allowing more time for energy to be absorbed and further promoting mixing and movement of the material broken down in the caecum which in turn may promote the fermentation process (Bruorton and Perrin 1988).

Stomach length and volume were significantly greater in *O. s. robertsi* than *O. angoniensis* and *O. irroratus*. Stomach fermentation is highly advantageous as it occurs just before protein digestion. A larger stomach volume furthermore provides a greater surface area for enzyme release (Perrin and Curtis 1980), thus promoting digestion. Also, larger quantities of ingested material can be digested at any one time. Lee and Houston (1993) maintained that an increase in stomach volume in bank (*Clethrionomys glareolus*) and field voles (*Microtus agrestis*) could decrease the time spent feeding in the open, thus reducing the risk of predation. It is possible that a larger stomach volume allows an animal to consume more food at one time, thus reducing the frequency of foraging bouts. It is uncertain whether the large stomach volume in *O. s. robertsi* has similar (secondary) functions in the exposed environments it occupies, as predation risk is low (U. Schwaibold, unpublished data), but structures that allow for minimal exposure to low ambient temperatures may be adaptive. It is known that increasing the rate of food intake results in an increased passage rate and thus a decrease in digestibility of food (Silby 1981; Gross et al. 1985). On the other hand, an increase in gut volume allows ingesta to pass at a slower rate as it is retained in each organ for a longer period. Therefore, the longer total gut length in *O. s. robertsi* may increase retention time and thus digestibility of food.

During summer, female *O. s. robertsi* showed an increase in the size of those regions of the gut that are essential for increased energy uptake, such as caecum and small intestine. Males did not show such increases. Similar findings were reported in wild rabbits (*Oryctolagus cuniculus*; Silby et al. 1990) and the South American field mouse (*Abrothrix andinus*; Bozinovic et al. 1990), a non-hibernating rodent found in the cold and harsh environments of the Andes. Bozinovic et al. (1990) reported significant increases in the length and mass of the whole gut and the lengths of the small and large intestines in winter, and significant differences in the dimensions of several digestive organs were found between males and females during the reproductive season. These female-biased sexual differences in gut dimensions between seasons are thought to reflect the need to improve energy acquisition during pregnancy and lactation (Weiner 1987; Sibly et al.1990). Female *O. s. robertsi* may be similarly constrained by the poor quality of the vegetation and the shorter growing season in their alpine habitats (Willan 1990).

In conclusion, our study reveals significant differences in the gastrointestinal morphology of *O. s. robertsi* on two levels. Interspecific comparisons within the otomyines suggest that the gut morphology of *O. s. robertsi* is adapted for cold environments because of the need to increase energy intake, although the gut structure may reflect also the poor quality diet of ice rats (U. Schwaibold, unpublished data). Intraspecific variation occurs during the reproductive season as energy demands differ between male and female ice rats, indicating a degree of phenotypic plasticity. Clearly, there is still a need for further physiological and biochemical studies to fully explain the results presented here.

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CHAPTER THREE:

Behaviour of free-living African ice rats *Otomys sloggetti robertsi*: strategies for coping with harsh environments

Abstract

In this study, environmental influences on the behaviour of the southern African ice rat, *Otomys sloggetti robertsi*, a herbivore endemic to the high altitude regions of the southern African Drakensberg and Maluti mountains, were investigated. Ice rats do not hibernate and are physiologically poorly adapted to low temperatures. *O. s. robertsi* was studied in its natural environment during both summer and winter and the behaviour of adult males and females was recorded by analysing the duration of behaviours as well as sequential transitions among behaviours. Gender and time of day did not influence ice rat behaviour and in both seasons ice rats spent most of their day foraging and basking, with much time spent in their underground burrows. Seasonal comparisons revealed that ice rats spent significantly more time foraging in winter whereas they remained belowground for longer periods of time in summer. Hoarding behaviour increased significantly from summer to winter and females showed higher levels of hoarding in summer than males. Sequential analysis of behaviours showed that most behavioural transitions in winter were strongly focused on foraging behaviours (searching, gathering and consuming food), basking and aggressive interactions. Behavioural transitions in summer were characterised by fewer transitions, with social interactions and basking decreasing in frequency. The data suggest that seasonal changes influence the motivation for, performance of, and sequences of behaviours in ice rats.

Key words: *Otomys sloggetti robertsi*, seasonal behaviour patterns, behavioural sequences, thermoregulation, motivation

Introduction

Thermoregulation in cold environments imposes great energetic demands on small mammals and coping with low temperatures is achieved by one or more of several physiological, morphological and/or behavioural adaptations (Johnson and Cabanac, 1982; Eckert *et al.*, 1988). Hibernation or entering into torpor are important physiological responses to low temperatures (Eckert *et al.*, 1988; Geiser and Ruf, 1995). When faced with ambient temperatures below their thermoneutral zones, small mammals which cannot reduce their metabolic rates need to modify their behaviour by either increasing calorific intake (e.g. by feeding) and mobilising stored energy (Johnson and Cabanac, 1982) or by reducing energy expenditure through basking and retreating into thermally stable shelters (Schultz *et al.,* 1999).

However, time spent acquiring energy (e.g. feeding) reduces the time spent in passive energy acquisition (e.g. basking) which would reduce overall energy loss, so that animals need to partition their time and energy among conflicting behavioural and physiological demands in order to maximise fitness benefits. In cold environments such trade-offs are crucial for survival and determine the behavioural strategy employed by small mammals in these habitats (Schultz *et al.,* 1999). Several small animal species such as chicks (Rovee-Collier *et al.*, 1997), house mice (Perrigo and Bronson, 1985) and rats (Johnson and Cabanac, 1982) reduce time spent on energetically costly behaviours in cold temperatures while increasing feeding time.

Behavioural strategies used by small mammals to regulate their body temperature can be temporally labile depending on prevailing environmental conditions. Behavioural responses can occur over a short term, such as when an animal moves from a shady, wind-protected burrow entrance to a sunny foraging site (Johnson and Cabanac, 1982), or they could occur in response to seasonal fluctuations in temperature (long-term response). Bertolino *et al.* (2004) maintain that seasonal changes in the behaviour of Finlayson's squirrels *Callosciurus finlaysonii* may be related to internal factors such as altered physiological demands (e.g. reproduction) and external factors such as differences in food type and quantity between seasons, and also predation risk. Activity patterns of the Arctic black-capped marmot *Marmota camtschatica bungei* change markedly throughout summer, increasing rapidly after the animals emerge from hibernation in spring and gradually decreasing towards late autumn (Semenov *et al.*, 2001). While behavioural changes from summer to late autumn/early winter in preparation for hibernation (e.g. Barash, 1989; Semenov *et al.,* 2001) have been studied for several years, research dealing with the winter behaviour patterns of non-hibernating alpine and subalpine animals has only recently emerged (see Kenagy *et al.*, 2002).

Hoarding food is an important behavioural strategy employed by animals living in cold environments (see Ellison, 1996). Typically, hoarding occurs when food is abundant and accessible in preparation for future shortages due to climatic changes and unpredictable food supply (Wood and Bartness, 1996) and is therefore common in hibernating species. However, caching can also occur for other reasons. For example, some diurnal animals store food for consumption overnight, as occurs in Brants' whistling rat *Parotomys brantsii* (Jackson, 2001). Many rodents also collect plants for use as nesting material (Barash, 1989). Whatever the reasons, time spent hoarding reduces time spent performing other behaviours and it is clear that when faced with thermoregulatory challenges, caching has to be traded off against feeding and basking behaviours.

The African ice rat *Otomys sloggetti robertsi* is a good model for studying behavioural strategies in harsh environments. This medium-sized (121-143g) murid rodent is confined to the altitudes above 2000m and is endemic to the harsh environments of the subalpine and alpine Drakensberg and Maluti mountains of southern Africa (Killick, 1978). Importantly, although it occupies some of the coldest habitats in the subregion, *O. s. robertsi* does not hibernate and apparently shows poor physiological adaptations to cold temperatures, such as an elevated metabolic rate and a thermoneutral zone above ambient temperature (Richter *et al.,* 1997), thus making the taxon particularly vulnerable to temperature extremes (Willan, 1990; Lynch and Watson, 1992). Instead, ice rats display a range of morphological (e.g. small tail, ear pinnae) and behavioural (e.g. sun-basking, huddling) adaptations to cope with the low temperatures (Willan, 1990; Richter, 1997). Ice rats live in colonies of up to 16 individuals and construct complex underground burrows, into which they retire when temperature and radiation levels are high in summer (Hinze *et al.*, submitted).

Like all other members of its subfamily Otomyinae (De Graaff, 1981; Skinner and Smithers, 1990), *O. s. robertsi* is strictly herbivorous, feeding on a wide range of plant material (Willan, 1990). None of the otomyines are ruminants (see Perrin and Curtis, 1980), necessitating frequent foraging bouts to acquire food to meet metabolic demands. In a recent study I reported that, although there are broad similarities in the overall gut morphology of ice rats compared with other mesic- and arid-living otomyines, *O. s. robertsi* has a larger small intestine, caecum and stomach, which may be adaptations for increased energy uptake and/or poor diet quality in cold alpine environments (Schwaibold and Pillay, 2003; Chapter 2). In addition, female ice rats increase the size of their gut in summer compared to winter, which apparently corresponds to times of greater energy need during the breeding season; male gut dimensions remain more or less unchanged seasonally (Schwaibold and Pillay, 2003).

Previous observations by Willan (1990) and by us, as well as anecdotal reports by local Basotho shepherds in my study site in the Sani Valley, indicate that predation pressure on ice rats is minimal in summer and virtually absent in winter, possibly due to excessive hunting of predators by local inhabitants (Willan, 1990). Mortality rates of ice rats appear to be regulated by snowfall and low winter temperatures (Lynch and Watson, 1992). Predation risk is an important determinant of the foraging behaviour of small mammals (Bozinovic and Simonetti, 1992; Kotler *et al.,* 1994; Vásquez, 1994; Lima, 1998) but in the absence of high predation levels it is possible that, at least at my study site, ice rat behaviour is primarily determined by environmental factors such as temperature, particularly between seasons.

Ice rats are easily observed in their natural habitat as they are diurnal, quickly habituate to the presence of observers, and because they inhabit areas with short vegetation. Despite this, little is known of the behaviour of ice rats in their natural environment. Even observations of their foraging and basking behaviour, which have been noted by several workers (e.g. Willan, 1990; Lynch and Watson, 1992), are anecdotal, despite these behaviours taking up much of their time as well as being important behavioural adaptation for thermoregulation.

The present study was designed to compare the aboveground diurnal behaviour of free-living ice rats between summer and winter. Generally, I asked whether *O. s. robertsi* displays seasonally varying behavioural strategies, and how ice rats trade off between various activities, particularly foraging and other behaviours, in winter when food quality is poor (Schwaibold and Pillay, 2003). Specifically, five questions were asked: 1) If ice rats are physiologically poorly adapted to cold environments, do they show seasonal differences in behaviour, that is, do they display higher levels of foraging and basking in winter than in summer to meet thermoregulatory demands? 2) Since environmental conditions change during the course of the day, do ice rats adjust their behaviour from morning to afternoon by increasing levels of hoarding and foraging in the afternoon before they retire into burrows for the night, and increasing levels of basking in the morning after they emerge from their burrows? 3) Because of the energetic demands of pregnancy and lactation, I expected that females would forage for longer in summer than males, but I also asked whether the increased gut capacity of females in summer might offset the need to increase time spent foraging. 4) Is hoarding behaviour greater in winter than in summer to compensate for the shorter foraging time available due to shorter day length? 5) Do females hoard more food in summer compared to males to meet the energetic requirements of reproduction?

To answer these questions, the duration of behaviours displayed by individual ice rats was recorded quantitatively. Such data are useful for understanding how animals distribute their time among various behaviours but do not tell us anything about the structure of the behaviour (Spruijt *et al.*, 1992). Behaviours are not static and do not usually occur in discrete bouts. With this in mind, the structure of the behaviour of ice rats was analysed using sequential transition matrices, since these may be more revealing of changes in activity of an animal and are perhaps more likely to show trade-offs between behaviours from moment to moment (Bakeman and Gottman, 1997).

Materials and Methods

Study site

Fieldwork was conducted on a 6 ha study site located in one of the Sani River valleys (29°37’ S; 29°14’ E) about 5 km west of Sani Top in the south-eastern Maluti mountains, Lesotho, at an altitude of about 2900 m. The study area was located along the edge of one of the many wetlands in the valley. Weather conditions in the Lesotho highlands are characterised by relatively low temperatures (mean temperatures around 0°C in winter and 6°C in summer; Grab, 1997) and high rainfall (mean annual rainfall is

1200 mm), and snow can be expected at any time of the year (Willan, 1990). These high plateaus of Lesotho are prone to strong winds blowing towards the escarpment during most of the day, although the early morning hours are usually calmest. Mist is common, providing valuable moisture for plants (Hilliard and Burtt, 1987). Shrubs and herbs (annuals and biennials, woody cushion plants and succulents, aquatics and alien plants) are found most commonly in the Sani Valley and trees are absent. Vegetation in the study area did not exceed 50 cm in height in the ice rat colonies.

Marking and behavioural observations

Experiments were conducted monthly in summer (October to March) and in winter (May to August). During these periods, metal live traps (26 x 9 x 9 cm), baited with a mix of fruits and vegetables (e.g. apple, cucumber, lettuce, spinach), were set during the early morning and late afternoon when ice rats are most active. Traps were checked every 30 minutes to minimise the time that trapped individuals were exposed to lethal temperatures. Trapped animals were weighed (to the nearest gram), sexed, fitted with a uniquely coloured plastic cable tie neck band (length 200 mm, width 4.7 mm) and released at the point of capture. 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. Collared individuals that were trapped later in my study did not show any signs of distress or injury due to the neck bands. These trapping and marking procedures were approved by the Animal ethics committee of the University of the Witwatersrand (clearance number 2000/21/2a).

The behaviour of 30 adult ice rats (14 males and 16 females) in summer and of another 28 adults (13 males and 15 females) in winter was studied. Care was taken to observe the animals on days with similar weather conditions in each season.

Observations of focal individuals were made from a raised surface (about 1 m above the ground) from a distance of approximately 5 to 20 metres, depending on the position and movement of the individual in the landscape. Occasionally, 10x50 binoculars were used when a focal individual was not clearly visible with the naked eye. Focal individuals were observed for a total of five sessions per season, each session lasting one hour. Because of seasonal differences in the timing of aboveground activity (i.e. mostly in the morning and afternoon in summer and for most of the day in winter), observation schedules were standardised by observing focal individuals in the mornings and afternoons in both seasons: 05h00-12h00 and 13h30-17h30 in summer and 08h00-12h00 and 13h30-17h00 in winter. A total of two or three sessions were conducted per individual in the morning and afternoon; whenever possible, the same animal was not observed in the morning and afternoon of the same day.

Using continuous focal sampling (Martin and Bateson, 1986), the duration of six behaviours was scored: 1) consuming (feeding on/grazing/ingesting food); 2) searching for food (moving between food patches/sampling food); 3) gathering food (collecting plant material, be it food or non-food plants, from a patch; it excludes actual consumption or transport of food); 4) basking/stationary (upright posture without locomotion mainly for basking or occasionally for vigilance); 5) social (socio-negative and socio-positive) behaviour, and 6) burrow maintenance (cleaning out and re-tunnelling of burrow entrances). The time spent belowground was also recorded, but it was not known what animals did during this time. The number of incidences of hoarding was also noted. Hoarding was assessed as the frequency of food transported by a given individual into a burrow (the individual usually remained underground for no longer than 5-8 seconds, indicating that food was not consumed).

Data analysis

Data for each focal individual were converted to proportions of the total time it was observed in the morning or afternoon sessions. Data sets were arcsine transformed and analysed using the general linear model (GLM) analysis for multiple dependents, in which season, time of day (morning or afternoon) and sex were the fixed response variables and the six behaviours and proportion of time spent underground were the dependent variables. Specific differences were tested using Tukey post-hoc tests. Incidences of hoarding between seasons and between morning and afternoon observation sessions were compared using a χ^2 test with Yates' correction. Two tailed tests were used throughout and $\alpha = 0.05$.

The behaviour of ice rats was also analysed using sequential transition matrices, as described by Van den Berg *et al.* (1999). Using the software Matman™ (de Vries *et al.,* 1993), the sequence of all behaviours and disappearance underground were transformed into transition matrices for each individual animal. These matrices contained succeeding behaviours in the columns and the preceding behaviours of the same individual in the rows. Transition matrices were summed per season, gender and time of day. These summed matrices were used to calculate adjusted residuals, which represented the difference between the observed and the expected values for the transition frequency. Both positive (transitions occurring more often than expected by chance) and negative (transitions occurring less often than expected by chance) residuals were calculated and expressed according to a Z-distribution (for details see Van den Berg *et al.,* 1999). Since this method generates effects only within, but not between, independent factors (e.g. season), matrices of adjusted residuals for each individual ice rat were generated and the data set was analysed using a 3-way GLM analysis, in which season, sex and time of day were fixed effects variables and a particular behaviour transition (e.g. gathering-consuming) was the dependent variable; negative and positive transitions were analysed separately and Tukey post-hoc tests were used to reveal specific differences. Using these results, drawings for positive and negative matrices for each season only were generated; drawings for gender and time of day are not provided here for the sake of simplicity and since they influenced <5% of all transitions.

Results

In both seasons, *O. s. robertsi* spent more than 50% of its aboveground activity consuming food and in stationary behaviour (i.e. mostly sun-basking; Table 1). In addition, ice rats spent a large proportion of the remaining time in their underground burrows. Statistical tests revealed that there were highly significant seasonal differences in behaviours ($F_{7,102} = 12.50$; $p<0.001$) due largely to higher levels of gathering and consuming food and basking behaviour in winter, and more time spent belowground in summer (Table 1). Neither time of day ($F_{7,102} = 1.21$; $p>0.05$) nor sex ($F_{7,102} = 0.85$; $p>0.05$) had any influence on the behaviour displayed. Likewise, no combination of the interactions between season, gender and time of day had any influence on behaviours.

Hoarding behaviour was observed significantly more often in winter than in summer ($\chi^2_1 = 39.60$; $p<0.001$), both in the mornings ($\chi^2_1 = 14.36$; $p<0.001$) and the afternoons ($\chi^2_1 = 7.30$; $p<0.01$; Figure 1). Hoarding was greater in summer afternoons compared to summer mornings, but this difference was not significant ($\chi^2_1 = 2.72$; $p>0.05$). This pattern was reversed in winter, with the incidence of hoarding increasing in the mornings, but again this increase was not significant ($\chi^2_1 = 0.65$; $p>0.05$). No gender differences occurred in the number of hoarding incidences in winter mornings ($\chi^2_1 = 0.14$; $p>0.05$) or afternoons ($\chi^2_1 = 0.09$; $p>0.05$; Figure 1), or in summer mornings ($\chi^2_1 = 0.01$; $p>0.05$) or afternoons ($\chi^2_1 = 1.08$; $p>0.05$).

Table 1. Comparison of seasonal, time of day and gender influences on the proportion (x 100) of time that *Otomys s. robertsi* engaged in six behaviours and time spent underground. Data presented as Mean (+SE).

	Summer				Winter			
	Morning		Afternoon		Morning		Afternoon	
Parameter	Female	Male	Female	Male	Female	Male	Female	Male
Gathering food ***	1.6 (0.6)	1.1 (0.5)	1.5 (0.4)	1.8 (0.6)	3.7 (0.7)	4.1 (1.0)	4.6 (1.5)	6.5 (1.5)
Searching for food	1.6(0.4)	1.2 (0.3)	1.7 (0.4)	1.1 (0.2)	1.5 (0.3)	1.1 (0.3)	1.6 (0.9)	2.7 (0.6)
Consuming food **	33.6 (2.4)	33.2 (3.2)	35.3 (2.5)	28.8 (2.0)	43.9 (2.9)	36.8 (5.0)	41.6 (3.7)	36.7 (2.6)
Stationary/Basking*	28.7 (3.1)	35.1 (2.9)	31.6 (4.6)	30.8 (3.6)	36.1 (3.1)	37.2 (5.4)	38.9 (4.4)	36.8 (1.9)
Social behaviour	0.06 (0.02)	0.04 (0.02)	0.14 (0.12)	0.05 (0.03)	0.13 (0.07)	0.01 (0.01)	0.06 (0.04)	0.79 (0.29)
Burrow maintenance	1.5 (0.6)	0.7 (0.3)	0.6 (0.2)	0.5 (0.1)	1.3 (0.5)	1.7 (0.6)	0.7 (0.3)	1.8 (0.4)
Time underground***	33.0 (3.4)	28.7 (4.1)	29.1 (3.6)	37.0 (2.7)	13.5 (1.9)	19.2 (2.8)	12.6 (3.5)	25.2 (4.5)

Asterisks = significant seasonal differences in behaviour: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ (Tukey post-hoc tests)

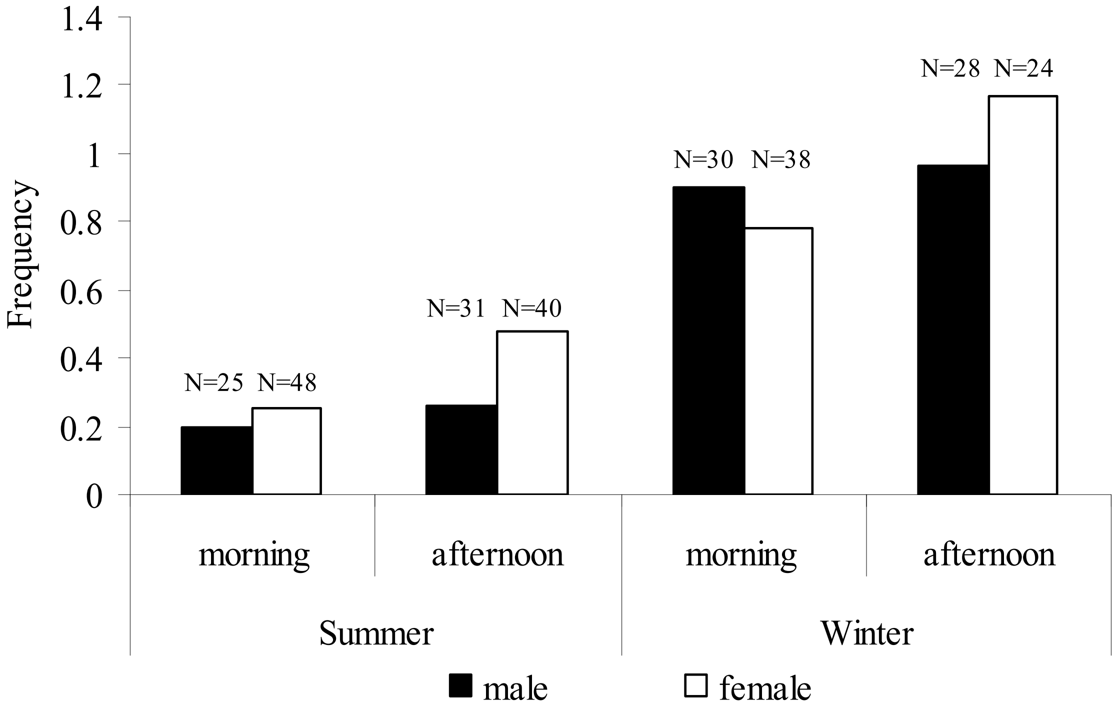
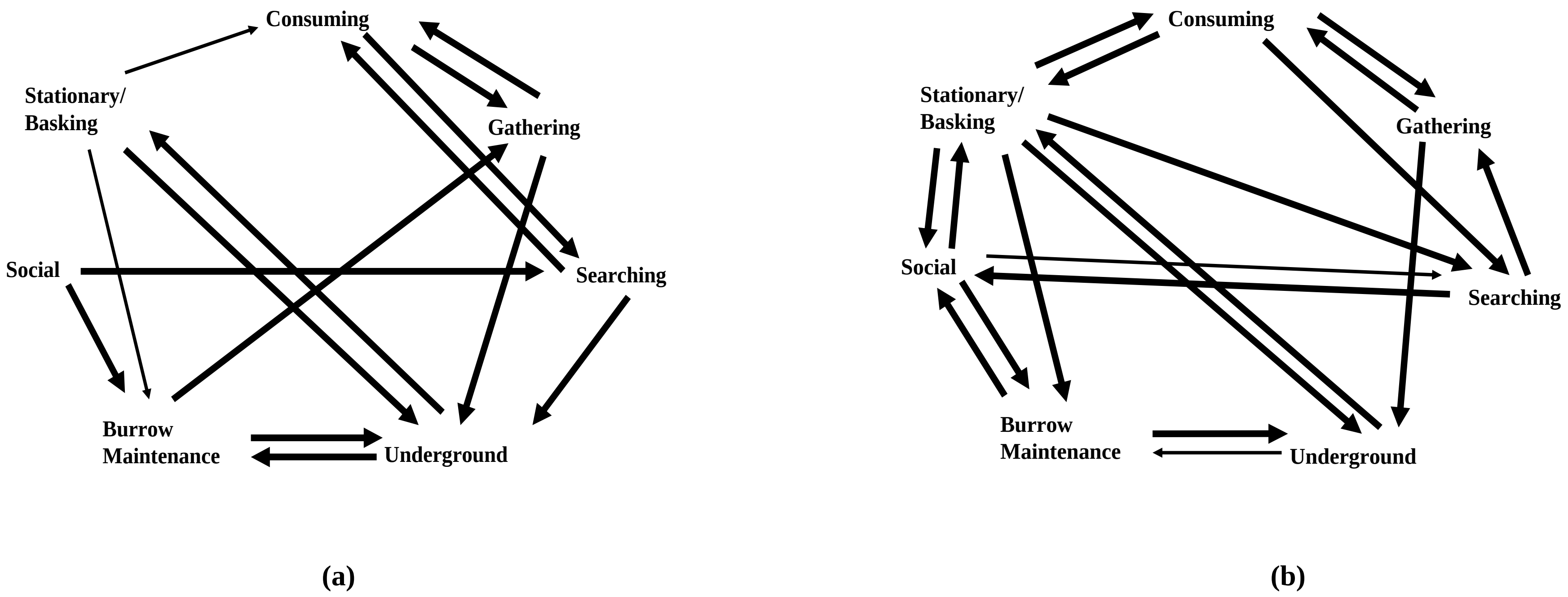


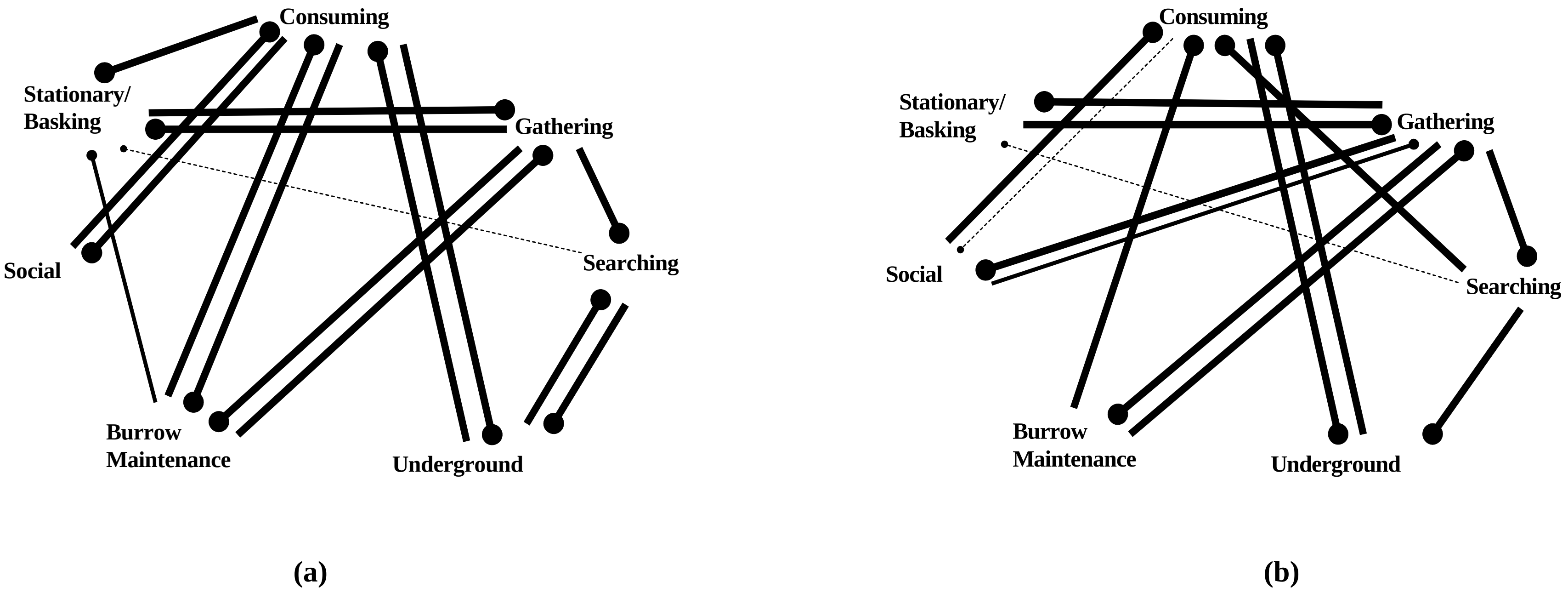
Figure 1. The number of incidences of hoarding per hour displayed by male and female *O. s. robertsi* in the mornings and afternoons in summer and winter. The number of hours of observation is shown above each bar.

There were fewer two-way positive transitions in summer (Figure 2a) than in winter (Figure 2b). In both seasons, strong two-way transitions occurred between burrow maintenance and disappearance belowground (underground), and consuming and gathering food. Seasonally-unique two-way transitions occurred between burrow maintenance and social behaviour, stationary/basking and social behaviour, consuming food and stationary/basking, and stationary/basking and disappearance underground (all in winter).

There were six two-way negative transitions in summer (Figure 3a) and five in winter (Figure 3b). Four transitions (consuming food and social behaviour, gathering food and stationary/basking, gathering food and burrow maintenance, consuming food and disappearance belowground) occurred less often than chance in both seasons. Other



Figures 2. Positive transitions in the sequential order of six behaviours and disappearance underground for *O. s. robertsi* in a) summer and b) winter. Transitions are depicted by lines and the thickness of the lines indicate the adjusted residual values in the transition matrix - thin lines = p<0.01; thick lines = p<0.001.



Figures 3. Negative transitions in the sequential order of six behaviours and disappearance underground for *O. s. robertsi* in a) summer and b) winter. Transitions are depicted by lines and the type and thickness of the lines indicate the adjusted residual values in the transition matrix - dashed lines = $p<0.05$; thin lines = $p<0.01$; thick lines = $p<0.001$.

two-way negative transitions were between burrow maintenance and consuming food and between searching for food and disappearance belowground in summer, and between gathering food and social behaviour in winter.

A total of 40 positive and 40 negative transitions were analysed for between independent factor effects. Nineteen positive and 17 negative transitions were influencedby season; sex and time of day influenced a total of four and three transitions respectively and are not considered further. One positive transition occurred significantly more often in summer than winter and 16 positive transitions occurred more frequently in winter than in summer (Table 2). Five transitions occurred less often than predicted by chance (i.e. negative transitions) in summer compared to winter, whereas eight negative transitions were more common in winter than summer (Table 2). The relationship between gathering and time spent underground (which demonstrates the sequence leading to hoarding) was significantly stronger in winter. Unlike the χ^2 tests, sequential analyses revealed that females were significantly more likely to hoard food than males, particularly in summer. Social interactions (predominantly socio-negative) followed various behaviours more often in winter than in summer.

Discussion

The present study examined the diurnal behaviour of a non-hibernating, alpine rodent, the ice rat *O. s. robertsi*, in its natural habitat, and tested whether ice rats have different behavioural strategies in summer and winter and at different times of the day. I also asked whether males and females behaved differently because of sex-specific reproductive investment and previously reported sex-specific differences in gut structure (Schwaibold and Pillay, 2003). My findings indicate that the diurnal activity of ice rats

Table 2. Significant seasonal negative and positive transitions for between sample effects for six behaviours and disappearance belowground displayed by *O. s. robertsi*. Seasonal effects were derived from post-hoc tests from GLM analyses.

Sequence		
From	**To**	**Seasonal effects**
Negative Transitions		
Consuming food	Time underground	winter > summer
	Stationary/Basking	summer > winter
Gathering food	Time underground	summer > winter
	Searching for food	winter > summer
	Social behaviour	winter > summer
	Stationary/Basking	winter > summer
Searching for food	Consuming food	winter > summer
	Gathering food	summer > winter
Social behaviour	Consuming food	winter > summer
	Gathering food	winter > summer
Stationary/Basking	Burrow maintenance	summer > winter
	Gathering food	winter > summer
Time underground	Gathering food	summer > winter
Positive Transitions		
Burrow maintenance	Searching for food	winter > summer
	Social behaviour	winter > summer
Consuming food	Searching for food	winter > summer
Gathering food	Time underground	winter > summer
	Social behaviour	summer > winter
	Consuming food	winter > summer
	Burrow maintenance	winter > summer
Searching for food	Social behaviour	winter > summer
	Burrow maintenance	winter > summer
Social behaviour	Stationary/Basking	winter > summer
	Burrow maintenance	winter > summer
Stationary/Basking	Burrow maintenance	winter > summer
	Consuming food	winter > summer
	Time underground	winter > summer
	Searching for food	winter > summer
	Social behaviour	winter > summer
Time underground	Stationary/Basking	winter > summer
	Gathering food	winter > summer

primarily reflects their behavioural responses to changes in environmental conditions between summer and winter.

Of the seven behaviours recorded, ice rats spent most time in energy acquiring (gathering and consuming food) and energy saving (basking and belowground in their burrows) activities. Small mammals have a high metabolic rate in relation to their size (Schultz *et al.*, 1999) and it was predictable that ice rats would spend much of their time in thermoregulatory activities. Moreover, as herbivores, ice rats need to spend most of their active time feeding, as less energy can be gained from low quality/high fibre plant material than from an omnivorous diet (see Perrin and Curtis, 1980, for review). However, the amount of time spent foraging is traded off against energy saving behaviours such as basking and seeking refuge underground.

Incidences of gathering and consuming food were higher in winter than in summer when conditions were more demanding. A similar pattern was found in desert-living Brant's whistling rat *Parotomys brantsii* (Jackson, 1998), a close relative of *O. s. robertsi*. There are possibly three explanations for the increased foraging in winter. Firstly, energy requirements are higher when temperatures are low, resulting in higher metabolic demands (Ellison, 1996) and accompanied by greater energy intake through feeding (see Hayne *et al.*, 1986; Schultz *et al.*, 1999). Secondly, since food availability and quality diminish dramatically in winter in the Lesotho wetlands (Schwaibold and Pillay, 2003; Chapter 2), high levels of foraging would increase net energy gain from the limited food resources to compensate for the increased energy loss due to low temperatures (Schultz *et al.*, 1999). Thirdly, intensive foraging bouts might be needed to compensate for the shorter day length in winter, since ice rats are not active aboveground after sunset (see also hoarding below).

Winter behaviour was characterised by high levels of basking. As the ice rat does not hibernate or enter bouts of torpor during extreme cold conditions, sun-basking is one of the behaviours adopted to cope with low temperatures. Many small mammals bask to overcome nocturnal hypothermia and to reduce the costs of metabolic heat production (Barash, 1989; Hainsworth, 1995; Geiser, *et al.*, 2002) and basking becomes increasingly important when animals are thermally stressed and when forage is scarce and of low quality. Sun-basking accelerates the warming-up process to a level that allows for uninterrupted activity with very little thermoregulatory cost (Sale, 1970; Geiser *et al.*, 2002). Ice rats spent extended periods of time sun-basking when temperatures dropped below 5°C (Hinze and Pillay, unpublished) and the energy gained through basking may compensate for the reduced energy intake from lower quality food, which may be adequate to meet metabolic requirements.

In contrast to winter, ice rats spent more time belowground in their burrows in summer. This is most likely a response to prevailing environmental conditions, since a concurrent study reported that ice rats avoid aboveground activity when ambient temperatures and levels of solar radiation are highest during the day (Hinze *et al.*, submitted), Similarly, black-capped marmots (*Marmota camtschatica bungei*) compensate for physiological limitations by seeking refuge in a burrow or lying on rocks to discharge excess heat when ambient temperatures were very high and potentially lethal (Semenov *et al.,* 2001). The South American degu (*Octodon degus*) also adjusts its activity patterns as temperatures increase and has been found to spend more time in shade or below-ground during the hottest times of the day (Kenagy *et al.,* 2002; Kenagy *et al*., 2004*).*

I predicted that ice rats would forage for longer in the afternoons since no aboveground activity occurs at night, and that they would bask for longer periods in the morning sun after they emerged from their burrows. Time of day had minimal influence on ice rat behaviour, indicating similar behavioural priorities in the mornings and afternoons. In contrast, the diurnal *P. brantsii* increases foraging and hoarding behaviour substantially in the later hours of the day, thereby permitting them to feed belowground at night when temperatures drop after sunset (Jackson, 2001). The weather in the Lesotho mountains is unpredictable so that foraging throughout the day might be an adaptation to optimise feeding when conditions are favourable.

An important aim of this study was to investigate the organization of behaviours. In general, behavioural sequences also revealed significant seasonal differences with little or no gender or time of day effects. Transitional matrices indicate the likelihood of one behaviour following another. Compared to summer, there were many more positive transitions in winter (i.e. one behaviour following another), strongly focussed on foraging, hoarding and thermoregulation, which indicates that these three behaviours are very likely to follow each other during the behaviour repertoire of an individual, while other behaviours became less important. While the fewer transitions in summer may be related in part to the increased time spent belowground, reasons for the greater number of transitions in winter are not obvious, particularly in their relevance to energy conservation, since one would have expected reduced activity and hence fewer transitions in winter when energy loss would have been greatest (see Kluger, 1979). It might be profitable in future to derive a cost-benefit analysis of energy gains and losses from increased and reduced activity. Equally, an investigation of the temporal motivational reorganisation of behaviours in summer and winter would be useful, since it is known that animals will interrupt energy saving behaviours for energy demanding ones in response to specific cues (Aubert, 1999).

More transitions led to aggressive encounters in winter, which were probably ultimately related to heightened tension because of competition for optimal feeding sites (Hinze and Pillay, unpublished). The relationship between searching, gathering and disappearance underground was very strong, both in summer and winter, supporting the increased incidence of hoarding described earlier.

No sexual differences were found in the time spent in each of the seven behaviours and sexual differences in behavioural transitions were negligible. Since female ice rats have post-partum oestrous (Willan, 1990), most would have been pregnant and/or lactating during the summer observations. Therefore, I expected that females would forage for longer than males in order to meet the energy requirements of pregnancy and lactation. While one cannot rule out other reasons for the lack of differences between the sexes, one reason for the similarity in foraging time may be that the larger gut dimensions in females compared with males (see Schwaibold and Pillay, 2003) would reduce the need for extended foraging times of females in summer.

Hoarding is an adaptive response to changes in food availability and/or energy needs (Wunder, 1984). Stored food and nesting material provide food and warmth during unfavourable aboveground conditions and a decline in ambient temperature can result in significant increases in hoarding (Barry, 1976; Masudu and Oishi, 1988) and explains the increase in hoarding behaviour by both male and female ice rats in winter. The shorter day length in winter may also have influenced hoarding, since hoarded food extends foraging times after dark. In addition, feeding belowground in winter would decrease the time that ice rats are exposed to extreme temperatures aboveground. Hinze *et al.* (submitted) found evidence of food storage chambers in ice rat burrow systems, confirming that food plants are hoarded when they are accessible during clear days in preparation for times when aboveground food is not accessible (e.g. cold nights, rainy days, snow days). Some of the plant species collected both in summer and winter were not part of the ice rat's diet (Schwaibold and Pillay, unpublished; Chapter 6), suggesting that plant material was collected for food as well as bedding, as also occurs in *Marmota* spp. (Barash, 1989).

Female rodents increase food hoarding behaviour when they are caring for young (Smith and Reichmann, 1984). Similarly, hoarding was seen significantly more often by female than male ice rats during summer. Compared to other members of its subfamily Otomyinae (Pillay, 2001), young ice rats complete weaning almost a week later at 16 days (Willan, 1990) and they emerge aboveground only about 4-5 weeks after birth (Hinze and Pillay, unpublished). Plant material taken belowground would be important both as food and as nesting material for physiologically weaned but dependent young.

An animal's fitness depends on its ability to effectively divide its time and energy among competing behavioural demands (Schoener, 1971; Schultz *et al.*, 1999). In cold environments, animals must have access to adequate food supplies and nesting opportunities to maintain their body weight and normal body temperature, but when they have to search for food elsewhere, they are faced with increased thermoregulatory demands (Johnson and Cabanac, 1982). This is especially crucial for small mammals because their high metabolic rate and high surface area: volume ratio results in high thermal conductance (Schultz *et al.*, 1999). Ice rats are faced with the conflicting demands of energy intake and energy saving, and this study indicates that they have adapted their behavioural patterns seasonally. Foraging and basking behaviours are traded off against reduced exposure to low temperatures in winter, while ice rats escape lethal ambient temperatures and solar radiation levels in summer by retreating belowground. Further studies are needed on how ice rats modify their behaviour patterns during short term environmental changes (e.g. under various weather conditions during summer), how they respond to periods of prolonged snowfall, and whether high energy demands in winter may be met by energy conservation and huddling belowground. Finally, since predation pressure in the Sani Valley is negligible, this study reveals that the behaviour *O. s. robertsi* in the Sani Valley, Lesotho is strongly dictated by environmental influences. It would be interesting to examine ice rat behaviour in areas with greater predation risk to define behavioural priorities under challenging environmental conditions (e.g. low temperatures) and predation risk.

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CHAPTER FOUR:

Flexible foraging decision-making in the African ice rat, *Otomys sloggetti robertsi*

Abstract

I investigated the foraging behaviour of the southern African ice rat, *Otomys sloggetti robertsi*, a diurnal herbivore endemic to the southern African Drakensberg and Maluti mountains at altitudes above 2000m. Ice rats do not hibernate and show little physiological adaptation to their cold environment. Instead, they rely on a range of behavioural and morphological adaptations. Ice rats are central place foragers and travel short distances (<50 cm) to forage. They display significant seasonal variation in their foraging patterns. The further a foraging site is from a burrow, the greater the tendency for consuming food at the foraging site in summer, but in winter ice rats mostly return to a burrow, regardless of distance travelled. No relationship was found between distance travelled and time spent at a foraging site in summer, although in winter there was a strong negative relationship between these two variables. Predation risk is negligible in ice rats, so while the costs of returning to a burrow after foraging in winter may be energetically demanding, these must be viewed against the benefits accrued through avoiding exposure to low temperatures by feeding in a burrow, as well as the loss of collected food and possible injury associated with aggressive interactions with conspecifics.

Key words: *Otomys sloggetti robertsi*, central place, diet, foraging behaviour

Introduction

Understanding foraging decision-making is best encapsulated by mathematical models generated by optimal foraging theory, which has attempted to show how foraging behaviours of animals are adapted, through natural selection, to maximise fitness by balancing their net rate of energy gain (foraging) against their rate of energy loss through optimal searching, feeding and diet selection (Charnov, 1976; Pyke *et al*., 1977; Sih, 1980; Lima and Dill, 1990; Hughes, 1993). As a derivative of the optimal foraging theory, central place foraging specifically describes the behaviour of animals that repeatedly return to a fixed point with food items collected elsewhere (Orians and Pearson, 1979; Stephens and Krebs, 1986). Support for these models has been provided by numerous empirical studies which largely consider the rate of energy intake as the critical determinant of foraging patterns (see Lima, 1985; Nonacs and Dill, 1990; Vásquez, 1994; Jackson, 2001) and fitness increases as a function of the rate of energy gain per unit of time spent foraging (Charnov, 1976).

Nonetheless, other conditions to which animals are exposed are sometimes overlooked in these models. For example, predation risk (see Lima and Dill, 1990; Lima, 1998), the presence of competitors (see Schröpfer and Klenner-Fringes, 1991; Krebs and Davies, 1993) and food handling times (see Guerra and Ades, 2002) can also affect foraging decisions. An important factor often ignored in most foraging models is the influence of environmental factors, such as prevailing weather conditions, on foraging decisions, possibly because of the difficulty of identifying appropriate empirical vectors (Jackson, 2001), but see Stouder (1987) and Sergio (2003). Since environmental conditions vary over time (e.g. from daily variations to seasonal changes), an animal might need to modify its foraging behaviour temporally in the face of changing energy demands associated with temperature fluctuations. When ambient temperature falls below the thermoneutral range, animals with access to sufficient food and a thermally stable refuge can maintain normal body temperature by eating more or higher quality food and by spending more time in the refuge. However, if animals must leave their stable microenvironments to obtain food elsewhere, they will face increased thermoregulatory challenges. This problem is especially acute for small mammals because of their large surface area to volume ratio (Johnson and Cabanac, 1982).

Intuitively, selection should favour flexible decision-making to maximise energy gain, which is often likely to be achieved as a series of trade-offs of various behaviours (Schoener, 1971; see Schultz, *et al.*, 1999, for review). Desert antelope ground squirrels *Ammospermophilus leucurus* (Hainsworth, 1995) and thirteen-lined ground squirrels *Spermophilus tridecemlineatus* (Vispo and Bakken, 1993), for example, 'shuttle' between hot desert surfaces to forage and cool burrows to escape high temperatures. In cold environments, small animals would be expected to trade off between foraging activity, which is the most common means of acquiring energy (Schultz *et al.*, 1999), and escaping prolonged exposure to low temperatures (Johnson and Cabanac, 1982b). For example, black-capped chickadees *Parus atricapillus* may gain some thermal benefit from carrying food items back to cover for consumption rather than eating in the open at the foraging patch, particularly on cold or windy days (Lima, 1985). Also, Caraco *et al.* (1990) found that yellow-eyed juncos (*Junco phaenotus*) changed their foraging patterns during the day in relation to ambient temperature by displaying risk-averse bahaviour during the warmer periods of the day when a positive energy budget could be expected, while colder periods of the day brought about risk-prone behaviour as the energy budget was expected to be negative.

The aim of the present study was to investigate the foraging behaviour of free-living African ice rats, *Otomys sloggetti robertsi*. This medium-sized (121-143 g), burrow-dwelling, diurnal murid rodent is an interesting subject for studying foraging decision-making because of its unique biology coupled with its geographic distribution. *Otomys s. robertsi* is confined to altitudes exceeding 2000 m, and is endemic to the harsh subalpine and alpine Drakensberg and Maluti mountains of southern Africa (Killick, 1978) but it does not hibernate and its physiology is apparently similar to congeners inhabiting warmer and lower altitudes (Richter *et al.*, 1997). Instead, it employs a range of behavioural adaptations (e.g. sun-basking and huddling) to cope with low temperatures (Willan, 1990; Schwaibold and Pillay, unpublished; Chapter 3).

Ice rats are specialist herbivores, feeding more or less exclusively on green plant material with a high fibre content, including stems, leaves, and grasses (Willan, 1990) and only have access to high-quality plant parts such as flowers and new shoots for a short time in summer (Schwaibold and Pillay, 2003; Chapter 2). This, coupled with the high metabolic rates of small animals (Schultz *et al.*, 1999) means that *O. s. robertsi* needs to maximise overall food intake in order to gain as much energy during foraging as omnivorous or granivorous rodents (Perrin and Curtis, 1980; Green and Millar, 1987). Moreover, the poorer diet quality of its herbivorous diet (Green and Millar, 1987; Hammond, 1993) and the short growing season in the alpine habitats (Killick, 1978) would presumably influence the foraging behaviour of ice rats. In recent examinations of gross gut anatomy, we reported that *O. s. robertsi* has a larger small intestine, caecum, stomach volume and parts of the colon compared to its relatives living at lower and warmer altitudes, and we suggested that these morphological adaptations increase energy uptake from a poor quality diet (Schwaibold and Pillay, 2003; Chapter 2). In addition, while male gut dimensions did not change seasonally, female ice rats showed increased gut dimensions in summer compared to winter, most likely because for increased energy requirements during pregnancy and lactation (Schwaibold and Pillay, 2003).

Predation pressure on *O. s. robertsi* in my study site in the Sani Valley appears to be minimal (Willan, 1990) and anecdotal reports from local Basotho shepherds and my own observations from 1999 to 2003 indicate that predation on ice rats is negligible in summer and virtually absent in winter. Instead, population numbers are regulated by snowfall and low winter temperatures (Willan, 1990; Lynch and Watson, 1992). In the absence of high predation levels, it is possible that, at least at my study site, ice rat foraging behaviour is mainly determined by environmental factors such as temperature.

Pilot studies have indicated that ice rats may possibly be central place foragers, collecting food and returning to a burrow for consumption. While returning to a central place may impose an energetic cost compared with staying at the foraging site (*in situ*), remaining *in situ* exposes the ice rat to potentially lethal temperatures, especially in winter. In summer, foraging occurs mainly during the cooler mornings and late afternoons, and aboveground activity is reduced during the middle of the day when temperatures and radiation levels are highest, whereas in winter, aboveground activity is more or less uninterrupted from morning to late afternoon; no aboveground activity has been observed at night (Hinze and Pillay, unpublished).

I asked whether the foraging decisions of ice rats could be influenced by seasonal changes in environmental conditions within the constraints of central place foraging. Specifically, three predictions were made: (1) Since winter in my study area is characterised by very low temperatures (often below 0º C), often far below the thermoneutral zone of ice rats (Richter *et al*., 1997; Hinze and Pillay, unpublished) and by poor food quality and availability (Schwaibold and Pillay, 2003), I asked how ice rats trade off between energy conservation and energy-acquiring foraging activities in winter, which would expose them to potentially lethal temperatures (ice rats are physiologically stressed at low temperatures, which may incur costs (Richter *et al*., 1997)). If avoidance of low temperatures is the primary concern for ice rats, I predicted that distances travelled for foraging would be comparatively short and that the incidence of returning to a protective burrow entrance with collected food items would be more common in winter compared to summer, regardless of the distance travelled. Alternatively, if acquisition of better quality food is more important, I predicted that ice rats would travel further in winter than in summer to find food and that, as distances from burrow entrances increased, ice rats would be more likely to consume food *in situ*, allowing them to feed for longer and increase energy intake. (2) Because of the energetic demands of pregnancy and lactation, I expected gender differences in foraging behaviour, but I also asked whether the increased gut capacity of females in summer might influence their foraging behaviour by compensating for the increased energy requirements, thereby making behavioural changes to increase energy intake unnecessary. (3) I also investigated the food type and quality of food and non-food plants in the ice rat's habitat and predicted that they would prefer food plants with lower levels of digestible fibre and higher levels of protein.

Materials and Methods

The study site

Fieldwork was conducted on a 4 ha site in the Sani Valley (29° 37' S; 29°14' E), about 5 km west of Sani Top in the south-eastern Drakensberg Mountains in Lesotho. The study site was located at an altitude of 2900 m along the edges of one of the many wetlands in the Sani Valley. Mean air temperature in the Lesotho highlands ranges from 0°C in winter to 6°C in summer (Grab, 1997). Precipitation is high (about 1200 mm per annum) and snowfall can be expected at any time of the year (Willan, 1990). Shrubs and herbs (annuals and biennials, woody cushion plants and succulents, aquatics and alien plants) are common in the Sani Valley, and trees are absent. Vegetation in my study area did not exceed 0.5 m in the colonies, making direct observations of ice rat behaviour possible.

Behavioural observations

The foraging behaviour of 18 adults (8 females and 10 males) was studied in summer (October to March) and of 14 adults (7 females and 7 males) in winter (May to August). Animals were live-trapped in three colonies and to facilitate later identification, each individual was fitted with a distinctively coloured plastic cable tie neck band (length 20 cm, width 4.7mm) and released at the point of capture. The procedure of using neck bands for identification is described by Jackson (1998). Females were fitted with a white cable tie and males with a black one. A distinctive colour combination of insulation tape was taped on to the cable tie for individual identification. This marking method permitted animals to be easily recognised in the field and was approved by the animal ethics committee of the University of the Witwatersrand (clearance number 2000/21/2a).

Tagged individuals were observed directly using 10x50 binoculars from a raised surface, about 1m above the ground, at a distance of between 10 and 30 m (ice rats habituate quickly to the presence of people). To allow tagged individuals to become accustomed to the neck bands, they were observed no earlier than five hours after tagging. Each individual was observed in one season only. Observations were made in the early morning (05h00 - 11h00) and afternoon (13h30 - 17h30) during summer and during most of the day (09h00 - 15h00) in winter, coinciding with the most active times in each season (Hinze and Pillay, unpublished). The foraging behaviour of each tagged individual was recorded using continuous focal sampling in 20 different foraging bouts per individual over several days and at various times of the day. A foraging bout started when the animal gathered and consumed food and ended when the animal changed behaviours, disappeared into its underground burrow or changed to a new location to forage. Data were collected whenever an individual was foraging, although no individual was observed more than once per day to allow for a representative data set over several days and at various times of the day; there was no time limitation to this data collection.

Ice rats consumed collected food *in situ* or took it back and consumed it in a burrow entrance (i.e. a central place). Incidences of hoarding behaviour were not scored because individuals often alternated between entrance holes during hoarding, and thus clear bouts could not be established. Also, since plant species were difficult to identify, it was uncertain whether the plant material gathered was used for nesting or caching. The distances that food was carried during foraging bouts were standardised against the body length of an ice rat. In addition, colour-coded wooden peg markers were arranged in a 4x4 metre grid over each colony. Using these indicators, the distances an ice rat travelled from a start point (e.g. burrow entrance) were categorized as follows: 1-15 cm (estimated from the length of an adult ice rat); 16-30 cm (up to twice the length of an ice rat); 31-50 cm (less than one eighth the length between two grid markers); 51-100 cm (up to a quarter the length between two grid markers); 101-150 cm (one quarter to one third the length between two grid markers); 151-200 cm (up to half the length between two grid markers); 200-400 cm (more than half the length between two grid markers). Food eaten at a central place was scored as 0 cm.

The habitat of ice rats consisted of a variety of plants such as small woody shrubs (*Helichrysum* spp.), various grass species, herbaceous plants and wetland vegetation, of which only the herbaceous and wetland vegetation were consumed. The plants present in the habitat were identified to species level where possible but as ice rats fed on very short grass and wetland plants, they usually collected as many different plant types as possible before consumption. This made it difficult to identify the species collected during a foraging bout (due to the small size of the sedges and lack of floral parts on grasses). Therefore, the plant species collected for consumption were categorised as wetland vegetation, herbaceous plants or grass. Foraging areas (i.e. areas regularly visited by ice rats during foraging bouts) were categorised according to the percentage cover of herbs (wetland and herbaceous vegetation) and grass present, which was determined in a 2 m radius around each burrow frequently used during foraging bouts. The frequency of visits to each of these patches was determined for each distance category in summer. Plant data were not collected in winter as it was very difficult to distinguish between the types of grasses and herbaceous vegetation when they were dry and often covered with ice. Samples of each of these plant types in the colonies under observation were collected and sent to the Institute for Commercial Forestry Research in Pietermaritzburg, South Africa, to obtain measurements of fibre (acid detergent fibre), protein and nitrogen levels. The size of the food items was not recorded because ice rats tended to collect as much plant material as would fit into their mouths before consumption, making estimation of size difficult.

Data analysis

The proportion of all bouts spent *in situ* and at a central place was calculated for males and females in summer and winter. The data set was arcsine transformed and a general linear model (GLM) was used to analyse whether season and gender (independent factors) influenced the proportion of times ice rats consumed food items *in situ* (calculated as a proportion of the total number of bouts per individual). A Tukey HSD post-hoc test was performed to determine specific differences. A Spearman Rank correlation with a Bonferroni adjustment was used to analyse the relationship between the frequency of foraging bouts and the distance travelled by each gender in summer and winter. The same tests were also used to establish the relationship between the distance travelled for foraging and the time spent at the foraging site, and between distances travelled and the frequency of staying *in situ*. I did not consider the colony affiliation of individuals in the analysis of foraging behaviour because of low sample sizes and since another study revealed no significant differences in the behaviour of ice rats of different colonies in a particular season (Schwaibold and Pillay, unpublished; Chapter 3). The time of day when observations were made did not statistically influence foraging behaviour and was not considered further.

The preference of ice rats for particular foraging areas was analysed using linear regression analysis, and chi-squared tests with Boferroni adjustment were used to assess differences between distances travelled and the type of food collected. The average proportion of fibre, protein and nitrogen content was calculated for the three plant types (i.e. grasses, herbaceous plants and wetland plants) consumed by the ice rat, the data were arcsine transformed and analysed using a GLM model and Tukey HSD post-hoc analyses.

Results

In approximately 65% of a total of 564 observations, ice rats left a burrow entrance, collected plants some distance away and returned to the same burrow entrance, strongly suggesting that ice rats are central place foragers. In the remaining 35% of observations, ice rats spent significantly more bouts *in situ* in summer than in winter ($F_{1,41} = 23.09$; $p<0.001$). There was no significant differences in the number of bouts spent *in situ* between males and females ($F_{1,41} = 0.40$; $p=0.53$; Figure 1). The season x sex interaction was also not significant ($F_{1,41} = 0.08$; $p=0.78$).

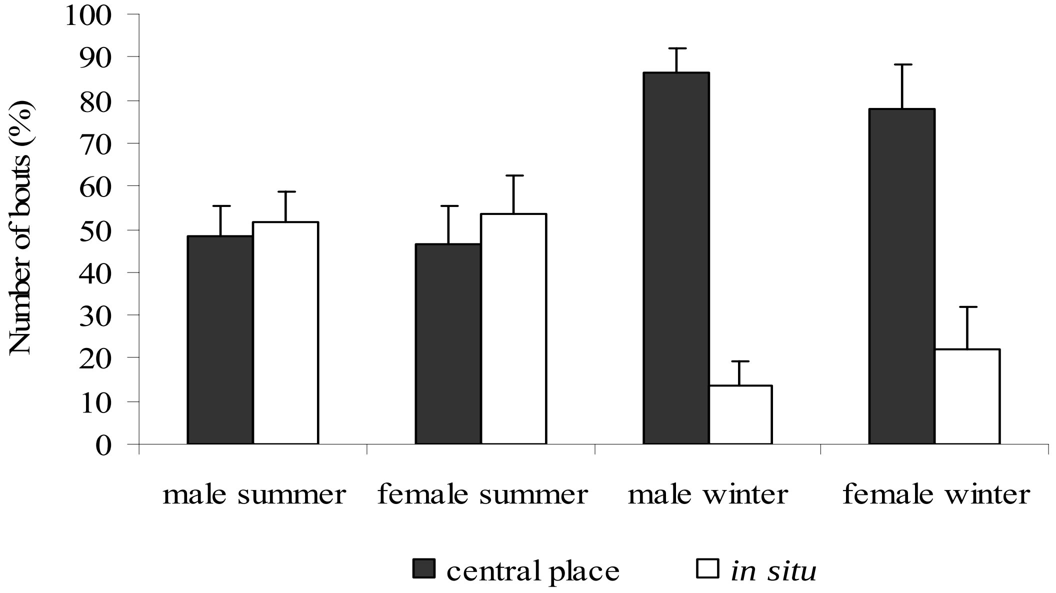

Figure 1. Mean (±SE) percentage of foraging bouts spent at a central place and *in situ* for male and female *O. s. robertsi* in summer and winter.

There was a strong negative relationship between the proportion of foraging bouts and distances travelled by ice rats in summer (r_{119}=-0.86; p<0.01) and winter (r_{70}=-0.82; p<0.0001). There were no gender differences in this relationship (Bonferroni tests). In both seasons, most foraging occurred within 10-15 cm of a burrow and foraging frequency decreased sharply towards 100 cm, with little foraging occurring beyond 100 cm of a burrow entrance (Figure 2).

The relationship between the number of times food was consumed *in situ* and distances travelled from a central place (i.e. burrow entrance) revealed dichotomous seasonal patterns (Figure 3). In summer, as the distance travelled from a central place increased, the frequency of remaining *in situ* also increased, resulting in a weak positive relationship (r_{45} = 0.39; p=0.01). In winter, however, there was a strong negative relationship between the frequency of bouts spent *in situ* and the distance from a central place (r_{22} = -0.71, p=0.0002).

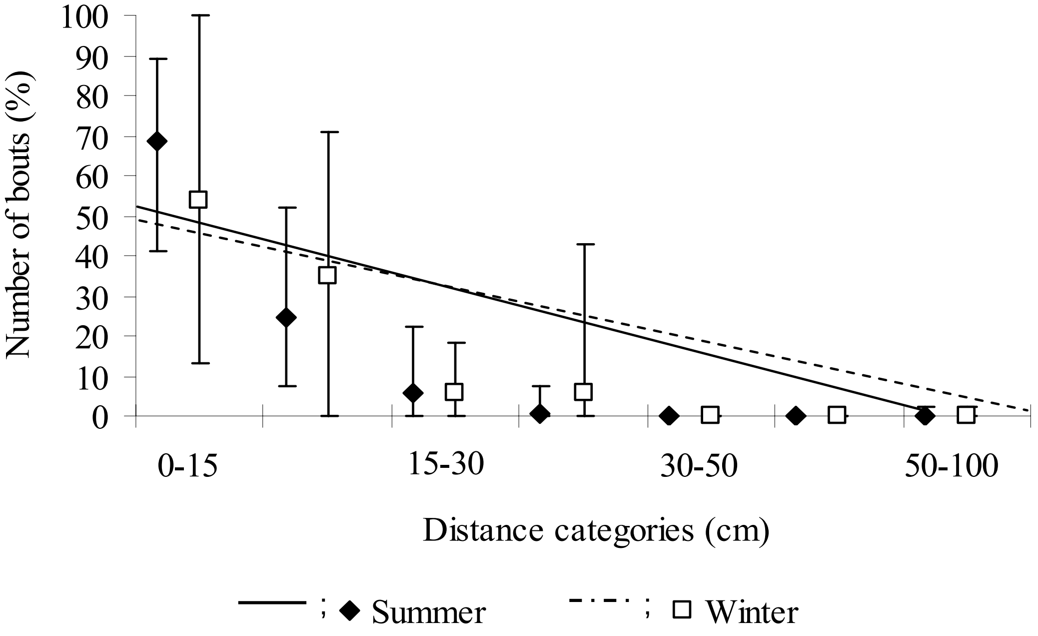

Figure 2. Mean percentage (including minimum and maximum values) of foraging bouts at each distance category in summer (N=17) and winter (N=13). Regression lines are included: summer: y = 48.19 - 0.849x; winter: y = 28.76 - 0.494x.

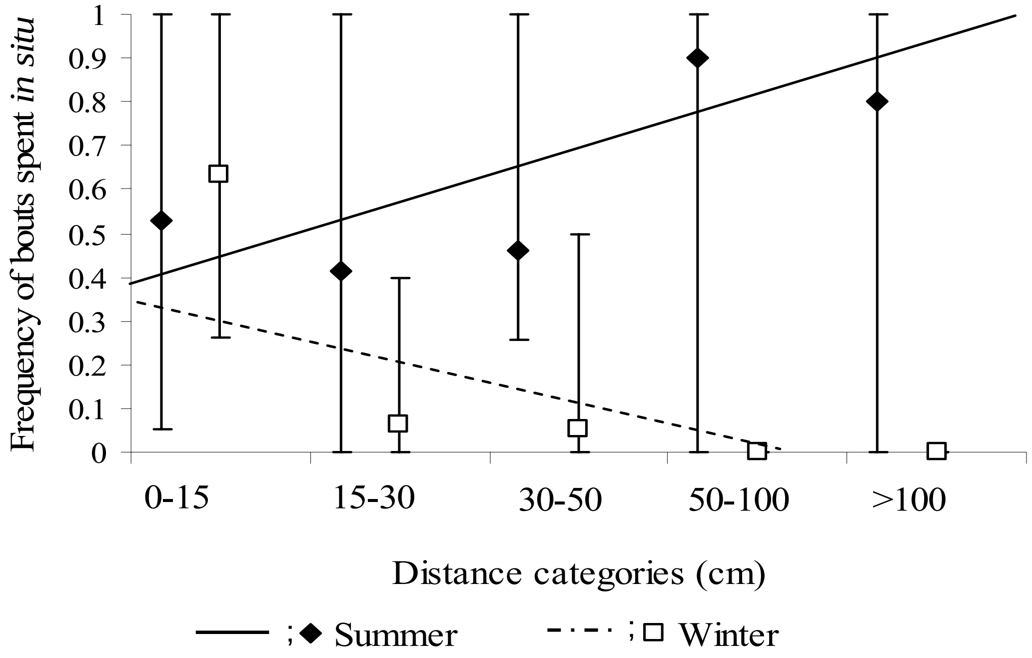

Figure 3. Mean frequency (including minimum and maximum values) of foraging bouts spent *in situ* for all distance categories in summer (N=17) and winter (N=13). Regression lines are included: summer: y = -895.0 + 9.29x; winter: y = 2015.1 – 19.45x.

In both summer and winter, as the distance from a central place increased, the time spent *in situ* decreased (Figure 4). A Kruskal-Wallis ANOVA showed no gender differences for any of the distance categories, but seasonal differences were found in the 15-30 cm ($H_{1,30}$=13.11, p=0.0003) and 30-50 cm ($H_{1,30}$ = 4.06, p=0.04) categories, and in both cases ice rats spent more time *in situ* in summer than in winter. In winter, there was a strong negative relationship between distance travelled and time *in situ*: foraging occurred for the longest period close to a burrow entrance and foraging bouts became shorter with increasing distance from a central place (r_{19} = -0.74; p<0.00032). A weak non-significant negative relationship was observed in summer (r_{49}= -0.24; p>0.10), indicating that ice rats spent a similar duration of time at each distance category. No gender differences were found in winter (r_{19}=0.39; p=0.10) or in summer (r_{49}=0.04; p=0.78).

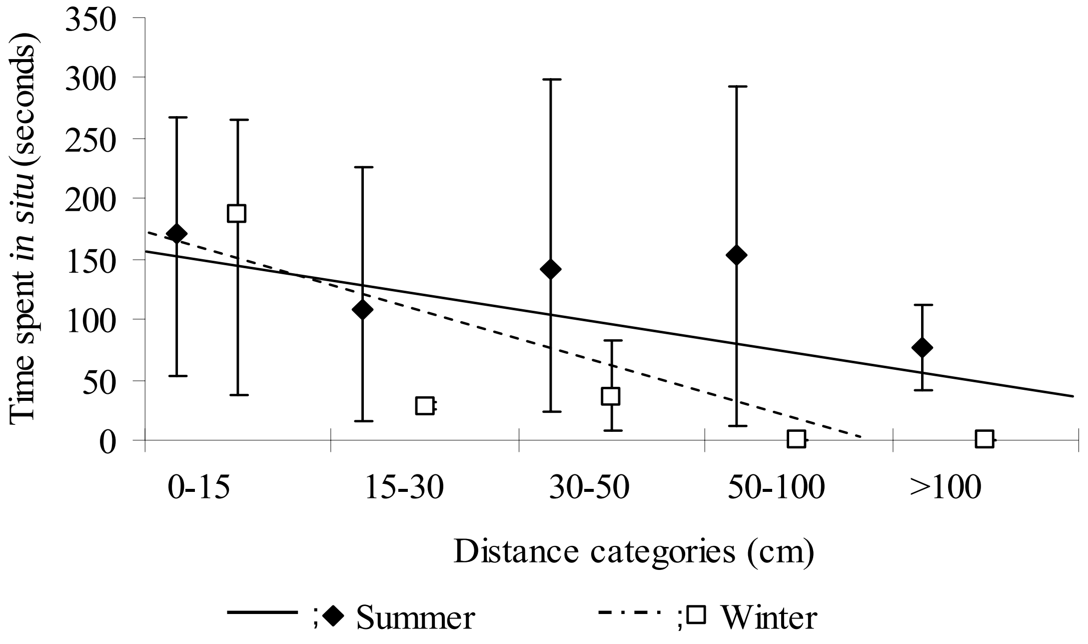

Figure 4. Mean duration (including minimum and maximum values) of time spent *in situ* by ice rats in summer (N=17) and winter (N=13). Regression lines are included: summer: y = 0.11 – 0.008x; winter: y = 0.19 – 0.06x.

In summer, ice rats displayed some preference for the areas visited for foraging. Those containing more than 50% herbaceous plants (of which most were wetland plants) were visited more often than those that contained more grass species, with the majority of visits taking place in areas containing 50-75% wetland/herbaceous plants (Figure 5). A regression analysis however showed that this relationship was neither strong nor significant (r_8= 0.41; p=0.32). This analysis was not performed in winter because plants were difficult to identify.

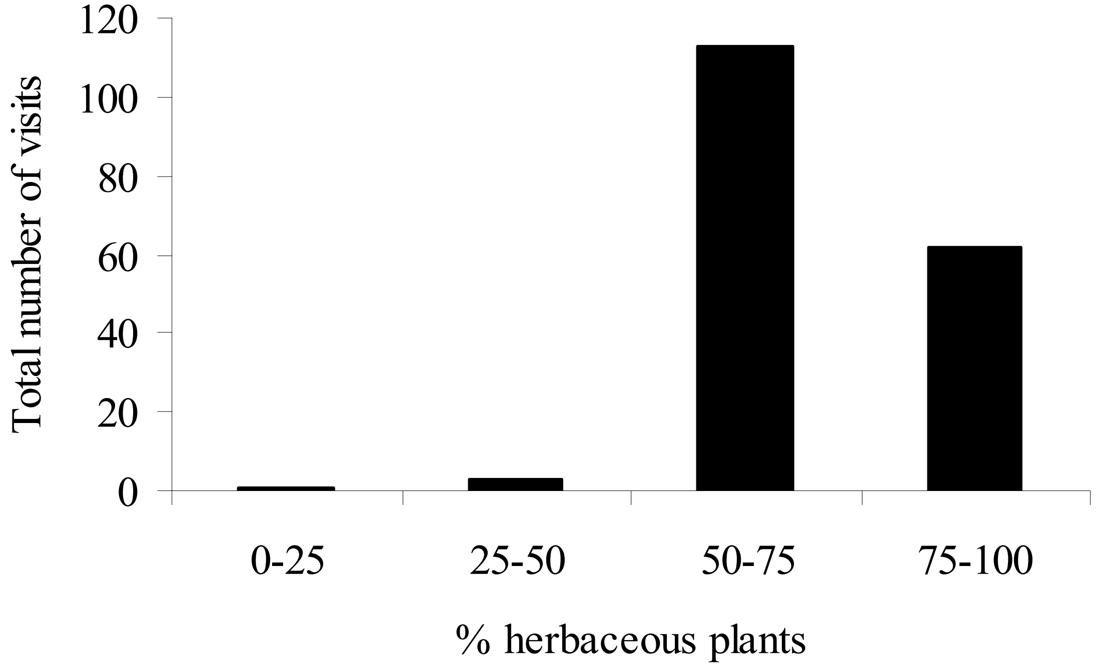

Figure 5. Foraging areas visited by *O. s. robertsi* during foraging bouts for all distance categories in summer.

The three plant types collected by ice rats varied significantly in fibre, nitrogen and protein content ($F_{6,24}$= 9.96; p= 0.00015), with wetland vegetation (the preferred food type) containing the lowest levels of digestible fibre and grasses (the less preferred food type) the highest (post-hoc tests). In contrast, grasses had the lowest levels of protein and nitrogen (Figure 6). Analyses of non-food plants such as *Helichrysum* spp. revealed very high levels of fibre (mean = 46.90%) and very low levels of protein (mean = 5.47%) and nitrogen (mean = 0.88%).

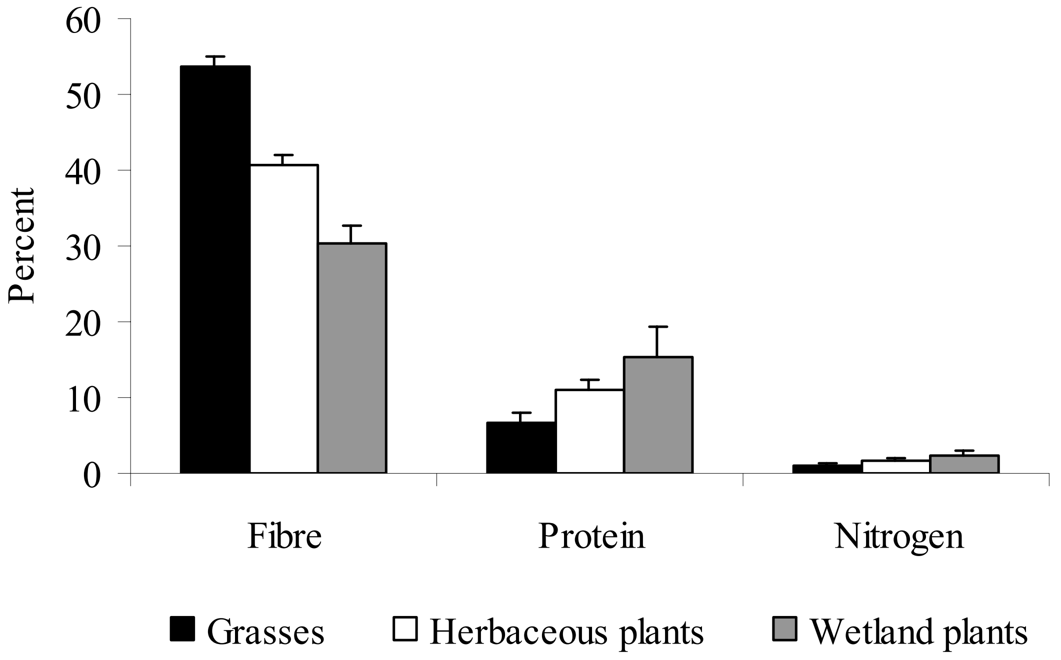

Figure 6. Mean (±SE) percentage of acid detergent fibre (ADF), protein and nitrogen in grasses, herbaceous plants and wetland plants determined on a 100% dry matter basis.

Discussion

During foraging bouts, ice rats mainly (65%) returned to a central place (i.e. the burrow) or sometimes (35%) remained and fed *in situ*. Ice rats are central place foragers and their foraging behaviour appears to be strongly influenced by seasonal changes in environmental conditions. Central place foraging theory maintains that animals return to a central place with collected food items if the distance travelled to the foraging site is short but that food should be consumed *in situ* if the distance travelled is further away. As the distance from a central place increases, the energy cost of travelling the distance outweighs the benefits of protection against risks such as predation (Orians and Pearson, 1979; Lima *et al.*, 1985). *Otomys s. robertsi* displayed such behaviour in summer: as distance travelled from a central place to a foraging site increased, the tendency to consume food *in situ* also increased. In winter, *O. s. robertsi* displayed a different foraging strategy. As the distance travelled from a burrow to a foraging site increased, the tendency to return with the collected food items increased. Not only did ice rats return from foraging bouts more often in winter than in summer, they also spent less time *in situ*.

Otomys s. robertsi travelled short distances to forage in both summer and winter and there were only a few occasions when foraging occurred more than 50 cm away from a burrow. In comparison, some small mammals which are of similar size and have a similar diet to ice rats travel further to forage. For example, Brants' whistling rat *Parotomys brant*sii (a close relative of the ice rat; Jackson, 2001) travels over 200 cm from its burrow to forage, and experiments by Anderson (1986) encouraged mice (*Peromyscus maniculatus*) and voles (*Clethrionomys gapperi* and *Phenacomys intermedius*) to travel distances over 14 meters in cold conditions. The short distances travelled by the ice rat may be explained by the short distances between burrows and food plants (Schwaibold and Pillay, unpublished; Chapter 6).

Lima (1985) proposed that animals concerned mainly with foraging efficiency would tend to feed *in situ*, whereas those at risk of predation would always return to the relative safety of cover, regardless of distance travelled. However, in most cases animals will trade off these two conflicting needs against each other (Caraco, 1979; Sih, 1980; Lima, 1985; Lima *et al.*, 1985). In many ways the foraging behaviour of ice rats, particularly in winter, appears to minimise risk and resembles the behaviour of animals subjected to high predation risk (Lima, 1985). However, potential predators in the Sani

Valley were rarely observed and predation risk is unlikely to have influenced foraging behaviour. If it did influence foraging decisions, I would have predicted higher incidences of returning to a central place and shorter time spent *in situ* in summer when a few raptors were sighted in the study area. I suggest that there are two non-mutually exclusive reasons for ice rats returning more frequently to a central place and spending less time *in situ* in winter. Firstly, ice rats reduce their exposure to low temperature if they spend less time *in situ*. Winter temperatures (Killick, 1978; Grab, 1997) are well below the thermoneutral zone of ice rats (see Richter *et al.*, 1997) and it appears that the benefits of returning to cover with forage may outweigh the costs of energy loss through travelling. Secondly, although ice rats in a colony nest communally, they display temporal territoriality aboveground and colony mates either ignore one another or interact aggressively (Hinze and Pillay, unpublished). Moreover, competition for limiting food resources among colony members is intense in winter, resulting in highly aggressive interactions (Hinze and Pillay, unpublished), leading to damaging fights (Willan, 1990). I suggest therefore that ice rats avoid competition with neighbours by consuming food at the burrow. Group-living striped mice *Rhabdomys pumilio* show a similar response by leaving a foraging site when another conspecific arrives, thereby avoiding aggressive encounters (Schradin, 2004).

No differences were found in the foraging patterns of male and female ice rats. Since female rodents generally have higher energy needs during the reproductive season (Weiner, 1987; Silby *et al.,* 1990), significant gender differences in foraging behaviour in summer were expected. However, in the harsh alpine habitats, reproductively active female *O. s. robertsi* have to compromise among caring for young, foraging, basking and territory defence (Schwaibold and Pillay, unpublished; Chapter 3). Female ice rats show a significant increase in gut dimensions during summer, which potentially allows them to extract more energy per unit mass of food than males (Schwaibold and Pillay, 2003; Chapter 2), which may explain why females may not need to change their foraging behaviour in summer.

Furthermore, a previous study has shown that ice rats spend more time basking in winter than in summer (Schwaibold and Pillay, unpublished; Chapter 3) and this is increasingly important when animals are thermally stressed and forage is scarce and of low quality. Marmots (*Marmota* spp.) have also been found to facilitate energy gain during cold periods by utilising radiant energy through basking (Barash, 1989). Energy intake through basking may compensate for the reduced energy intake from lower quality food in winter, thus allowing metabolic requirements to be met.

Fibre, nitrogen and protein analysis of various plants found in the ice rat's habitat revealed that wetland sedges such as *Haplocarpa nervosa* have the lowest levels of digestible fibre (ranging from 27% to 35%), followed by herbaceous plants, while the grass species have relatively high levels of fibre (40% - 53%). As patches consisting predominantly of herbaceous and wetland vegetation were preferred by ice rats, this comparatively low fibre contents may allow the rodents to gain as much energy as possible from easily digestible food items. In comparison, non-food plants such as the *Helichrysum spp* were found to have very high levels of fibre and comparatively low levels of protein and nitrogen, possibly making them unpalatable to ice rats. This is supported by the animal's patch preferences. Although most patches visited in summer contained grasses and very few non-food plants, mainly wetland plants and herbaceous vegetation were consumed. Unfortunately, no winter data were available, but if the levels of digestible fibre are in fact the driving force behind patch choice, I would predict the same pattern in winter with a stronger emphasis on the presence of wetland vegetation and herbaceous plants.

In conclusion, this study reveals that ice rats modify their foraging behaviour between seasons. In summer their behaviour is typical of animals following a central place foraging strategy, but in winter they almost always return to a central place, possibly to minimise exposure to low temperatures and competitive neighbours. *Otomys s. robertsi* is physiologically poorly adapted to low temperatures (Richter *et al.,* 1997), so its flexible foraging behaviour pattern is no doubt an adaptation for life in a harsh environment. In order to fully understand the foraging efficiency of *O. s. robertsi*, future studies should investigate which food items are collected in summer and in winter, and the size and energy values of the food items relative to the distances travelled should be established, both of which could not be established in this study. A future consideration should be to study the foraging patterns of ice rat populations which experience significant predation risk.

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CHAPTER FIVE:

Foraging in the African ice rat *Otomys sloggetti robertsi*: conflicting demands of energy conservation and predator avoidance

Abstract

According to optimal foraging theory, an animal is expected to make foraging decisions which maximise energy gain. However, many environmental factors shape foraging decisions and thereby the potential for energy maximisation. I investigated the influences of two environmental factors, predation pressure and cold temperatures, on the foraging behaviour of the African ice rat, *Otomys sloggetti robertsi*. Ice rats are diurnal herbivores endemic to the subalpine regions of the southern African Drakensberg and Maluti mountains, but are physiologically poorly adapted to low temperatures. In a population with negligible predation (Sani Top), foraging behaviour was seasonally variable: in summer, ice rats only returned to their burrow with forage as distance travelled increased, whereas they always returned to a burrow in winter. In another population (Katse Dam) experiencing higher predation pressure, ice rats always returned to a burrow entrance with forage when predators were present. Similar behaviours were observed when predators were absent, but ice rats also modified part of their foraging repertoire, which resembled that of their counterparts at Sani Top. Ice rats responded to the two environmental cues in a hierarchical manner, with foraging decisions being primarily determined by predation risk. However, foraging decisions in winter in the absence of predation resembled foraging decisions made when predators where present, indicating that low temperatures also pose a risk. Such facultative responses are adaptive in response to multiple cues.

Key words: *Otomys sloggetti robertsi*, foraging behaviour, predation risk, multiple cues, facultative decision making

Introduction

Optimal foraging theory has been used to describe and understand the foraging behaviour of many animals (reviewed in Stephens and Krebs, 1986). This theory highlights how animals trade-off between different behaviours (e.g. what to eat, how long to remain in a food patch) to optimise energy gain (Lima and Dill, 1990). Many factors have been shown to influence foraging behaviour, such as competition among conspecifics (Giraldeau *et al*., 1994; Rita and Ranta, 1998), food availability (Bautista *et al*.,1998), thermoregulatory costs (Bozinovic and Vásquez, 1999; Krijgsveld *et al*., 2003), weather patterns (Sergio, 2003), reproductive activity (Frey-Roos *et al*., 1995) and predation risk (Lima and Dill, 1990).

Predation risk is possibly the most important underlying determinant of foraging behaviour, especially for small mammals (Lima, 1985; Lima and Dill, 1990; Lima, 1998). As a result, many small mammals facing high levels of predation display a central place foraging strategy, by repeatedly returning to a fixed point with forage collected elsewhere to consume it under the protection of cover (Orians and Pearson, 1979; Lima, 1985; Lima and Dill, 1990; Lima *et al*., 1985; Anderson, 1986). Although returning to the safety of a central place reduces the risk of predation, there are energetic costs associated with carrying food to cover rather than feeding at the foraging site (Orians and Pearson, 1979; Lima *et al*., 1985; Vásquez, 1994). Therefore, most foragers trade off the demands of maximising foraging efficiency with the need to minimise time exposed to danger. For example, remaining at a foraging site (*in situ*) to consume food increases overall energy intake by reducing energy loss, but increases time exposed to risks such as predation and other environmental influences (Lima, 1985).

Ambient temperatures influence time and energy allocation to different behaviours (Huey, 1991; Bozinovic and Vásquez, 1999). Anderson (1986) suggested that exposure to cold temperatures may be viewed as a significant risk to small mammals, particularly in winter. Since thermal physiology may be a significant factor influencing foraging behaviour (Caraco *et al*., 1990), endothermic animals select microhabitats with temperatures close to their thermoneutral zone, but several behaviours such as foraging and mating require that the animal leaves this favourable microenvironment (Johnson and Cabanac, 1982) such as a burrow or nest, resulting in exposure to extreme environmental temperatures. Harsh environmental conditions may therefore limit the use of space and time for foraging and other maintenance behaviours in small endotherms such as rodents (Melcher *et al*., 1990; Kenagy *et al*., 2002), as activity time (and therefore time available for foraging) is traded off against other thermoregulatory costs (Belovsky and Slade, 1986). Although returning to a suitable microhabitat while foraging reduces exposure to low temperatures, energy will be lost through carrying food to cover rather than consuming it *in situ* (Schwaibold and Pillay, unpublished; Chapter 4). Therefore, there must be a trade off between the demands of maximising foraging efficiency and the need to minimise time exposed to the cold.

While most studies focus on the influence of only one factor on foraging decisions and efficiency (see Lima, 1985; Lima and Dill, 1990; Schröpfer and Klenner-Fringes, 1991; Jackson, 2001; Powell and Banks, 2004), little is known about how the foraging behaviour of small mammals is determined by a combination of factors (e.g. predation and low temperature). Such studies could answer questions about the motivation of animals to make decisions when faced with multiple cues (see Morrell, 2004). For example, are there predictable trade-offs between cues in relation to prevailing conditions and do the response to the cues follow hierarchical rules (i.e. response is stronger to some cues than others; Balasko and Cabanac, 1998; Morrell, 2004)?

The African ice rat *Otomys sloggetti robertsi* is an ideal model for studying how environmental factors influence foraging behaviour in small endothermic animals. The ice rat is a medium-sized (121-143 g), herbivorous, diurnal murid rodent, endemic to the harsh subalpine and alpine environment of the Drakensberg and Maluti mountains of southern Africa (Killick, 1978) at altitudes exceeding 2000 m. Ice rats do not enter into torpor or hibernate and are physiologically poorly adapted to the temperature extremes in their habitats (Richter *et al.*, 1997). Instead, they display a range of morphological (e.g. short limbs and tails; Richter, 1997) and behavioural (e.g. sun-basking and huddling; Willan, 1990) adaptations to cope with their environment, particularly with low temperatures. In addition, ice rats live in colonies of up to 16 individuals and construct complex underground burrow systems with insulated nests, which create favourable microclimatic conditions and also provide opportunities for social huddling (Hinze *et al.*, submitted).

In a previous study, I reported that ice rats are central place foragers (Schwaibold and Pillay, unpublished; Chapter 4) since they collect food in open areas which is consumed when ice rats return with it to a burrow (central place). This study population, located at Sani Top, Lesotho, was exposed to little or no predation risk, and I concluded that returning to a central place was related to environmental cues, particularly low ambient temperatures (Chapter 4). I recently located another ice rat population (i.e. near Katse Dam, Lesotho) that is subjected to significantly higher levels of predation than the population in my earlier study. Ice rats here also experience similar environmental conditions to those at Sani Top, and so afford the opportunity for studying how both predator risk and low temperatures influence foraging. If predator avoidance is the main priority, one would expect these animals to consume food at a central place. However, if the priority is energy conservation, forage should be consumed *in situ* (Lima, 1985), although these probably represent extreme responses along a continuum because of the spatio-temporal distribution of both predation risk (Lima and Dill, 1990) and environmental temperature (Johnston and Bennett, 1996).

I compared the foraging behaviour of individual ice rats exposed to moderate levels of predation (Katse Dam) with data from a previously completed study on an ice rat population near Sani Top (only two predation attempts were observed during more than 625 hourse of study, about 0.3%). My aim was to compare the foraging behaviour of ice rats when they are faced with little or no predation risk (Schwaibold and Pillay, unpublished; Chapter 4) with that of ice rats which experience moderate levels of predation, both when predators were present and absent, since foraging decisions are shaped by a perceived risk (Lima and Dill, 1990; Ylönen and Magnhagen, 1992). I asked two questions: (1) Does the foraging behaviour of ice rats follow hierarchical rules (i.e. foraging is primarily shaped by predation risk and then by thermoregulatory cost) or do they trade off between predation and thermal costs? (2) Do ice rats in predation risky areas respond differently to an immediate threat (i.e. predator present) than when predators are absent?

Materials and Methods

Study site

The study was conducted near the Sengu River, about 7km south-east of the Katse Dam (29°21' S; 28°32' E) in Lesotho. The site was situated at an altitude of approximately

2000 m. The ice rat population experienced moderate predation pressure, and predation attempts were observed on 27 occasions during the five months of study, mainly (74%) by jackal buzzards *Buteo rufofuscus* (20 occasions) and occasionally by barn owls *Tyto alba*. Ice rats are also hunted by indigenous Basotho herdsman, but I did not observe hunting during my study. The study area comprised mainly shrubs and herbs and trees were absent, and vegetation never exceeded 0.5 m.

The data collected for this study will be compared to data obtained from Sani Top in the Sani valley, located in eastern Drakensberg Mountains in Lesotho (29° 37' S; 29°14' E; altitude: 2900m). While predation pressure in this area is negligible, temperature means in the Lesotho highlands are low (from 0°C in winter to 6°C in summer; Grab, 1997). Rainfall is high (around 1200mm per annum) and snow can be expected at any time of the year (Willan, 1990).

Behavioural observations

The methods used here were similar to those of a previous study (Schwaibold and Pillay, unpublished; Chapter 4). The foraging behaviour of 20 adult ice rats (10 of each sex) was studied in summer (January to March) and 20 different ice rats (8 males, 12 females) were studied in winter (May to August). Animals were live-trapped (metal live traps, 26 x 9 x 9 cm) in four colonies. Each individual was fitted with a uniquely coloured plastic cable tie neck band (length 20 cm, width 4.7 mm) and released at the point of capture (see Chapter 4). Females were marked with a white cable tie and males with a black one, and a unique colour combination of insulation tape was taped onto the cable tie for individual identification. Excess cable was cut off. This marking method facilitated easy recognition of individual ice rats in the field, and was approved by the animal ethics committee of the University of the Witwatersrand (clearance number

2000/21/2a). Individuals were not observed on the day they were tagged to allow them to become familiar with the neck bands. Each individual was observed in one season only, as it was not always possible to find marked individuals again in the next season.

Collared individuals were observed directly using 10x50 binoculars from a raised surface at a distance of between 30-50 m; this distance was further away from colonies than observations in my other study (3-30 m) but I could not approach ice rats too closely in the Katse colonies. Observations were made in the early morning (05h00 - 11h00) and afternoon (13h30 - 17h00) during summer, and during most of the day (09h00 - 15h00) in winter, coinciding with the most active times in each season (Hinze and Pillay, unpublished). Continuous focal sampling was used to study the foraging behaviour of each individual ice rat during 20 foraging bouts over several days and at various times of the day. A foraging bout began when an ice rat gathered and consumed food and ended when it changed behaviour, disappeared into an underground burrow or changed its central place. Data were collected whenever an individual was found to be foraging, although no individual was observed more than once per day. Times were adjusted based on the presence/absence of predators at Katse Dam.

The distances that food was carried during foraging bouts were estimated relative to the body length of an ice rat. Furthermore, wooden peg markers were arranged in a 4x4 metre grid over each colony and used to categorise the distances an ice rat travelled from a start point (e.g. burrow entrance) as follows: 1-15 cm (estimated from the length of an adult ice rat); 16-30 cm (up to twice the length of an ice rat); 31-50 cm (less than one third the length between two grid markers); 51-100 cm (up to a quarter the length between two grid markers); 101-150 cm (one quarter to one third the length between two grid markers); 151-200 cm (up to half the length between two grid markers); 200-400 cm (more than half the length between two grid markers). Food consumed at a central place was scored as 0 cm.

Data were collected when predators were visible in the vicinity of the colonies (i.e. flying overhead) and also when no predators were observed. For the predator absent treatment, I collected data no earlier than one hour after a predator was seen.

Data analysis

I compared the data collected here with those obtained in my other study at Sani Top (Schwaibold and Pillay, unpublished; Chapter 4). Data were averaged for each individual and tested for normality before analysis. Data sets were transformed when necessary. General linear models (GLM) were used to analyse both the number of foraging bouts per hour and the proportion of times ice rats consumed food items *in situ* (calculated as a proportion of the total number of bouts per individual), in which location/predation, season and gender were independent factors. A Tukey HSD post-hoc test was used to determine specific differences in foraging patterns.

A Spearman Rank correlation with Bonferroni adjustment was used to analyse the relationships between three sets of variables in relation to location/predation risk and gender, including 1) frequency of foraging bouts and the distance travelled by each individual, (2) distances travelled and the frequency of staying *in situ*, and (3) distances travelled for foraging and the time spent at the foraging site. I did not consider the colony affiliation of individuals in the analysis of foraging behaviour because of low sample sizes and since another study revealed no significant differences in the behaviours of ice rats of different colonies in a particular season (Chapter 4).

Results

The average number of foraging bouts per hour was significantly influenced by location/predation risk categories ($F_{2,100} = 17.07$, $p<0.001$) but not by season ($F_{1,100} = 0.16$, $p=0.69$), gender ($F_{1,100} = 1.91$, $p=0.17$) and the interactions between these variables ($F_{1,100} = 0.91$; $p=0.34$; Figure 1).

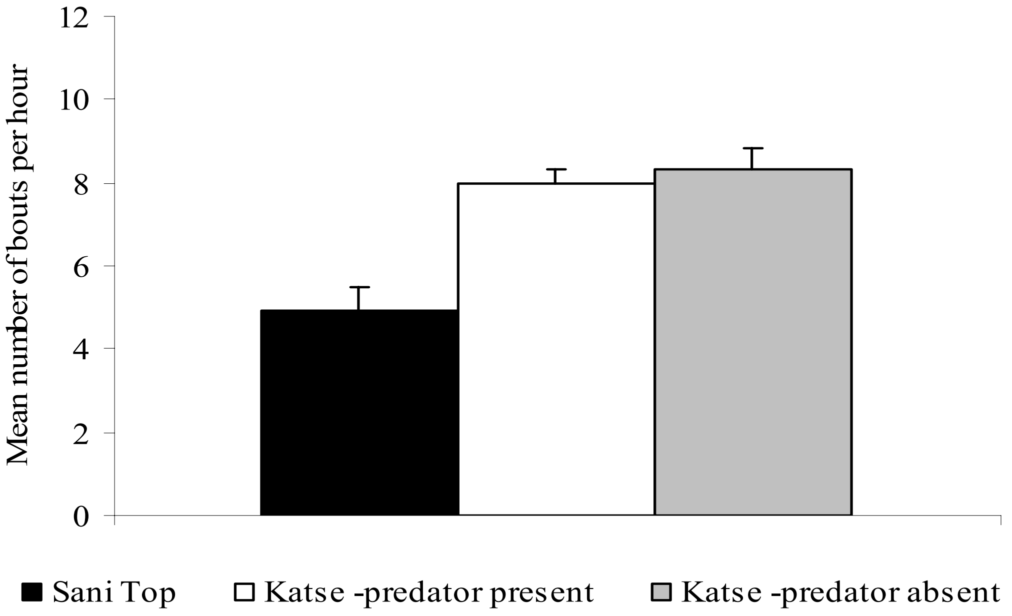


Figure 1. Mean (±SE) number of foraging bouts spent per hour for *O. s. robertsi* at Sani Top and at Katse Dam in the presence and absence of predators in summer and winter.

A GLM analysis for the foraging bouts spent *in situ* (Figure 2) revealed no gender differences ($F_{1,113} = 0.0001$, $p=0.99$) but significant differences in location/predation risk ($F_{2,113} = 11.27$, $p<0.001$), with ice rats at Sani Top remaining *in situ* more frequently than those at Katse Dam (predator: $p=0.0001$; no predator: 0.04). Interestingly, ice rats at Katse Dam were more likely to stay *in situ* when predators were absent than when predators were present. Irrespective of location/predation risk, ice rats were twice as likely to remain at a foraging site in summer than in winter ($F_{1,113} = 37.04$, $p<0.001$). The statistical interaction between location/predation risk and season also

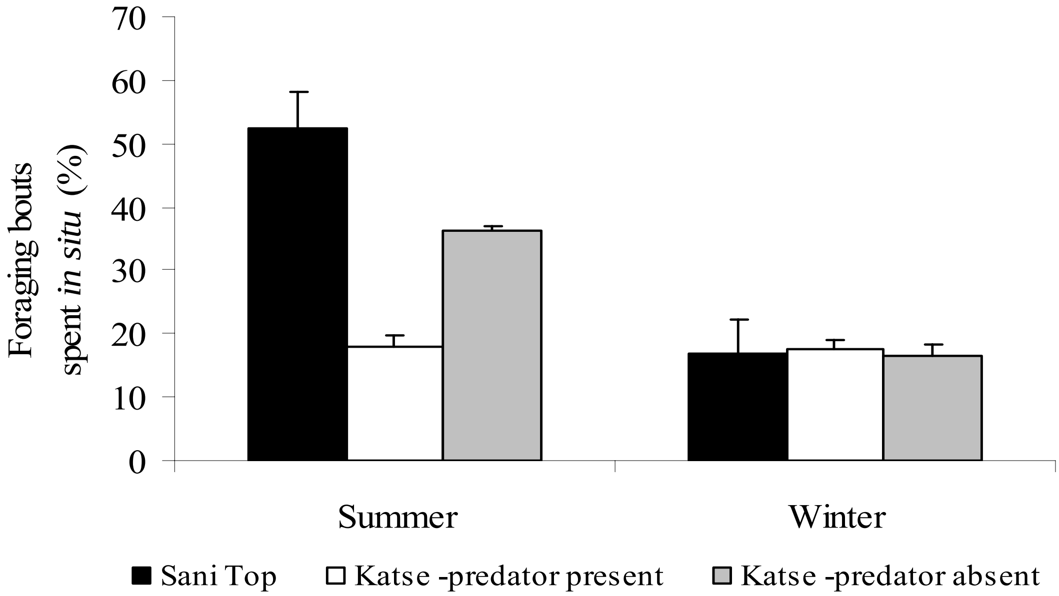
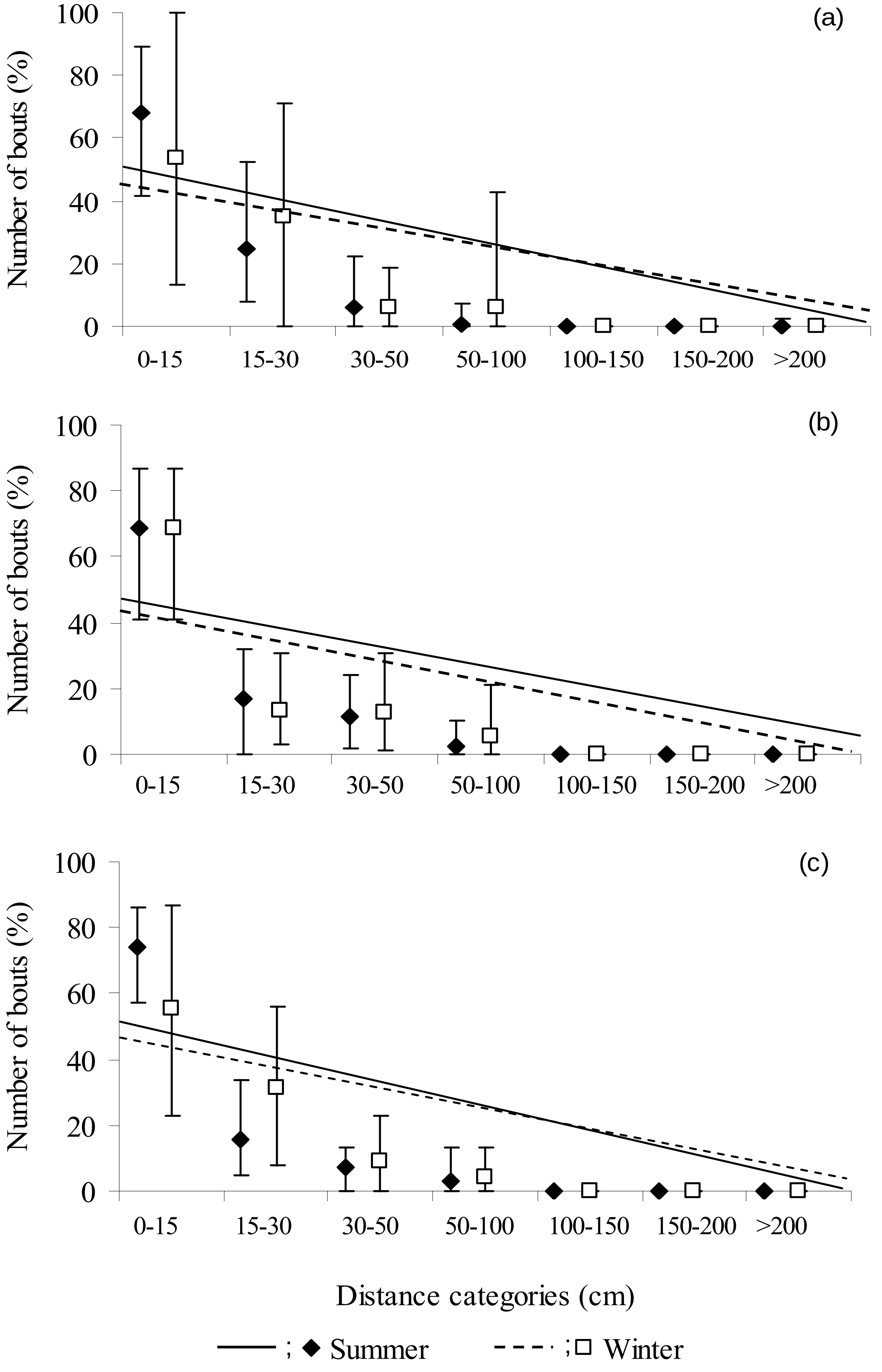


Figure 2. Mean (±SE) percentage of foraging bouts spent *in situ* at various distances from a burrow entrance (central place) by *O. s. robertsi* in summer and winter at Sani Top and at Katse Dam in the presence and absence of predators.

influenced the frequency of foraging bouts spent *in situ* ($F_{2,113}$ = 10.92, $p<0.001$), being greatest at Sani Top in summer, followed by Katse Dam/predators absent in summer, while the remainder of the season-location/predation risk categories were significantly lower (Figure 2).

In both summer and winter, there were significantly negative relationships between the distance categories travelled and the frequency of travel in the Katse Dam population in the presence of predators (summer: r_{140} = -0.91; $p<0.01$; winter: r_{140}= -0.89; $p<0.01$; Figure 3b = -0.89; $p<0.01$; Figure 3b) and the absence of predators (summer: r_{140} = -0.91; $p<0.01$; winter: r_{140} = -0.92; $p<0.01$; Figure 3c) and at Sani Top (summer: r_{119} = -0.86; $p<0.05$; winter: r_{70} = -0.82; $p<0.005$; Figure 3a). I found no seasonal or gender patterns ($p>0.05$).



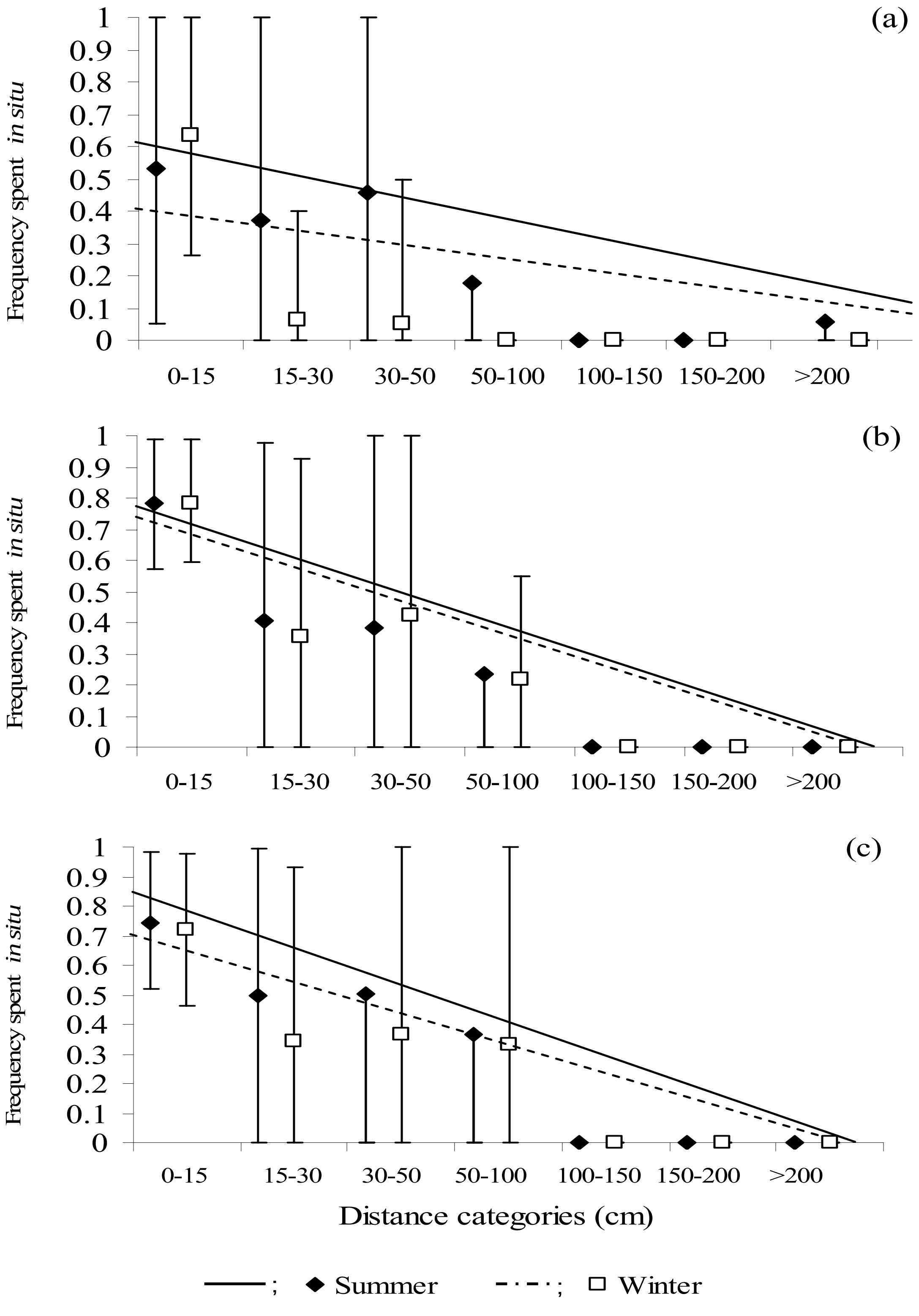
Figures 3. Mean frequency (including minimum and maximum values) of foraging bouts at each distance category in summer and winter at Sani Top (a) and at Katse Dam in the presence (b) and absence (c) of predators. Regression lines: Sani Top - summer: y = 51.44 – 9.29x; winter: y = 47.99 – 8.43x; Katse Dam predators present - summer: y = 52.27 – 8.99x; winter: y = 49.31 – 8.76x; Katse Dam predators absent - summer: y = 48.21 – 8.48x; winter: y = 51.64 – 9.34x.

The relationship between the distance travelled and frequency of foraging bouts spent *in situ* revealed several patterns in relation to location/predation risk and season. In summer, ice rats in Sani Top displayed a significant but weak positive relationship between distance travelled and the frequency of bouts spent *in situ* ($r_{46} = 0.38$, $p=0.01$) (Figure 4a). In winter, this population had a strong negative relationship between these variables ($r_{22} = -0.71$, $p<0.0001$). In the Katse Dam population in the presence of predators (Figure 4b) there was a significant but weak negative association between distances travelled from a burrow and the frequency of remaining *in situ* decreased, both in summer ($r_{59} = -0.38$, $p=0.003$) and in winter ($r_{58} = -0.49$, $p<0.0001$). Similar patterns occurred when predators were absent (Figure 4c), although this relationship was only significant in winter ($r_{59} = -0.27$, $p=0.04$) and not in summer ($r_{64} = -0.16$, $p=0.20$).

In winter, ice rats at Sani Top spent less time *in situ* as the distance from a burrow entrance increased ($r_{19} = -0.74$, $p<0.001$) but no clear pattern was observed in summer ($r_{49} = -0.24$, $p>0.05$; Figure 5a). At Katse Dam, this relationship was weakly negative but significant when predators were present (summer: $r_{80} = -0.40$, $p<0.0005$; winter: $r_{80} = -0.56$, $p<0.0005$; Figure 5b) but strongly negative and significant when predators were absent (summer: $r_{80}=-0.60$, $p<0.0001$; winter: $r_{80} = -0.83$, $p<0.0001$; Figure 5c). In all cases, no gender differences were found.

Discussion

I compared the foraging behaviour of ice rats at Katse Dam, a population that experiences moderate predation pressure, with ice rats exposed to minimal or no predation (i.e. Sani Top; Schwaibold and Pillay, unpublished; Chapter 4). By studying foraging in summer and winter and when predators were absent and present at Katse



Figures 4. Mean frequency (including minimum and maximum values) of foraging bouts spent *in situ* in each distance category by ice rats in summer and winter at Sani Top (a) and at Katse Dam in the presence (b) and absence (c) of predators. Regression lines: Sani Top - summer: y = 0.06 – 0.09x; winter: y = 0.40 – 0.74x; Katse Dam predators present - summer: y = 0.77 – 0.13x; winter: y = 0.75 – 0.12x; Katse Dam predators absent - summer: y = 0.83 – 0.13x; winter: y = 0.71 – 0.11x.

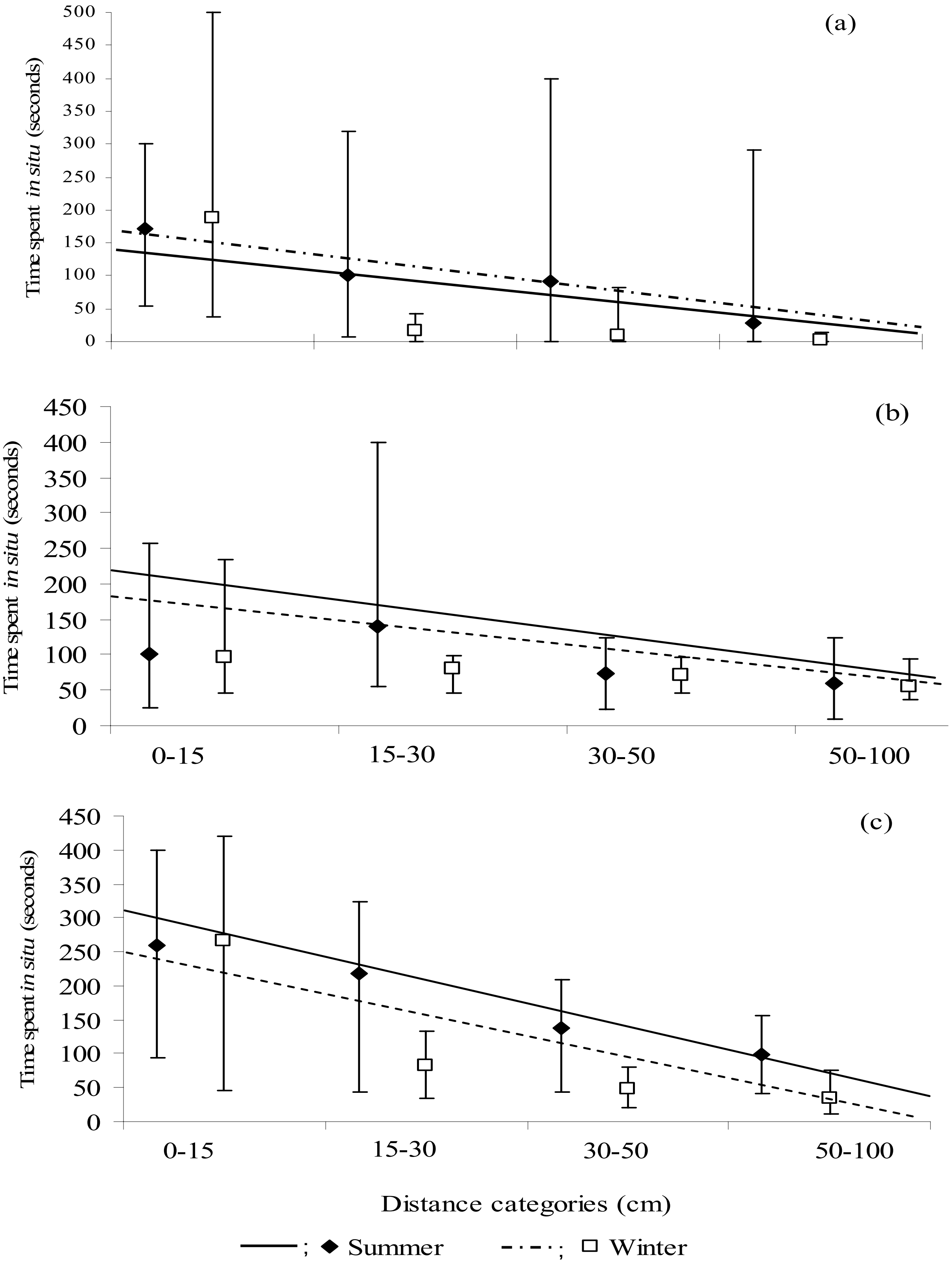


Figure 5. Mean duration (including minimum and maximum values) of time spent *in situ* by ice rats in summer and winter at Sani Top (a) and at Katse Dam in the presence and absence (b) of predators (c). Regression lines: Sani Top- summer: y = 172.49 – 34.46x; winter: y = 138.31 – 39.19x; Katse Dam predators present- summer: y = 124.51 – 15.92x; winter: y = 108.52 – 13.11x; Katse Dam predators absent- summer: y = 317.73 – 55.64x; winter: y = 270.15 – 66.93x.

Dam, I investigated how ice rats respond to two environmental cues: low temperatures and predation risk.

My data revealed several location/predation risk and seasonal patterns. In response to predation threat at Katse Dam, *O. s. robertsi* foraged close to a burrow and for shorter periods, which would reduce exposure to predators and characterises rodents foraging in risky habitats (Brown, 1988; Mohr *et al*., 2003). I recorded similar foraging behaviour patterns when predators were not observed at Katse Dam, suggesting that the perceived threat of predators shapes foraging decisions. Perceived safety strongly influences foraging decisions for animals (Whishaw *et al*., 1992). However, the frequency of bouts spent *in situ* was higher in summer than in winter, indicating that some decision-making rules change in the absence of predation. I observed a similar seasonal pattern at Sani Top (minimal predation risk), which I related to higher thermoregulatory costs in winter (Schwaibold and Pillay, unpublished; Chapter 4). However, in summer ice rats at Sani Top tended to stay *in situ* the further they travelled from a burrow and their foraging time was similar at different distances travelled. While ice rats at Sani Top made fewer foraging trips regardless of season, ice rats at Katse Dam foraged more frequently but for shorter periods. Such a trade-off is presumably a response to predation risk and the need to obtain sufficient energy to meet thermoregulatory needs (Ludwig and Rowe, 1990; Duriez *et al*., 2005). Interestingly, ice rats at Sani Top did not show a similar trade-off in winter (i.e. fewer and shorter foraging bouts).

The number of foraging bouts spent *in situ* in summer was significantly greater than in winter for ice rats at Sani Top (52% in summer and 16% in winter). Similarly, when no predators were observed at Katse Dam, ice rats spent 35% of their foraging bouts *in situ* in summer and only 15% in winter. However in the presence of predators ice rats spent only about 16-18% of their bouts *in situ* in both seasons. Thus ice rats respond to low, potentially lethal temperatures in the same way as they do to predation risk, suggesting that cold temperatures in winter may represent a significant risk. Winter temperatures (mean air temperatures range from 0°C in winter to 6°C in summer; Grab, 1997) are well below the thermoneutral zone (25.3°C to 28°C) of ice rats (Richter *et al*., 1997), so that the benefits of returning to a favourable microclimate, such as a burrow, with food items may outweigh the costs of energy lost through travelling. Moreover, individual ice rats defend individual territories aboveground and colony members compete for limited food in winter (Hinze and Pillay, unpublished), so that returning to a central place may also reduce intraspecific competition and damaging fights (Willan, 1990).

Central place foraging theory maintains that animals travelling relatively short distances to a foraging site should return to a central place with food items collected elsewhere, but should consume food items at the foraging site if the distance travelled is greater, since the energetic cost of travelling back to cover would be high (Orians and Pearson, 1979; Lima *et al*., 1985). Ice rats at Sani Top adopted a central place foraging strategy in summer (see also Chapter 4): the tendency to consume food items *in situ* increased as distance travelled from a central place to a foraging site increased, while in winter they returned to cover with forage even when the distance travelled increased. In contrast, in the presence of predators, ice rats displayed the same foraging patterns in summer and winter and always returned to a central place. Lima (1985) suggests that animals concerned predominantly with increasing foraging efficiency (i.e. reducing energy loss) should never carry food back to cover, but if risk avoidance is the main concern, food items should always be carried back to safety. Several studies indicate that, in most cases, animals will trade off between these two conflicting needs (Caraco, 1979; Sih, 1980; Lima, 1985; Lima *et al.*, 1985).

While it appears that ice rats primarily respond to predation risk, most biotic and abiotic variables are not constant and vary in time and space. Therefore decision-making during foraging, like any other behaviour, is motivated by several non-mutually exclusive internal and external factors. Internal factors include several physiological mechanisms such as levels of hunger (Milinski and Heller, 1978; Croy and Hughes, 1991; Gentle and Gosler, 2001), previous activity and cumulative thermal budgets (Bozinovic and Vásquez, 1999). Two examples of external factors include (i) patch quality, which would promote differential exploitation of patches (Stephens and Krebs, 1986; Valone and Brown, 1989), assuming that foraging rate is a function of resource density (Brown, 1988; Arcis and Desor, 2003); and (ii) food handling time, which would result in different strategies for staying *in situ* or returning to a central place, so that if handling time is very short, one could predict that animals would consume food *in situ*, even in risky patches (Lima *et al.*, 1985; Newman, 1991). When faced with physiological stress, it is predicted that the optimal foraging strategy of a food-deprived animal would be to maximise instantaneous harvest rate and reduce feeding time (Bozinovic and Vásquez, 1999), thereby minimising exposure to extreme temperatures. Although I did not quantify the factors motivating foraging behaviour in ice rats, as a herbivorous rodent they are restricted to a low-calorific high fibre diet (Van Soest, 1982) and this decreased food quality means that they need to forage for most of the day as they need to consume more food to gain sufficient energy for survival (Green and Millar, 1987) Also, ice rats are faced with increased energy demands in their cold environment (Green and Millar, 1987), further reinforcing the need to maximise foraging efficiency. Harvest time in the absence of predation is relatively short, with ice rats collecting up to 12 mouthfuls per foraging session (U. Schwaibold, pers. obs.). Handling time was variable but never exceeded one minute. No data are available for the harvest rate for ice rats at risk of predation and as it was difficult to define patch entities within wetland vegetation, patch use time could not be established for the Sani Top and the Katse Dam populations. These factors should be considered in future studies to establish a more definite measure of foraging efficiency in ice rats.

Predation pressure in any environment also varies in space and time (Kotler *et al.*, 1994), however few studies consider temporal variation in predation risk and its effects on the foraging behaviour of prey aninmals. Vásquez (1994) found that the nocturnal leaf-eared mouse *Phyllotis darwini* adjusts its foraging pattern according to a perceived risk of predation related to an environmental cue (levels of illumination). Sundell *et al.* (2004) reported that the foraging behaviour of bank voles *Clethrionomys glareolus* (housed in 0.25 ha outdoor enclosures) did not change in response to temporal variation in predation risk, but foraging effort was significantly lower in high risk areas compared to low risk areas. In contrast, ice rats did not show spatial variation in predator response, but rather temporal/seasonal variation (i.e. staying *in situ* in summer in the absence of predators). One reason could be differences in habitat structure between the species, with the bank voles benefiting from cover provided by bush and tall grass vegetation, and ice rats always occurring in open habitat and therefore being more likely to detect predators.

In laboratory experiments, Sih (1980) and Nonacs and Dill (ants; 1990) reported that, if energy demands and predation risk are experimentally manipulated, individuals will trade off one variable against the other, thereby neither maximising energy gain nor minimising predation risk. In contrast, in this study, which examined the influence of more than one environmental cue on foraging behaviour in free-living animals, foraging behaviour was influenced by predation risk and ambient temperatures (i.e. mainly low temperatures in winter) in a hierarchical fashion. In the presence of predators, the foraging behaviour of ice rats was similar in summer and winter, indicating that predation risk is a primary determinant of foraging decisions. The influence of predators on foraging behaviour is a universal phenomenon (Lima, 1985; Lima *et al.*, 1985; Milinski and Heller, 1978; Brown, 1988; Lima and Dill, 1990; Kotler *et al.*, 1994; Mohr *et al.*, 2003; Powell and Banks, 2004; Sundell *et al.*, 2004). In the absence of predators, *O. s. robertsi* at Katse Dam still responded to a potential threat, but there were some differences in behaviour in summer. Moreover, foraging in winter at Sani Top resembled foraging under predation risk, and it is clear that thermoregulatory homeostasis also influences foraging behaviour in ice rats (see also Bozinovic and Vásquez, 1999). Facultative foraging responses are adaptive in habitats where animals experience multiple environmental cues.

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CHAPTER SIX:

Microhabitat selection by the ice rat *Otomys sloggetti robertsi* in the Sani Valley, Lesotho

Abstract

We studied the relationship between several environmental factors and the distribution of the ice rat *Otomys sloggetti robertsi* in the Sani Valley, Lesotho. Ice rats are herbivorous burrow-dwelling rodents, endemic to the southern African Drakensberg and Maluti mountains at altitudes above 2000m. Several parameters including aspect, soil compactness, soil types and moisture content, percentage vegetation cover and percentage cover of various plant types were measured along three 500-1000m transect lines starting at the top of a hill and ending in a wetland. The correlation between the parameters measured and the presence of occupied ice rat burrows, revealed that the presence of food plants (i.e. wetland vegetation and other herbaceous plants) were the main determinants of the presence of ice rats. Unexpectedly, soil characteristics and vegetation cover were of less importance. Vegetation cover as well as plant community structure differed significantly between areas occupied and unoccupied by ice rats in both summer and winter. The data indicate that habitat selection by the ice rat is primarily determined by proximity to food plants, thereby reducing the distances travelled to forage and thus decreasing the time exposed to low temperatures.

Key words: *Otomys sloggetti robertsi*, alpine environment, habitat selection, vegetation

Introduction

The ice rat *Otomys sloggetti robertsi* (Muridae, subfamily Otomyinae) is endemic to the alpine and subalpine regions of the Drakensberg and Maluti mountains in southern Africa, and is restricted to altitudes above 2000 m (Killick, 1978). Despite its occurrence in such harsh environments, it does not hibernate (Willan, 1990) and shows little physiological adaptations to cold conditions (Richter *et al*., 1997). Instead, ice rats have morphological (e.g. small ears and tail; Richter, 1997) and behavioural adaptations (e.g. sun-basking, timing aboveground activity with favourable conditions; Willan, 1990; Hinze and Pillay, unpublished). They are diurnal and live in colonies of up to 16 individuals which construct complex underground burrow systems that provide opportunities for social huddling (Hinze *et al*., submitted), even though aboveground social interactions are generally characterised by high levels of aggression among colony members, especially in winter (Hinze and Pillay, unpublished). An important consideration is that the growing season in the ice rat's habitat is restricted to six to seven months in a year, interrupted by very cold winters, often characterised by heavy snowfall (Killick, 1978), which limits the availability of high quality food (Willan, 1990).

Like their otomyine relatives, which occur in the driest (e.g. whistling rats *Parotomys* spp.) and wettest (e.g. vlei rats *Otomys* spp.) parts of southern Africa (Skinner and Smithers, 1990), ice rats are specialist herbivores, feeding more or less exclusively on plant material including herbaceous stems, leaves, flowers and grasses (Schwaibold and Pillay, unpublished data). I reported in an earlier study that ice rats have a longer small intestine compared to its closest mesophyllic and xerophyllic relatives, which is likely to facilitate an increased energy uptake from a high fibre herbivorous diet to meet greater metabolic requirements in cold environments (Schwaibold and Pillay, 2003).

The ice rat has been poorly studied in the past, possibly because of the remote areas it occupies. However, information is available for microhabitat selection in some of its relatives occurring at lower altitudes. Like *O. s. robertsi*, *Parotomys brantsii* and *P. littledale,* which are endemic to the arid western parts of southern Africa, also construct complex underground burrows (Jackson, 2000). Due to the complexity of these burrow systems, the distribution of *P. brantsii* and *P. littledale* is strongly influenced by suitable soil to construct burrows (du Plessis and Kerley, 1991; Jackson, 2000). While *P. brantsii* constructs burrows in both closed areas and areas with limited plant cover, *P. littledale* is restricted to areas with cover (Jackson, 2000). Similarly the bush Karoo rat *O. unisulcatus,* another arid-living relative, is restricted to areas with good plant cover (du Plessis and Kerley, 1991). This species constructs characteristic 'lodges' with collected sticks under or in which it nests, and habitat selection seems to be driven by the nature of the woody vegetation, which provide opportunities for constructing these lodges (Vermeulen and Nel, 1988; Brown and Willan, 1991) and for food (Brown and Willan, 1991).

Comparative information is available for only two mesic occurring otomyines in southern Africa. The vlei rats *O. irroratus* and *O. angoniensis* inhabit the more mesic eastern parts of southern Africa (Skinner and Smithers, 1990), with the former inhabiting areas along wetlands or vleis, and the latter being restricted to the drier areas close to water bodies or wetlands (Skinner and Smithers, 1990), particularly when these two species occur syntopically. Both species nest under overhanging grass or rocks, although they will use abandoned burrows of other animals (Davis, 1972; Packer, 1980; Phillips *et* *al*., 1997). Therefore, the habitat requirements of both species are strongly associated with cover provided by plants (Willan, 1982; Pillay, 1993; Phillips *et al*., 1997).

Our study was designed within a framework of a broader behavioural ecological investigation to ascertain the microhabitat requirements and use by *O. s. robertsi*. In a recent review of microhabitat use by small mammals, Jorgensen (2004) argued that the concept of microhabitat is clouded by imprecise definition and biased by modest sampling effort, mainly because of the use of small spatial scales and because the responses of small mammals to similar and different microhabitats in adjoining vegetation are not considered. To address these concerns, I define microhabitat as being composed of environmental variables that affect individuals (after Morris, 1987) within their home range (after Johnson, 1980; Morris, 1987). In addition, I studied the distribution of ice rat colonies at two spatial scales. Firstly, I sampled along three transect lines with varying aspect, vegetation type and cover, and soil characteristics, to establish the relationships between these parameters and colony location. Secondly, I compared vegetation types and cover in areas occupied by ice rats and in adjoining unoccupied areas; measurements were made in summer and winter to investigate seasonal changes. I asked two broad questions. 1) Is the ice rat microhabitat distribution limited by soil qualities appropriate for burrowing? In particular, do ice rats prefer areas with softer, drier soils? 2) Does plant type influence their microdistribution? How do the distribution of wetland and herbaceous vegetation (food) and woody vegetation (cover) influence the distribution of ice rats?

For central place foragers like the ice rat (Schwaibold and Pillay, unpublished; Chapter 4), microhabitat selection is coupled with the optimal use of resources (Rosenberg and McKelvey, 1999). The distribution of these resources within a selected microhabitat will affect the size of the animal's home range (Rosenberg and McKelvey, 1999). It is not clear though what drives the choice of habitat for a central place forager. Choice can be based on the proximity of resources, but also on the habitat requirements of that central place, such as a nest or burrow (Rosenberg and McKelvey, 1999).

Study area

The study was undertaken in one of valleys of the Sani River (29° 37' S; 29°14' E), about 5 km west of Sani Top in the south- eastern Maluti Mountains, Lesotho at an altitude of about 2900m. The weather conditions in the Lesotho highlands area are harsh and unpredictable, with mean air temperatures ranging from 6° C in summer to 0° C in winter (Grab, 1997). Rainfall is high (mean annual ~1200 mm), and snow can be expected at any time of the year (Willan, 1990). The high plateaus of Lesotho are prone to strong winds blowing towards the escarpment during most of the day; the early morning hours are usually calmest. Shrubs and herbs (annuals and biennials, woody cushion plants and succulents, aquatics and alien plants) are found most commonly in the Sani Valley, and trees were absent in my study area; vegetation rarely exceeded 0.5m.

After an extensive search of Sani Top and the surrounding areas for the presence of ice rats (ice rats are easily observed in nature because of the short vegetation) and the presence of their distinctive burrow entrances (Hinze *et al.*, submitted), I selected an area of 6 ha for my study, which comprised an area located along the fringes of one of the many wetlands in this valley.

Materials and methods

The study took place between May 2000 and January 2002 inclusive. Fieldwork totalled 14 days. Reference collections of all plants species collected on site have been prepared as voucher specimens and are housed in the CE Moss Herbarium of the University of the Witwatersrand.

Transect sampling

To ascertain the microhabitat selection of *O. s. robertsi* in the study site, several parameters were measured along three different transect lines of between 500 and 1000 m long, starting from the edge of the wetland to the top of the hills surrounding the wetland (Figure 1). At every 50 m interval, I noted the presence or absence of active burrows (i.e. burrows that were inhabited by ice rats) and measured the slope (aspect) using a dumpy level and soil compactness using a penetrometer. In addition, soil samples (approximately 100-150 g) were collected at a 20 cm depth, weighed and taken back to the University of the Witwatersrand in sealed airtight plastic bags to calculate soil moisture content. Soil types (or classes) were established by determining the proportions of silt, clay and sand in the soil samples through a particle size distribution (Hillel, 1982). The particle size distribution data were used to determine soil texture using a texture triangle (Hillel, 1982). At each 50m interval, I also estimated the overall percentage vegetation cover from 10 1m^2 quadrates, as well as the mean percentage cover of the major vegetation type (i.e. *Helichrysum* bushes, grass, herbaceous and wetland vegetation).

Plant community structure

I compared the vegetation in 10 occupied (identified by the presence of burrows that were being used by ice rats) and 10 unoccupied areas using a paired designed. I selected occupied areas of at least 5m^2 in size and sampled the vegetation using a semi-random sampling method: a 5m x 5m string frame subdivided into 0.5 x 0.5 m blocks was laid

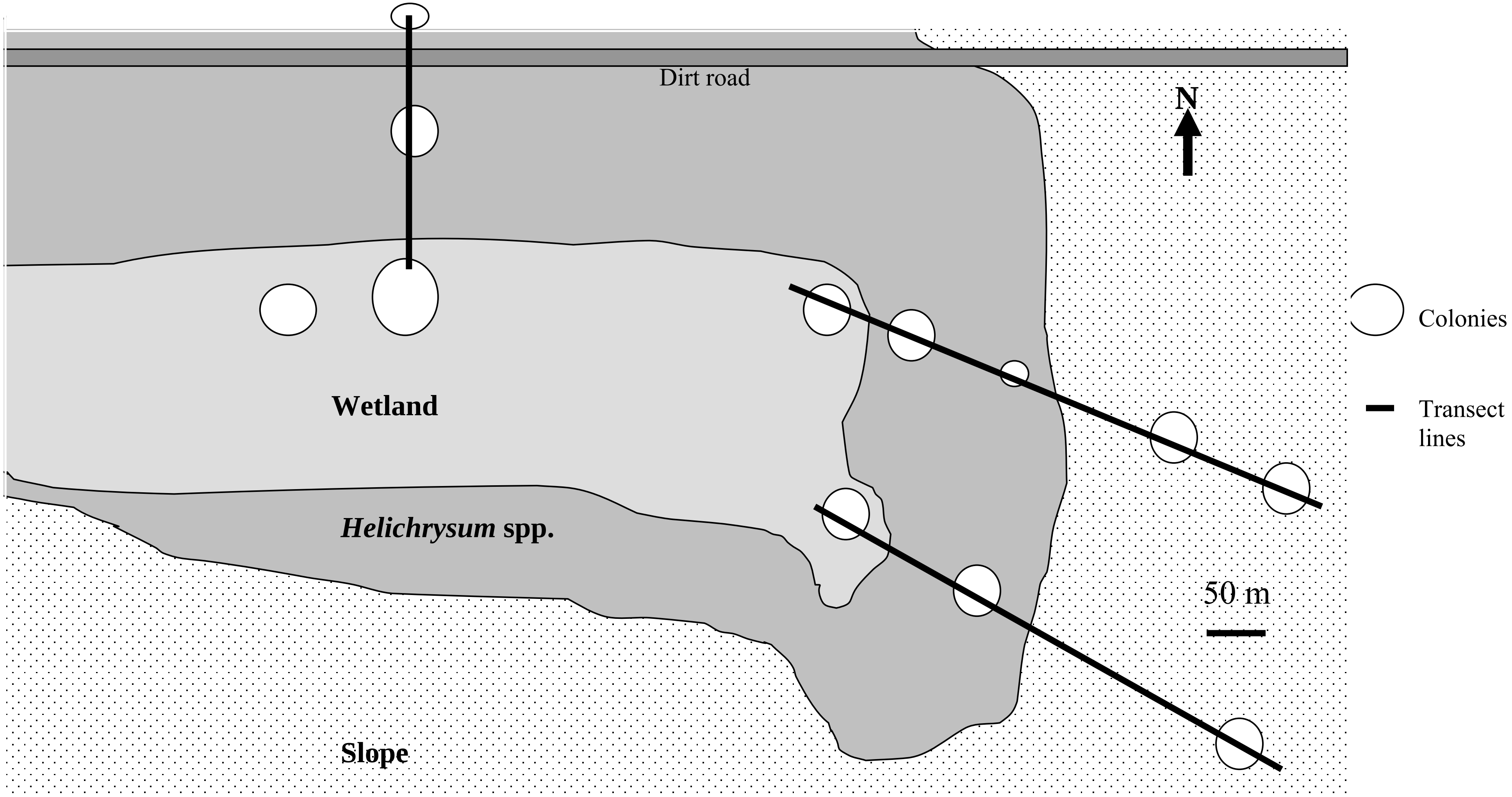

Figure 1. Map of the study site near Sani Top, Lesotho, indicating the position of the colonies selected for study as well as the transect lines. Since the boundaries of the wetland and *Helichrysum* sections were seasonally dynamic, boundary lines are estimated for summer.

over the sampling area. In 10 random 0.5m x 0.5m blocks (selected using a random numbers table), I calculated the plant species composition and frequency (proportion of blocks within which a species occurred), mean percentage vegetation cover (proportion of the ground covered by the aerial parts of the plant) as well as mean percentage cover of woody vegetation (predominantly *Helichrysum* spp.), grasses, herbaceous plants and wetland vegetation. Using the same techniques, measurements were also made in unoccupied areas, which were 15 m away from occupied areas; unoccupied areas were selected if they contained the same broad vegetation type (e.g. wetland plants, bushes) to avoid biasing the sampling.

Diet

The general diet of the ice rat was determined during 150 hours of direct observations using 10x50 binoculars. I recorded the foraging behaviour of ice rats in different patches, and determined the vegetation types present and, where possible, food plants were identified to species level.

Data analysis

Regression analyses were used to assess the relationships between the presence of active burrows and each of the environmental factors measured along the transects. A general discriminant analysis was then performed to establish the relationship between combinations of environmental parameters and the presence of ice rats.

For the analysis of plant community structure, mean percentage cover was calculated for each occupied and unoccupied patch, and a Wilcoxon paired rank test (abbreviated H) was used to compare the vegetation cover between occupied and unoccupied areas in all four sample months (two months per season). Bonferroni adjustments were used to establish specific differences. Seasonal differences in plant cover were established by calculating the difference between the percentage cover of occupied and unoccupied areas and comparing the relative difference using a Mann-Whitney-U test (abbreviated Z). The frequency of species occurring in occupied and unoccupied areas was compared for each sample month using a χ^2 contingency table.

Results

Transect sampling

General regression analyses revealed that the presence of occupied ice rat burrows was correlated with only two environmental factors measured. There was a significant relationship with the presence of herbs (wetland plants and herbaceous vegetation; $r_{63} = 0.45$, $p<0.001$) and the absence of *Helichrysum* (taller bushy vegetation; $r_{63}= -0.44$, $p<0.001$). A discriminant analysis revealed that a high percentage cover of herbaceous vegetation (excluding all woody vegetation and grasses) significantly influenced the presence of ice rats ($\lambda_{1,54} = 4.89$, $p=0.03$). The data indicate that slope/aspect was not important ($\lambda_{1,54} = 2.20$, $p=0.89$), which was confirmed by my observations of burrows in both the flattest and steepest areas along the transects. Soil moisture content was also not significant ($\lambda_{1,54} = 0.01$, $p=0.97$), since burrows were found in the wettest and driest areas. Burrows also occurred in both compact and the soft soils ($\lambda_{1,54} = 1.03$, $p=0.32$), in various soil types ($\lambda_{5,54} = 1.39$, $p=0.24$) and with varying overall vegetation cover ($\lambda_{1,54} = 0.86$, $p=0.36$).

Plant community structure

There were no differences in respect of vegetation cover between months of the same season, and the data were pooled by season. Predictably, vegetation cover (Table 1) was

Table 1. Mean (± SE) percentage vegetation cover and dominant species/vegetation types in areas occupied and unoccupied by *O. s. robertsi* in summer and winter.

Season	**Use**	**% Cover**	**Dominant Vegetation**[1]
Winter	occupied	57.96 ± 4.61	grasses wetland plants *Geranium multisectum* *Helichrysum* sp
	unoccupied	86.58 ± 3.27	grasses wetland plants *Haplocarpha nervosa* *Ranunculus multifidus*
Summer	occupied	56.28 ± 1.86	grasses wetland plants *Geranium multisectum*
	unoccupied	83.76 ± 2.73	grasses wetland plants *Geranium multisectum* *Ranunculus multifidus*

[1] Taxonomic name provided if known.

significantly greater in unoccupied areas than in occupied areas, both in summer ($H_{10,10}$ = 3.92, $p<0.0001$) and winter ($H_{10,10}$ =3.88, $p<0.0005$). Relative differences in vegetation cover between occupied and unoccupied areas (i.e. mean cover in occupied areas – mean cover in unoccupied areas) revealed no significant variation between summer (27.49%) and winter (28.62%; $Z_{10,10} = 0.15$, p=0.88).

Woody vegetation was sparse in both occupied and unoccupied patches, while herbaceous vegetation cover ranged from 30-100% in both patch types. Grasses and herbs occurred most frequently in both occupied and unoccupied areas, although there was no consistent difference between occupied and unoccupied areas with regard to the most common plant species present (Figure 2). *Haplocarpha nervosa* was the dominant wetland species, followed by *Ranunculus multifidus* (wetland plants present are listed in Table 2). No significant differences were found in overall plant frequencies between occupied and unoccupied areas in May ($\chi^2_{11}= 6.33$, p>0.05), August ($\chi^2_{8}= 4.60$, p>0.05), October ($\chi^2_{11}= 3.70$, p>0.05) and November ($\chi^2_{11} = 5.48$, p>0.05).

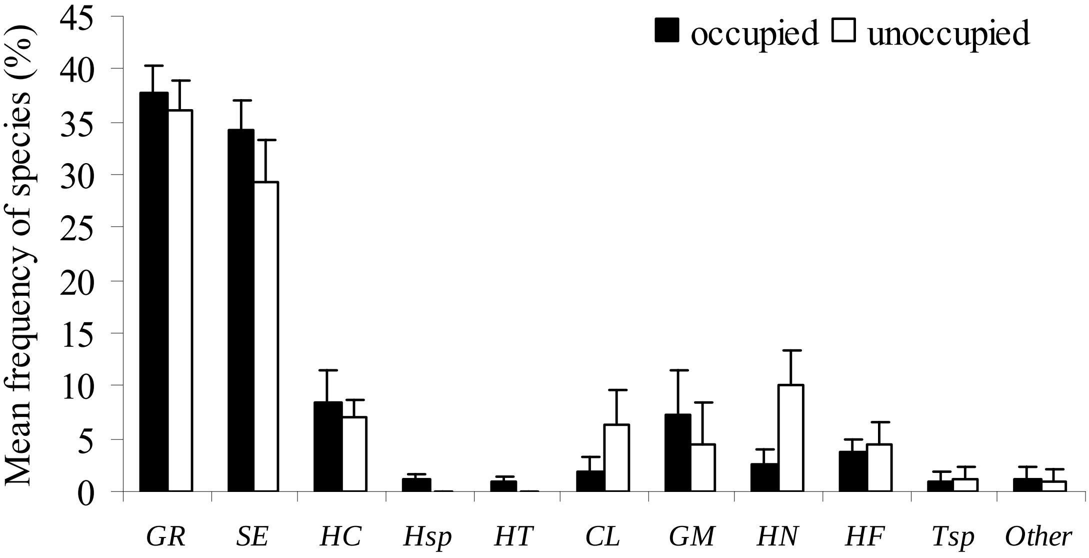

Figure 2. Mean (±SE) percentage frequencies of various plant species in areas occupied and unoccupied by *O. s. robertsi* (GR=*Pentaschistis* sp; SE=Wetland plants; HC = *Helichrysum cymosum*; Hsp=*H.* sp; HT=*H.trilineatum*; CL = *Crassula lanceolata*; GM = *Geranium multisectum*; HN = *Haplocarpa nervosa*; HF = *Helichrysum flanaganii*; Tsp = *Taraxacum sp.*

Table 2. Dominant species of the woody and herbaceous vegetation in areas occupied and unoccupied by *O. s. robertsi* at Sani Top and the plant species consumed by ice rats.

Vegetation Type	**Species**	**Consumed by ice rats**
Grasses	*Pentaschistis oreodoxa*	Yes
Wetland Plants	*Limosella vesiculosa*	Yes
	Trifolium burchellianum	Yes
	Ranunculus multifidus	Yes
	Haplocarpha nervosa	Yes
	Cotula paludosa	Yes
	Saniella verna	Yes
Helichrysum sp.	*H. cymosum*	No
	H. subglomeratum	No
	H. trilineatum	No
	H. flanaganii	No
Other herbaceous vegetation	*Crassula lanceolata*	No
	Geranium multisectum	Yes
	Selago flanaganii	Yes
	Selago galpinii	No
	Eumorphia sericea	No

Diet

Behavioural observations of the foraging patterns of *O. s. robertsi* revealed that its diet consisted predominantly of wetland plants and herbaceous vegetation (Table 2). Both the green and floral parts of *H. nervosa* were consumed and collected by ice rats. Herbaceous and floral parts of *R. multifidus* and *Trifolium burchellianum* were also eaten but to a lesser extent. I did not observe ice rats feeding on *Helichrysum* spp.

Discussion

The microhabitat selection and use by burrowing small mammals is influenced by several environmental parameters, including food availability (Rosenberg and McKelvey, 1999), plant species composition (Brown and Willan, 1991), cover (Falkenberg and Clarke, 1998; Jackson, 2000) and soil characteristics (du Plessis and Kerley, 1991).

The Afro-alpine giant molerat *Tachyoryctes macrocephalus* appears to select suitable habitats according to, among other factors, soil moisture content, as burrows were found mainly along seasonally waterlogged swamps (Sillero-Zubiri *et al.*, 1995). Neither aspect nor soil composition (i.e. soil type, moisture content) were good predictors of the location of *O. s. robertsi* colonies. Ice rats are known to construct burrows in soil substrates differing in water content, such as harder organic and softer mineral soils, and interestingly, burrow systems were more extensive and complex in the harder organic soils than in softer sandy soils (Hinze *et al.*, submitted). Reasons for the these differences in burrowing behaviour are not fully understood but may be related to soil compactness, although both this study as well as the study by Hinze *et al.* (submitted) suggest that soil characteristics do not influence habitat choice. However, I found that previously waterlogged tunnel systems (i.e. burrows that were flooded due to spring rains and melting ice in the wetland) were not re-inhabited and no burrows were found in the wetland (which was not included in the transect; pers. obs.), possibly due to the high risk of flooding in summer and freezing over in winter.

Of the five environmental variables measured, only the presence of herbaceous plant material and the absence of woody *Helichrysum* species influenced the microhabitat distribution of ice rats. The diet of ice rats consists mainly of relatively fresh plant material, such as wetland vegetation and other herbaceous species. Two advantages appear to accrue to *O. s. robertsi* as a result of occupying patches with food plants. 1) Travelling short distances to forage may be related to a need to minimise energy loss through exposure to cold temperatures (Johnson and Cabanac, 1982), particularly since ice rats are physiologically poorly adapted to extreme cold (Richter *et al.*, 1997). As herbaceous food quality decreases in winter (Van Soest, 1982) and more food needs to be ingested to meet increased metabolic requirements (Batzli and Cole, 1979), reducing energy loss through travel is essential. Indeed, ice rats are central place foragers, which very rarely forage more that a metre away from the nearest burrow entrance (Schwaibold and Pillay, unpublished; Chapter 4). 2) Despite its colonial existence, members of an ice rat colony maintain defined territories aboveground apparently to defend food patches, and interactions between colony members are rare but mostly aggressive when they meet (Hinze and Pillay, unpublished). Therefore, feeding within the confines of the home range may reduce intraspecific competition. Similarly, *P. brantsii* is able to reduce competition with its two potential counterparts, *P. littledalei* and *O. unisulcatus*, by foraging almost entirely within the limits of its burrow system, thereby gaining access to otherwise unavailable resources and eliminating the need for extensive plant cover for protection (Jackson, 2000).

In many rodents, predation pressure may drive selection for areas with extensive cover, whereas interspecific competition may result in the use of areas with poor cover (reviewed in Falkenberg and Clarke, 1998), and the rationale for many studies of microhabitat use in small mammals has been to understand microhabitat partitioning between syntopic species (see Jorgenson, 2004). Both of these factors do not appear to influence ice rat distribution. Based on our observations over the past 13 years, predation pressure in the Sani Valley is negligible (as it is in most localities where ice rats occur; Willan, 1990), and the ice rat here does not share its habitat aboveground with other small mammals, although the appearance of distinctive mounds suggests that mole-rats also occurred at my study site.

The absence of woody vegetation in ice rat colonies was unexpected, as *Helichrysum* spp. bushes would provide adequate cover from possible predators (which are discounted here) and, more importantly, would act as a wind break (see Willan, 1990). However, *Helichrysum* spp. is not consumed and its presence may affect the microclimate experienced close to the ground due to shading (Eurola *et al.*, 1984), thereby influencing the growth of food plants consumed by ice rats. In another study, I showed that ice rats spend a large proportion (28-38%) of their aboveground activity engaged in sun-basking (Schwaibold and Pillay, unpublished; Chapter 3). Basking is an important behavioural thermoregulatory activity, shared by many other alpine rodents (e.g. marmots *Marmota* spp.; Barash, 1989), and which may compensate for the reduced energy intake from lower quality food in winter by accelerating the warming-up process to a level that allows for uninterrupted activity with very little thermoregulatory cost (Sale, 1970; Geiser, *et al.*, 2002). Marmots also facilitate energy gain during cold periods by utilising radiant energy through basking as this may compensate for the reduced energy intake from lower quality food in winter and thus allow for metabolic requirements to be met. I suggest that excess woody vegetation in an ice rat colony, which can reach up to 50 cm in height, may result in increased shading of the colonies which in turn may negatively influence basking opportunities.

Vegetation cover in areas occupied by ice rats was significantly less than in unoccupied areas in both summer and winter. One reason may be that they select areas with less cover due to the need for sun-basking. This is unlikely, however, and a more plausible explanation may be that the foraging activity of ice rats reduces cover. This highlights the fact that cover is not an important determinant of ice rat microdistribution.

The arid-occurring otomyine *Parotomys brantsii* requires deep sandy soils to construct complex burrow systems (du Plessis and Kerley, 1991), which determine the habitats it occupies within its distribution range. In contrast, ice rats are not limited by soil type, and instead locate their colonies in food patches. Although I did not measure the production of edible plant material, the high density of ice rats (up to 100 individuals per ha; Hinze and Pillay, unpublished), suggests that the carrying capacity for ice rats in my site is high. Nonetheless, 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, coupled with prolonged periods of snowfall.

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CHAPTER SEVEN: Discussion

The ice rat *Otomys sloggetti robertsi* is an interesting model to study the effects of low temperatures on the behaviour patterns of small mammals as it is one of only few high altitude small mammals that does not hibernate or display torpor. It shows poor physiological adaptations (Richter *et al.*, 1997) and apparently shows a range of morphological and behavioural adaptations for life in cold alpine habitats (De Graaff, 1981; Willan, 1990; Richter *et al.*, 1997). Little was known about the ice rat before this study, and I studied the behavioural and morphological responses in respect of foraging in *O. s. robertsi* by investigating its gut morphology, aboveground behaviour (mainly foraging behaviour) and habitat choice.

Gut structure

The aim of the study was to establish whether the gut of ice rats is modified for low food quality and high energy demands associated with the cold Lesotho environment. The morphology of the digestive system of ice rats is well adapted for a high fibre, herbivorous diet, as is the case with all other otomyines (Perrin and Curtis, 1980). Compared to both its mesic and xeric-occurring relatives, there were directional modifications of the gut including an increase in length of the large intestine and colon, and an increase in stomach volume. Both hibernating and non-hibernating small mammals in cold environments display an increase in size of these organs (Silby, 1981; Hammond and Wunder, 1991), suggesting that such anatomical modifications may be adaptations to coping with cold conditions as they facilitate increased energy uptake through improved breakdown of low quality/high fibre plant material and increase the surface area available for absorption of high energy dietary components (Silby, 1981; Schieck and Millar, 1985).

Seasonal gender differences were also found with females increasing dimensions of the stomach, small intestine, caecum, and large intestine in summer. This sexual dimorphism in gut structure may be related to increased energy requirements of females during pregnancy and lactation (Weiner, 1987; Silby *et al.*, 1990).

Seasonal variation in aboveground behaviour patterns

An animal's fitness depends on its ability to effectively allocate its time and energy to competing behavioural demands (Schoener, 1971; Schultz *et al.*, 1999). I investigated the variation in aboveground behaviour of *O. s. robertsi* in response to seasonal changes in temperature. Ice rats face the conflicting demands of energy gain and energy conservation, and my study suggests that foraging behaviour is traded off against thermoregulation in winter, while ice rats escape high ambient temperatures and solar radiation levels during the middle of the day in summer by disappearing belowground.

Due to the increased metabolic rate of small mammals (Schultz *et al.*, 1999) it is predictable that ice rats should spend most of their time on energy acquisition and energy conservation. Furthermore, the food available in the habitats of ice rats is of low quality due to a high fibre content (Killick, 1978; Green and Millar, 1987), resulting in an increase in foraging activity to meet metabolic requirements, particularly in winter when ambient temperatures were around freezing point. In winter, ice rats also spent much time basking, thus gaining energy through radiant heat. Similar behaviour patterns are found in other high-altitude small mammals such as marmots (*Marmota* spp.), which show seasonal changes in activity with foraging increasing in preparation for hibernation

(Barash, 1989). Marmots spend much of their day basking to facilitate energy gain through radiant heat (Barash, 1989), but they will avoid the afternoon heat by escaping underground (Türk and Arnold, 1988).

Foraging strategies – predation versus thermoregulation

Foraging behaviour is strongly influenced by a variety of environmental factors (e.g. weather conditions; Sergio, 2003; food availability; Belovsky and Slade, 1986). I investigated the effects of seasonal differences on the foraging decisions of *O.s. robertsi.* Ice rats are central place foragers and their foraging behaviour at my primary field site (i.e. Sani Top) in the absence of predators appears to be strongly influenced by seasonal changes in environmental conditions: in summer, ice rats remained *in situ* as the distance from a burrow increased, conforming to predictions made by central place foraging theory. In contrast, in winter, foraging patterns were determined by low temperatures, with ice rats returning to the protection of their burrows with forage regardless of distance travelled.

Since predation risk is often regarded as the main factor dictating foraging behaviour in small mammals (Lima, 1985; Brown, 1988; Lima and Dill, 1990; Kotler *et al.*, 1994; Mohr *et al.*, 2003; Powell and Banks, 2004; Sundell *et al.*, 2004), I also studied the foraging behaviour of ice rats near Katse Dam; this population experiences moderate levels of predation, particularly from birds of prey. I tested how ice rats respond to two environmental cues: low temperatures and predation risk. In addition, I established foraging behaviour in the presence and absence of predators. Ice rats responded to the presence of predators by always foraging close to a burrow and for shorter periods in both summer and winter, in contrast to ‘optimal’ foraging patterns in the absence of any predation threat in summer, when ice rats were more likely to forage *in situ* as distances from a burrow increased, indicating that predation is the main determinant of foraging behaviour. The foraging behaviour of ice rats in winter without the risk of predation matched the behaviour of ice rats facing predation pressure, indicating that low temperatures pose as significant a threat as predation.

Habitat choice

I set out to identify the microhabitat requirements of *O. s. sloggetti.* Of all the environmental factors recorded, the presence of herbaceous vegetation and the absence of woody vegetation appeared to constitute suitable microhabitats for ice rats, suggesting that habitat choice may be related to the presence of food plants and reduction of shade.

Habitat selection is influenced by multiple variables including the intrinsic features of an animal as well as biotic and abiotic environmental factors (Vásquez, 1996), of which predation risk is thought to be one of the most important factors influencing space use (Kotler *et al.*, 1994). As food patches within any given habitat will vary with regards to the effort required to select suitable forage, habitat selection is often dependent on physiological trade-offs and constraints (Bozinovic and Vásquez, 1999) and the choice of habitat translates as fitness consequences (Jorgensen, 2004). For central place foragers, microhabitat selection is usually associated with the optimal use of resources as well as the habitat requirements of their central place, such as a nest or burrow (Rosenberg and McKelvey, 1999). The proximity to forage allows them to reduce exposure to risks such as predation (Lima, 1985) and temperature.

Biology of 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 (De Graaff, 1981; Skinner and 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.

Ice rats are apparently closely related to arid-occurring southern African otomyines species (see introduction). One of these, Brants' whistling rat *Parotomys brantsii*, prefers areas with deep sandy soils within relatively open areas (Jackson, 2000) to construct complex underground burrow systems (du Plessis and Kerley, 1991) which provide a suitable microclimate, buffering temperature extremes above ground (Jackson, 2000). In contrast, not much is known about the habitat requirements of Littledale's whistling rat *P. littledalei* which also constructs complex underground burrow systems with several nest chambers, although it is thought that the association of these warrens with areas providing good cover could reduce risk of predation (Jackson, 2000). The bush Karoo rat *O. unisulcatus* prefers areas with suitable woody vegetation to construct its stick lodges and for food (Brown and Willan, 1991). Although little is known about the behaviour of *P. littledalei* or the thermal characteristics of lodges of *O. unisulcatus*, it is likely that their nesting habits are adapted for life in harsh arid environments (Brown and Willan, 1991; Jackson, 2000). All three species forage in close proximity to the nest site, apparently to reduce predation risk (Brown and Willan, 1991; Coetzee and Jackson, 1999; Jackson, 2001).

Unlike the arid-occurring otomyines, the mesic-occurring vlei rats *O. irroratus* and *O. angoniensis* do not excavate complex underground warrens. Instead they nest under overhanging grass or rocks and will occasionally use abandoned burrows of other animals (Davis, 1972; Packer, 1980; Phillips *et al.*, 1997), and the habitat requirements of both species are strongly associated with adequate plant cover (Willan, 1982; Pillay, 1993; Phillips, *et al.*, 1997).

Details of foraging behaviour are available only for *P. brantsii*, possibly because, like *O. s. robertsi*, it is easily observed in nature. Jackson (2000) reported that *P. brantsii* is a central place forager. Individuals travel up to 200 cm from their burrows to forage, generally carrying larger food items back to be consumed under cover or storing them underground, and foraging bouts increase significantly in the afternoons in preparation for the night (Jackson, 2001). In turn, *P. littledalei* is hardly ever found to leave the protective cover of bushes and shrubs to forage (Coetzee and Jackson, 1999).

Although the foraging patterns of the other otomyine species has not been studied in great detail, some general information is available. *Otomys unisulcatus* forages on the ground or aboreally and restricts its foraging activity to between 5-10 m of cover, sometimes retreating to cover with collected food items, possibly as an anti-predator tactic (Brown and Willan, 1991), suggesting that it, too, is a central place forager to some degree.

Coping with cold conditions

Optimal foraging theory maintains that an animal performs a particular activity depending on associated costs and benefits (Schoener, 1971). Models generated from optimal foraging theory emphasise foraging strategies, since these form the major components of energy acquisition (Stephens and Krebs, 1986). When foraging, an animal makes particular decisions that are thought to be optimal in terms of energy intake rate (Stephens and Krebs, 1986), although this depends on the ecological context in which foraging takes place (Bozinovic and Vásquez, 1999). Theoretically, maximising energy gain through foraging enhances fitness (Schoener, 1971).

While the role of predation in influencing foraging is well documented (Lima, 1985; Lima *et al.*, 1985; Milinski and Heller, 1987; Brown, 1988; Lima and Dill, 1990;

Kotler *et al.*, 1994; Powell and Banks, 2004; Sundell *et al.*, 2004), thermal conditions also influence foraging decision making (Bozinovic and Vásquez, 1999) because ambient temperatures influence thermoregulatory homeostasis in animals. Since physiological states influence behavioural motivation (Dugatkin, 2004), it is predicted that in cold environments (i.e. under physiological stress) animals should follow energy-maximising foraging patterns. Indeed, animals exposed to cold conditions adjust their behaviour patterns to facilitate increased foraging, thus increasing overall energy intake (see Johnson and Cabanac, 1982; Perrigo and Bronson, 1985). Lima (1985) suggests that returning to cover for food consumption could provide thermal benefits compared to foraging in the open, and the conflict between the benefit of reduced exposure to cold and the cost of travelling back to cover may resemble foraging responses under predation risk. Thus, depending on the extent of thermal stress, it would be expected that food would be consumed under cover if the benefits of foraging in a thermally stable microenvironment outweigh the costs of travel, while foraging *in situ* should occur if energy lost through travel outweighs energy saved from foraging under cover.

The climate of the Lesotho highlands is characterised by a low temperature profile and high rainfall; the growing season is short and primary productivity is low (Killick, 1978). Willan (1990) describes the climate within the distributional range as predictably harsh. Ice rats are adversely affected by low temperatures in their habitats and they experience density-dependent mortality in winter because of diminishing food resources (Willan, 1990).

While many small mammals in cold environments hibernate or go into torpor to conserve energy during cold periods (Müller, 1986; Barash, 1989; Geiser and Ruf, 1995), non-hibernating small mammals might compensate for the lack of hibernation and torpor by maximising energy gain during this time. The results of my study indicate that *O. s. robertsi* appears to be very efficient in its energy gain by reducing exposure to low temperatures. It travels short distances to forage and, in winter, it returns to a burrow with forage, regardless of distance travelled. Colonies are established in areas with food plants. Apart from providing a thermal buffer against lethal temperatures and high levels of solar radiation aboveground, the complex underground burrow system of ice rats (Hinze *et al*. submitted) would promote foraging in close proximity to food, thereby reducing excess energy expenditure and ultimately resulting in central place foraging. Basking in winter and social huddling belowground (Hinze and Pillay, unpublished) are likely to result energy savings. Moreover, the gut morphology of ice rats appears to be adapted to increase energy uptake from poor quality forage and sexual dimorphism in gut structure in summer may compensate for the lack of other gender differences in behaviour and morphology by providing physiological means for females to extract more energy from their food source...

The similarity in foraging behaviour in winter at Sani Top and in the presence of predators in both seasons at Katse Dam suggests that low temperatures pose a risk for foraging and highlights how foraging decisions are shaped by thermal conditions. *Otomys s. robertsi* shares similar foraging behaviour with its arid-occurring relatives, the *Parotomys* species, suggesting phylogenetic influences, but is possibly more a reflection of similar phenotypic characteristics in the extreme habitats inhabited by these otomyines.

Based on the physiological limitations of *O. s. robertsi*, Richter *et al*. (1997) maintained that the allopatric distribution of *O. s. robertsi* and *O. iroratus* might have been a consequence of interspecific competition for available resources, resulting in ice rats being restricted to higher altitudes. Nonetheless, the data presented here suggest that ice rats have modified their foraging behaviour and gut morphology for life in alpine habitats, both of which are phenotypic characters that often show high levels of plasticity (see Bozinovic *et al.*, 1990; Stirling and Roff, 2000).

Conclusions and further research

My research has significantly increased our understanding of the biology of *O. s. robertsi* by providing new insights into its foraging biology in its natural environment. The variation in predation levels at the two study sites allowed me to study the effects of predation on foraging behaviour under natural conditions and without using surrogate measures of predation (e.g. predator odours; Powell and Banks, 2004; illumination; Kotler, 1984 and Vásquez, 1996). The Sani Top site provided ideal conditions to study the response of ice rats to cold temperatures with little or no influence from predation or interspecific competition; ice rats were the only non-fossorial small mammal at this site.

This study has shown similarities in behaviour of the ice rat compared to its otomyine relatives, but several differences were identified, mostly reflecting the harsh alpine habitats inhabited by ice rat. I set out to provide broad background information on the foraging biology of this taxon, since little data were available regarding its behaviour in its natural environment. Thus, my research focussed mainly on the behavioural strategies employed by the ice rat to maximise energy gain while minimising energy loss. Further quantitative research is needed on the energetic costs and benefits of various behaviours. Due to the seasonal variation in temperature and the associated changes in energy requirements, metabolic rates of free-living ice rats should be examined, for example, by using implanted data loggers (see Taylor *et al.*, 2004). Such devices may be able to also relate internal physiological states to foraging need (i.e. internal motivation). More precise measurements are also needed of external factors which influence foraging decisions such as patch quality and food handling time, which are traditionally used to investigate foraging decision making (Lima and Dill, 1990; Bozinovic and Vásquez, 1999).

It would also be interesting to investigate the histology of the gastrointestinal tract of the ice rat in more detail to determine any physiological adaptation in gut structure (e.g. intestinal nutrient transporters; Karasov and Diamond, 1988). Other anatomical adaptations to cold temperatures could be revealed by investigating seasonal changes in adipose and cardiovascular tissue (Quay, 1984). Finally, a more detailed investigation of digestive efficiency should be conducted by examining the energy assimilation from their food plants.

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