Habitat use in the ice rat
Otomys slogetti robertsi

Ute Schwaibold* & Neville Pillay
School of Animal, Plant and Environmental Sciences, University of the Witwatersrand,
Private Bag 3, WITS, 2050 South Africa
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We documented the habitat selection and use in the ice rat, *Otomys slogetti robertsi*, in Lesotho. Ice rats are herbivorous, burrow-dwelling rodents, endemic to the southern African Drakensberg and Maluti mountains at altitudes above 2000 m. We predicted that ice rat habitat selection is associated with soil qualities suitable for burrowing, as well as the availability of food plants and cover. We also tested whether space use changed seasonally and differed between the sexes. We studied habitat selection at different spatial scales, and recorded several biotic and abiotic environmental variables. We found that the presence of food plants (*i.e.* wetland sedges and herbaceous plants) were the main determinants of the presence of ice rats. Contrary to expectations, soil characteristics and woody vegetation cover were not key determinants of ice rat colonies, regardless of season. Space use was greater in summer than winter, and females utilized larger areas than males in summer. The close association of ice rats with their food plants is also observed in some of its relatives in other habitats. However, unlike other otomyines, ice rats occupy cold environments, and their close proximity to food and distance from cover may be a response to reduce exposure to low temperatures.

Key words: *Otomys slogetti robertsi*, alpine environment, diet, habitat selection, space use.

INTRODUCTION
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 because, due to the limited size of their home range or dispersal range, they can sample only a small area within an otherwise extensive and possibly diverse habitat (Johnson 1980).

The literature provides many examples of animal species showing 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 include predation pressure, in which case animals tend to select habitats with more vegetation cover, and interspecific competition (Falkenberg & Clarke 1998; Schradin & Pillay 2005), which may result in habitat partitioning at various scales (Jorgensen 2004). In cold environments, factors such as protection from low ambient temperatures may influence habitat selection. Furthermore, vegetation and topography may affect the microclimate experienced by animals and may therefore significantly determine their habitat and microhabitat choice within the limits of their distribution (Barash 1989; Happold 1998).

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. Thus, for the present study, we define habitat as being composed of environmental variables that affect the biology of an individual within their home range (Johnson 1980; Morris 1987).

Our study was designed within a framework of a broader behavioural ecological investigation to ascertain the habitat requirements and use by the ice rat *Otomys slogetti robertsi*. The ice rat is a medium-sized (150–170 mm; 120–140 g; Willan 1990), diurnal, murid rodent, endemic to the alpine and subalpine regions of the Drakensberg and Maluti mountains in southern Africa (Skinner & Smithers 1990) above 2000 m (Killick 1978). It
is the only southern African mammal occurring exclusively at these altitudes. Despite its occurrence in such harsh environments, it does not hibernate (Willan 1990) and shows poor physiological adaptations to cold conditions (Richter et al. 1997). Instead, ice rats have morphological (e.g. small ears and tail; Richter 1997) and behavioural characteristics (e.g. sun-basking, huddling; Willan 1990; Hinze & Pillay 2006) to cope with low temperatures. Ice rats live in colonies of up to 16 individuals, constructing complex underground burrow systems (Hinze et al. 2006). While they show colonial behaviour below ground (e.g. huddling), they exhibit temporal territoriality and high levels of aggression above ground (Hinze 2005).

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 & Smithers 1990), ice rats are specialist herbivores, feeding almost exclusively on plant material, including herbaceous stems, leaves, flowers and grasses. The growing season in ice rat habitats is restricted to 6–7 months a year, interrupted by very cold winters often with heavy snowfall (Killick 1978), which limits high-quality food availability (Willan 1990). Perhaps in response to poor food quality, ice rats have a longer small intestine than their closest mesophytic and xerophytic relatives, which may facilitate increased energy uptake from a high-fibre herbivorous diet to meet the greater metabolic requirements in cold environments (Schwaibold & Pillay 2003). Moreover, females increase their gut capacity in summer, which corresponds to greater energy need during the breeding season; male gut dimensions remain more or less constant (Schwaibold & Pillay 2003).

Despite their abundance in suitable habitats (Willan 1990), not much is known about the ecology and behaviour of ice rats, possibly because of their remote locations. Here, we investigated the habitat use and requirements of O. s. robertsi. We studied the distribution of ice rat colonies at two spatial scales. Firstly, we compared vegetation types and cover in areas occupied by ice rats and in adjoining unoccupied areas. Secondly, we sampled along three transect lines to establish the association between ice rat presence/absence and plant structure and selected abiotic factors (e.g. soil characteristics). Finally, we documented the space use of adult females and males within colonies seasonally, and established the general dietary preferences of ice rats by recording vegetation types (identified to species where possible) consumed during behavioural observations in summer when plant species/vegetation types were easily identifiable.

We made four predictions. 1) Ice rat habitat use is associated with features (e.g. soil qualities, aspect) appropriate for burrowing. Particularly, ice rats prefer areas with softer, drier soils on flat ground. 2) The distribution of wetland, herbaceous (food) and woody vegetation (cover) positively influences the distribution of ice rats. 3) Ice rats are central place foragers (Schwaibold 2005) (i.e. they repeatedly return to a fixed point such as a burrow entrance with food items collected elsewhere; Orians & Pearson 1979), which may reduce exposure to unfavourable conditions above-ground. However, food quality and availability are poor in winter, and we predicted that ice rats would travel longer distances to find better quality forage in winter (Rosenberg & McKelvey 1999). 4) We expected that, in summer, females would require more food than males, because of the energetic demands of pregnancy and lactation, but we also predicted that the increased gut capacity of females in summer might offset the need to increase their space use during summer.

METHODS
The study took place between May 2000 and January 2001. Field work totalled 102 days. Reference collections of all plants species collected on site have been prepared as voucher specimens and are housed in the C.E. Moss Herbarium of the University of the Witwatersrand.

Study area
The study was undertaken in one of the Sani River valleys (29°37′S, 29°14′E), about 5 km west of Sani Top in the southeastern Maluti Mountains, Lesotho, at about 2900 m a.m.s.l. The mean annual temperature is about 6°C (Grab 1997). Mean annual rainfall is 1200 mm, and snow may occur 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; vegetation rarely exceeds 0.5 m in height. Based on observations over the past 15 years, predation pressure and interspecific competition in the Sani Valley are negligible as predatory species are hunted by local farmers, and no other small mammals were found in the ice rat’s environment.

Ice rats are easily observed in nature because of
the short vegetation and because of the presence of their distinctive burrow entrances (Hinze et al. 2006). Our primary study site was 6 ha, situated along the fringes of one of the many wetlands in the Sani Valley. In addition, we sampled along transects from our study site into the surrounding slopes.

Plant community structure

We compared the vegetation in 20 areas occupied by ice rats (identified by the presence of burrows) and 20 unoccupied areas using a paired design. Comparisons were made in summer and winter (n = 10 per season), over a two-month period per season. Unoccupied areas were located approximately 15 m away from occupied areas, and were selected on the basis of similar broad vegetation type (e.g. wetland plants, bushes) to occupied areas. In both occupied and unoccupied areas, we sampled the vegetation using a semi-random sampling method: a 5 × 5 m string frame subdivided into 0.5 × 0.5 m blocks was laid over the sampling area. Within this string frame, we selected 10 random 0.5 × 0.5 m blocks, and recorded: 1) plant species composition and frequency: percentage of blocks within which a species occurred; and 2) percentage vegetation cover: proportion of the ground covered by the aerial parts of the plant (plant species with the highest percentage cover were considered to be the dominant species). To ascertain the percentage cover (overall and vegetation type) in each block, we used a modified Braun-Blanquet scale (after Hill et al. 2005).

Space use

We studied the space use of marked adult individuals in 10 ice rat colonies in summer and winter by recording their locations within their colony. We studied 24 females and 19 males in summer, and 20 females and 18 males in winter from the same colonies. These individuals were trapped in metal live-traps (26 × 9 × 9 cm), baited with fruits and vegetables (e.g. apple, cucumber, lettuce and spinach). Traps were set during early mornings and late afternoons when ice rats are most active. The traps were checked every 30 minutes. Focal individuals were sexed and fitted with a coloured plastic cable tie (length 200 mm, width 4.7 mm) neck band (Jackson 1999). Females were fitted with white neck bands and males with black ones. A distinctive colour combination of insulation tape was taped on the neck bands for individual identification. Animals were then released at the point of capture. Collared individuals that were trapped subsequently showed no 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).

Each colony was marked off into 4 × 4 m grid squares, coinciding with the maximum surface area of an ice rat colony (i.e. 15.75 m²; Hinze et al. 2006), and numbered consecutively. The corners of the grid were demarcated with clearly visible coloured pegs (30 cm high) to serve as landmarks. Observations of adult focal individuals were made directly, using 10 × 50 binoculars, and each individual was observed for a total of 4–7 hours per season, during the day when ice rats were most active (05:00–12:00 and 13:30–17:30 in summer and 08:00–12:00 and 13:30–17:00 in winter; Hinze & Pillay 2006).

To calculate the space use of an individual during observations, we recorded the square in which the individual was located at the start of an observation session (one hour each, continuous sampling) and then in all subsequent squares into which the focal ice rat moved. When the focal individual travelled belowground within the burrow system of the colony, we noted the square containing the burrow into which it had disappeared and the square with the burrow from which it reappeared.

We investigated the space use of individuals by using the minimum polygon method (Schradin & Pillay 2005). The number of squares and half grids within this convex polygon were summed to calculate the home-range size in square metres. We excluded obvious excursions, such as rare visits of >20 m from the cluster of other recordings for a focal ice rat. The dominant vegetation types (herbaceous plants, wetland sedges, grasses, woody vegetation) were identified in each square, and plants were identified to species level where possible.

Diet

We ascertained the basic dietary preference of ice rats during 150 hours of direct observations using 10 × 50 binoculars. Observers were usually situated 10–30 m from the focal animal. These observations were made in summer only as plant species were very difficult to identify in winter. We recorded the foraging behaviour of ice rats in different plant patches, which we defined as a
square (discussed above) to which ice rats returned regularly and by the presence of a dominant vegetation type. Where possible, food plants collected or consumed were identified to species level based on floral characteristics easily identifiable from the observation point.

**Transect sampling**

We laid three transect lines of between 500 and 1000 m long, starting from the edge of the wetland to the top of the surrounding hills (mean difference in altitude = 80 m). At 50 m intervals, we recorded the presence or absence of active burrows (i.e. burrows that were inhabited by ice rats; burrows used for plant community structure were not used for this part of the study) and the following habitat parameters: 1) slope (using a dumpy level); 2) soil compactness (using a penetrometer); 3) soil moisture (approximately 100–150 g soil samples were collected at 20 cm depth, weighed and taken to the University of the Witwatersrand in sealed airtight plastic bags and oven-dried to calculate soil moisture content); 4) soil types (a soil texture triangle was used to categorize soils into sand/loam/clay; Hillel 1982); and 5) percentage vegetation cover (from ten 1 m$^2$ quadrates as described earlier). We also recorded the percentage cover of the major vegetation types, including *Helichrysum* bushes, grasses, and herbaceous plants and wetland sedges. Sampling was done in late spring, summer and early autumn only, as the ground was usually frozen in winter, thus affecting penetrometer and soil moisture readings.

**Data analysis**

For the analysis of plant community structure, percentage cover was calculated for each occupied and unoccupied area and a Wilcoxon paired rank test with sequential Bonferroni adjustments (adjusted $\alpha' = 0.013$) was used to compare the vegetation cover between occupied and unoccupied areas in all four sample months (two months per season). Seasonal differences in plant cover were established by comparing the difference between the percentage cover of occupied and unoccupied areas using a Mann-Whitney $U$-test. A generalized linear model (GLZ) with a multinomial error structure and logit link structure was used to analyse interdependence between plant types; season and colony presence/absence were included as categorical predictors in the model (Statistica ver. 6.0; Statsoft Inc.). Data for space use were tested for sex and seasonal differences using Mann-Whitney $U$ analyses. For the transect sampling, we used a GLM (variance component covariance structure) to analyse whether the nine variables measured (percentage data were arcsin transformed) differed between burrow absent and present burrow locations (fixed factor); transect was included as a random factor in the model to account for the idiosyncrasies associated with each transect.

**RESULTS**

**Plant community structure**

There were no differences in vegetation cover between months of the same season for both occupied and unoccupied areas, so the data were pooled by season. Vegetation cover was significantly greater in unoccupied areas than in occupied areas, both in summer (median (min, max): 85 (64, 98)% vs 56 (45, 79); $H_{10,10} = 3.92, P < 0.001$) and winter (90 (49, 100) vs 58 (21, 93)%; $H_{10,10} = 3.88, P < 0.001$). Relative differences in vegetation cover between occupied and unoccupied areas (i.e. cover in occupied areas—cover in unoccupied areas) revealed no significant variation between summer (27.49%) and winter (28.62%; $U_{10,10} = 0.15, P = 0.881$).

A GLZ showed no significant interdependence of plant species occurring in occupied and unoccupied areas in both seasons (colony presence/absence: Wald $\chi^2_{11} = 0.41; P = 1.00$; season: Wald $\chi^2_{11} = 4.31; P = 0.96$; colony presence/absence*season: Wald $\chi^2_{11} = 1.91; P = 0.99$). The vegetation recorded was grouped into four categories (Table 1). Woody vegetation (*Helichrysum* spp.) was sparse in both occupied and unoccupied areas, while herbaceous plant cover was similar in both areas. Grasses and sedges occurred frequently in both areas. There was no consistent difference between occupied and unoccupied areas with regard to the most common plant species present in winter ($\chi^2_{11} = 6.33, P = 0.850$) and summer ($\chi^2_{11} = 5.48, P = 0.906$).

**Space use**

Space use was significantly greater in summer than winter for both males (median and range: summer = 264.74 (131.67–454.57) m$^2$, winter = 134.59 (56.91–300.12) m$^2$; $U_{19,18} = 251, P = 0.043$) and females (summer = 453.10 (214.1–623.32) m$^2$, winter = 129.20 (98.2–433.34) m$^2$; $U_{24,20} = 359, P < 0.001$). Space use did not differ significantly between the sexes in winter ($U_{18,20} = 231, P = 0.21$), but females utilized larger areas than males in summer ($U_{24,19} = 325, P = 0.021$).
We observed *O. s. roberts* feeding on herbaceous plants and wetland sedges predominantly and grasses to a lesser extent (Table 1); interestingly not all the dominant herbaceous plant species were consumed. Both the green and floral parts of these plants were collected and consumed. We did not observe ice rats feeding on *Helichrysum* spp.

**Transect sampling**

A summary of parameters recorded along transects in the presence and absence of ice rat burrows is given in Table 2. A GLM analysis revealed that sites with ice rats contained significantly more herbaceous plants ($F_{1,65} = 16.83, P < 0.001$) and wetland sedges ($F_{1,63} = 5.45, P = 0.023$) and significantly fewer *Helichrysum* bushes ($F_{1,63} = 15.45, P < 0.001$) than in sites where ice rats were absent (Table 2). Slope was not a good predictor of ice rat presence (Table 2), which was confirmed by our observations of burrows in both the flattest and steepest areas along the transects. Soil moisture content was also not a good predictor of the location of colonies, because burrows were found in the wettest and driest areas. The location of colonies was not influenced by the presence/absence of grass, vegetation cover, soil compactness or soil type. Transect was not a significant predictor of any of the nine parameters (Table 2).

**DISCUSSION**

Although the habitat selection and use by burrowing small mammals is influenced by several environmental parameters, such as food availability (Rosenberg & McKelvey 1999; Schradin & Pillay 2006), plant species composition (Brown & Willan 1991) and cover (Falkenberg & Clarke 1998; Jackson 2000), it is obvious that soil characteristics are likely to have a major influence on habitat selection (Jackson 2000). Soil characteristics influence burrowing ability (Shenbrot et al. 2002). For example, the Afro-alpine giant mole rat *Tachyoryctes macrocephalus* appears to select habitats according to, amongst others, soil moisture content, as burrows were found mainly along seasonally waterlogged swamps (Sillero-Zubiri et al. 1995). Similarly, we predicted that ice rats would select habitats that would facilitate burrowing. However, neither slope nor soil composition (i.e. soil type, moisture content) was a good predictor of the *O. s. robertsi* colony location. Indeed, ice rats are known to construct burrows in soil substrates differing in water content, such as harder organic and softer mineral soils (Hinze et al. 2006). However, previously waterlogged tunnel systems (i.e. flooded burrows) were not re-inhabited and no

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**Table 1.** Dominant species of the woody and herbaceous vegetation and their percentage occurrence in areas occupied and unoccupied by *Otomys slogetti robertsi* at Sani Top; plant species consumed by ice rats are also indicated.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Dominant species</th>
<th>Consumed by ice rats</th>
<th>Percentage cover median (range) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasses</td>
<td><em>Pentaschistis oreodoxa</em></td>
<td>Yes</td>
<td>13 (0–100)</td>
</tr>
<tr>
<td><em>Helichrysum</em> spp.</td>
<td><em>H. cymosum</em></td>
<td>No</td>
<td>0 (0–100)</td>
</tr>
<tr>
<td></td>
<td><em>H. subglomeratum</em></td>
<td>No</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>H. trilineatum</em></td>
<td>No</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>H. flanaganii</em></td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Herbaceous vegetation</td>
<td><em>Crassula lanceolata</em></td>
<td>No</td>
<td>75 (30–100)</td>
</tr>
<tr>
<td></td>
<td><em>Geranium multisectum</em></td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Selago flanaganii</em></td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Selago galpinii</em></td>
<td>No</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Eumorphia sericea</em></td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Wetland sedges</td>
<td><em>Limosella vesiculosa</em></td>
<td>Yes</td>
<td>40 (0–100)</td>
</tr>
<tr>
<td></td>
<td><em>Trifolium burchellianum</em></td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Ranunculus multifidus</em></td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Haplocarpha nervosa</em></td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Cotula paludosa</em></td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Saniella verna</em></td>
<td>Yes</td>
<td></td>
</tr>
</tbody>
</table>
burrows were located in the wetland, possibly due to the high flooding risk in summer and freezing-over in winter.

Of the five environmental variables measured along transects, the microhabitat distribution of *O. s. robertsi* was influenced only by the presence of herbaceous plants, which form a large component of their diet, and the absence of woody *Helichrysum* species. Ice rats feed on fresh plants mainly, and they hoard smaller quantities of food (Schwaibold & Pillay 2006). Therefore, occupying patches with food plants decreases travelling distances for foraging, which minimizes energy loss through exposure to cold temperatures (Johnson & Cabanac 1982), particularly since ice rats are poorly-adapted physiologically to extreme cold (Richter et al. 1997). As herbaceous food quality decreases in winter (Van Soest 1982) and more food is required to meet increased metabolic requirements (Batzli & Cole 1979), reducing energy loss on travel may be beneficial; ice rats are central place foragers, and very rarely forage more than a metre away from the nearest burrow entrance (Schwaibold 2005).

The absence of woody *Helichrysum* spp. bushes in ice rat colonies was unexpected, as these would have provided adequate cover, and would have been effective windbreaks (Willan 1990). However, ice rats do not consume *Helichrysum* and its presence may affect the microclimate close to the ground due to shading (Eurola et al. 1984), thereby influencing the growth of food plants. Moreover, shading by *Helichrysum* bushes, which can reach up to 50 cm in height, may negatively influence sun basking, which constitutes a large proportion (38%) of their daily above-ground activity (Schwaibold & Pillay 2006). Basking is an important thermoregulatory activity, which may compensate for reduced energy intake from lower quality food in winter by accelerating the warming-up process to a level allowing for uninterrupted activity with reduced thermoregulatory cost (Sale 1970; Geizer et al. 2002; Schradin et al. 2007). Indeed, in our study of space use, basking occurred more frequently away from *Helichrysum* bushes (*n* = 343) than within a 1-m radius of the bushes (*n* = 15; $\chi^2 = 300.51, P < 0.001$), and ice rats sometimes climbed and basked at the top of bushes if these obscured the sun.

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 & Clarke 1998; Jorgensen 2004). Both predation and interspecific competition do not appear to influence microhabitat distribution in *O. s. robertsi* as both

### Table 2. Habitat variables and soil type along transect lines in the presence and absence of *O. s. robertsi* colonies. Values given as mean ± S.E. Significant results are highlighted in bold.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Sites with ice rat burrows</th>
<th>Sites without ice rat burrows</th>
<th>Statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass (%)</td>
<td>50.36 ± 4.90</td>
<td>50.67 ± 2.29</td>
<td>Burrow: <em>F</em>$_{1,64.8}$ = 0.53, <em>P</em> = 0.469</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect: <em>F</em>$_{2,63.0}$ = 2.84, <em>P</em> = 0.066</td>
</tr>
<tr>
<td><em>Helichrysum</em> bushes (%)</td>
<td>11.32 ± 2.84</td>
<td>26.91 ± 2.70</td>
<td>Burrow: <em>F</em>$_{1,63.0}$ = 15.45, <em>P</em> &lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect: <em>F</em>$_{2,63.0}$ = 2.46, <em>P</em> = 0.059</td>
</tr>
<tr>
<td>Herbaceous plants (%)</td>
<td>51.69 ± 6.10</td>
<td>30.01 ± 3.55</td>
<td>Burrow: <em>F</em>$_{1,65.0}$ = 16.83, <em>P</em> &lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect: <em>F</em>$_{2,63.0}$ = 3.12, <em>P</em> = 0.094</td>
</tr>
<tr>
<td>Wetland sedges (%)</td>
<td>23.92 ± 4.99</td>
<td>11.61 ± 1.25</td>
<td>Burrow: <em>F</em>$_{1,63.0}$ = 5.45, <em>P</em> = 0.023</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect: <em>F</em>$_{2,63.0}$ = 1.12, <em>P</em> = 0.294</td>
</tr>
<tr>
<td>Vegetation cover (%)</td>
<td>79.64 ± 2.61</td>
<td>80.14 ± 1.84</td>
<td>Burrow: <em>F</em>$_{1,64.0}$ = 1.86, <em>P</em> = 0.177</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect: <em>F</em>$_{2,63.0}$ = 1.84, <em>P</em> = 0.167</td>
</tr>
<tr>
<td>Slope (degrees)</td>
<td>20.18 ± 2.06</td>
<td>17.86 ± 0.83</td>
<td>Burrow: <em>F</em>$_{1,5.4}$ = 0.95, <em>P</em> = 0.372</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect: <em>F</em>$_{2,63.0}$ = 2.73, <em>P</em> = 0.073</td>
</tr>
<tr>
<td>Soil moisture content (%)</td>
<td>22.44 ± 1.92</td>
<td>20.95 ± 0.94</td>
<td>Burrow: <em>F</em>$_{1,64.0}$ = 2.37, <em>P</em> = 0.539</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect: <em>F</em>$_{2,63.0}$ = 1.99, <em>P</em> = 0.144</td>
</tr>
<tr>
<td>Soil compactness (psi*)</td>
<td>9.38 ± 0.76</td>
<td>7.73 ± 0.39</td>
<td>Burrow: <em>F</em>$_{1,64.0}$ = 2.69, <em>P</em> = 0.106</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect: <em>F</em>$_{2,63.0}$ = 2.14, <em>P</em> = 0.126</td>
</tr>
<tr>
<td>Soil type</td>
<td>Sandy/loamy soil</td>
<td>Sandy/loamy soil</td>
<td>Burrow: <em>F</em>$_{1,64.0}$ = 0.38, <em>P</em> = 0.539</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect: <em>F</em>$_{2,63.0}$ = 2.00, <em>P</em> = 0.144</td>
</tr>
</tbody>
</table>

*Penetration resistance index.*
are negligible in our study area. Ice rat colonies were situated in areas with reduced cover compared to adjacent unoccupied areas; reduced cover in occupied areas is probably a consequence of their foraging behaviour. Moreover, based on observations over the past 15 years, predation pressure in the Sani Valley is negligible (as it is in most localities where ice rats occur; Willan 1990), and ice rats here do not share their aboveground habitat with other small mammals.

Willan (1990) reported that ice rats are absent from boggy areas and steep slopes but prefer level areas or gently sloping ground with abundant rocks. In contrast, substrate type did not influence colony absence/presence in our study. While it is possible that food plants, the primary positive determinant of ice rat microhabitat distribution, occur on many substrate types, we suggest that increased ice rat population density is another important and more recent factor (Mokhotjomela 2007), forcing ice rats into previously uninhabited substrates. The high population density is the result of improved ice rat survival in winter. In the absence of significant predation pressure, ice rat population numbers are apparently regulated by low temperatures coupled with prolonged periods of snowfall in the Maluti Mountains (Willan 1990; Lynch & Watson 1992). The winters over the past few years have been relatively mild with little snowfall and while maximum temperatures have remained mostly constant, minimum temperatures have increased substantially over the last decade (Lesotho Weather Service; Schwaibold 2005).

Since the distribution of resources within a microhabitat influences the home range size of an animal (Rosenberg & McKelvey 1999), we expected that space use would be directly proportional to food availability (i.e. ice rats would travel longer distances to find better quality forage in winter). However, space use was greater in summer than winter. It is not always apparent what drives habitat choice for a central place forager, because 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 & McKelvey 1999). An important consideration for ice rats is the thermoregulatory challenge imposed by low temperatures. It is possible that ice rats may be modifying their foraging behaviour temporally in response to changing energy needs (Schultz et al. 1999), particularly under thermally challenging conditions, resulting in a trade-off between foraging efficiency and reduced exposure to extreme temperatures (Johnson & Cabanac 1982). Therefore, travelling short distances in winter may reduce exposure to low temperatures but has to be traded-off against consuming poor quality food. In a previous study, we showed that the aboveground activity of ice rats was greatly influenced by low temperatures in winter, resulting in very predictable behavioural sequences (routines) to minimize energy loss (Schwaibold & Pillay 2006).

As predicted, females utilized a larger area of their colonies than males in summer. One reason for sex differences in space use may be the need to increase foraging opportunities in order to meet the energy requirements of pregnancy and lactation. It also appears that females do not capitalize on their larger gut size (Schwaibold & Pillay 2003) in summer. However, in a recent study, we showed that there were no sex differences in levels of foraging behaviour in summer (Schwaibold & Pillay 2006). Clearly, other factors for greater space use by females should be investigated in future, such as territorial defence to reduce infanticide risk (Wolff 1993).

Comparison with other otomyines

The subfamily Otomyinae is widespread in southern Africa, and predictably, their habitat use reflects the habitats they occupy (Table 3). All otomyines are herbivores, and thus associate with potential food plants. Another important consideration is cover, which reduces predation risk and buffers extreme temperatures. Mesic-living O. angoniensis and O. irroratus nest on the surface, and are thus associated with dense vegetation. The arid-living O. unisulcatus constructs stick-lodges and is associated with areas with woody plants. Both Parotomys species and O. s. robertsi construct complex underground burrows in open (desert/alpine) environments.

Parotomys spp. construct burrows situated in deep sandy soils at or near food, which determines the environment they occupy within their distribution ranges. Contrary to our predictions, O. s. robertsi is not limited by soil type for its burrows. Instead, ice rat distribution is determined primarily by the distribution of food plants, which ultimately decreases exposure to low temperatures and maximizes energy gain. Although we did not measure the productivity of edible plants, the high density of ice rats (up to 100 individuals per ha; Willan 1990; Mokhotjomela 2007), suggests that the carrying capacity for ice rats in our site is high.
although this may also reflect better survival of ice rats in the recent past.

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