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Life in an African Alpine Habitat: Diurnal Activity Patterns of the Ice Rat *Otomys sloggetti robertsi*

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Abstract

We studied the diurnal activity patterns of the African ice rat *Otomys sloggetti robertsi*, a murid rodent endemic to the harsh alpine and sub-alpine habitats of southern Africa. The taxon is poorly adapted physiologically to cold conditions, and we investigated whether the activity of free-living *O. s. robertsi* is modified by prevailing environmental conditions. *O. s. robertsi* displayed a bimodal diurnal activity profile in summer, retreating into underground burrows during the middle of the day when ambient temperatures and solar radiation levels were at their highest. In contrast, during winter, *O. s. robertsi* displayed a unimodal activity profile by spending most of the day foraging aboveground and extending its foraging bouts for about half an hour after sunset. More time was spent foraging than basking in winter compared to summer. Levels of foraging decreased and levels of basking increased during periods of snow cover, although runways beneath the snow could have provided access routes to foraging areas. *O. s. robertsi* activity is dictated by environmental conditions seasonally, time of the day, and the absence or presence of snow, and the taxon responds to these conditions by trading off between behaviors critical for meeting thermoregulatory requirements.

Introduction

There is overwhelming evidence that environmental variables have a strong influence on both the daily and seasonal activity patterns of small mammals living in temperate environments (Chappell and Bartholomew, 1981; Türk and Arnold, 1988; Bacigalupe et al., 2003). For example, alpine marmots *Marmota marmota* which nest in burrows reduce aboveground activity during the hottest times of the day, resulting in a bimodal activity profile, and they remain aboveground for most of the day during cool days (Türk and Arnold, 1988). Such bimodal activity appears to be a strategy for avoiding times when temperature and solar radiation levels are at their highest during the middle of the day (Walsberg, 1988). Most alpine rodents hibernate in winter, but rodents that do not hibernate modify their behavior (increase foraging time or sun basking) to maximize energy gain (Barash, 1973; West and Dublin, 1984; Drew and Bissonette, 1997). However, the actual time individuals can spend outside their refuges is lower in winter than summer because of a need to minimize exposure to the cold, especially before sunrise and after sunset (Zielinski et al., 1983).

An interesting model for studying how small mammals cope with temperate climatic conditions is the African ice rat *Otomys sloggetti robertsi*. This medium-sized (121–143 g) murid rodent is endemic to altitudes exceeding 2000 m in the southern African Drakensberg and Maluti mountains (Willan, 1990), a distribution which restricts it to the cold, harsh sub-alpine and alpine phytogeographic belts in Africa (Killick, 1978). *O. s. robertsi* is colonial, herbivorous, and diurnal. Importantly, it is poorly adapted physiologically to the temperate habitats it occupies and its physiology resembles that of its congeners inhabiting warmer climates (Richter et al., 1997). Unlike most small mammals that inhabit similar environments in the northern hemisphere, *O. s. robertsi* does not enter torpor or hibernate during winter. The low temperatures and prolonged snow cover in winter in the Maluti

Mountains apparently regulate *O. s. robertsi* population numbers (Willan, 1990; Lynch and Watson, 1992).

In response to low temperatures, *O. s. robertsi* has developed some morphological characteristics, such as a short tail and small ear pinnae (Richter, 1997), and a modified gut structure (Schwaibold and Pillay, 2003). In addition, *O. s. robertsi* displays behavioral strategies, including basking and huddling (Schwaibold and Pillay, 2006). Members in a colony also construct an intricate interlinking belowground tunnel system, located 280–357 mm deep in the soil, within which grass padded nest chambers provide thermal shelters from extremely cold temperatures during the night (Hinze et al., in press).

Apart from anecdotal information of its basking behavior (Willan, 1990), little is known about the diurnal activity of *O. s. robertsi*. The present study examined whether *O. s. robertsi* may have modified its activity pattern in relation to prevailing environmental conditions. Direct observations were made of the aboveground behavior of free-living *O. s. robertsi* to ascertain seasonal differences in its diurnal activity patterns. The influences of seasonal variation in solar radiation and temperatures on activity were also examined, as was the presence of snow on the ground. A bimodal activity profile was expected during summer, with aboveground appearance and activity taking place in the morning and afternoon/evening. In contrast, a unimodal activity profile was expected in winter, but we predicted that activity would be reduced when snow was present, since the opportunities for foraging would be diminished and low ambient temperatures would pose a thermoregulatory challenge aboveground. Since *O. s. robertsi* is poorly adapted physiologically to low temperatures, we expected seasonal differences in behavior, in particular higher levels of foraging and basking in winter than in summer to meet thermoregulatory demands (Johnson and Cabanac, 1982; Schultz et al., 1999).

Methods

Fieldwork was conducted in a 4 ha site in the Sani Valley located in the Maluti Mountains, Lesotho (29°33'S, 29°14'E). The study site lies at an elevation of 2800 m and comprises a wetland surrounded by gentle slopes. The mean minimum daily temperature during winter is approximately -5°C and the mean maximum is 9°C. During summer, the mean minimum is 5°C and the mean maximum reaches 16°C (Lesotho Weather Service). The mean annual precipitation, often in the form of snow, is over 1200 mm (Killick, 1963). The vegetation comprises mainly *Helichrysum* species on the slopes, while the wetlands contain several flowering plants, such as *Haplocarpa nervosa*, *Trifolium burchellianum*, *Saniella verna*, *Limosella vesiculosa*, *Cotula paludosa*, and *Ranunculus multifidus*.

Observations were conducted in two phases. In phase 1, field work was done during 10 d (140 h) in summer (October and November) and 10 d (100 h) in winter (May and August) over 2000 and 2001. In each season, observations were made on days with similar weather conditions. On different days, we observed the activity of *O. s. robertsi* belonging to three colonies, situated at a minimum of 75 m apart. Detailed observations were made from a raised vantage point approximately 3 m from a colony; *O. s. robertsi* quickly habituates (within 5 min) to human presence.

The activity of colony members was recorded on datasheets continuously from first light in the morning (5:00 in summer; 7:00 in winter) until it became too dark in the evening (17:00 in winter; 19:00 in summer) to observe colony members. Using instantaneous scan sampling (Martin and Bateson, 1993) with one minute intervals, we recorded whether the majority of the colony members (>50%) were foraging (searching, handling, and ingesting food), basking (sitting motionless aboveground), or had retreated belowground into their burrows. Rare activities, such as social behavior, were not included in the present analysis. The maximum number of individuals observed in a particular colony during the observation period was used to calculate the proportion of individuals aboveground per minute.

In phase 2, we studied the relationship between environmental parameters (solar radiation and ambient temperature) and activity of *O. s. robertsi*. Equipment for measuring environmental conditions was available for only 3 d in summer (2002) and 3 d in winter (2002). Based on the data collected during phase 1, we increased the sampling interval to 5 min for the instantaneous scan sampling. Ambient temperature and solar radiation were measured using, respectively, a TinytagTM data logger within a radiation shield and TinytagTM data logger without a shield, both of which were calibrated at the start of the experiment and logged readings in 5 min intervals. Both probes were set up alongside one colony under observation and at a similar height (5 cm) above the ground at which the rodents were active. Readings taken of solar radiation, temperature, and behavior of the colony were synchronized, so that activity could be correlated with the environmental parameters.

Otomys s. robertsi activity was also recorded on three separate occasions (8 d in total) when the habitat was covered in a thick layer of snow using the same recording techniques as described in phase 1. Snow was rare during our study, and we used the opportunity to study how snow on the ground influenced *O. s. robertsi* behavior. For comparison, we also recorded *O. s. robertsi* activity a week after the snow had melted. For comparison of activity in the presence and absence of snow, we recorded activity from 10:00 to 16:00.

Data Analysis

All data were analyzed for normality. We used a general linear model (GLM) with a repeated measures (time of day) design to compare the levels of foraging and basking behaviors and time spent belowground between seasons for phase 1; we did not use a multivariate approach because the number of degrees of freedom were comprised by the 2 (treatment) × 30 (dependent variables) matrix. Because of seasonal differences in the number of hours of daylight, data were collected over more hours in summer than winter, so we statistically compared data collected during the same times (7:00 to 17:00) in both seasons. A GLM with a repeated measures design was also used to compare foraging and basking behaviors and time spent belowground when snow was present and absent. The influence of environmental parameters on activity was analyzed using a GLM with a nested design: location above or belowground (fixed effects variable) was nested in time of day (random effects variable) and both of these were nested in season (fixed effects variable); and temperature and radiation were the response variables. Tukey post hoc tests were used to reveal specific differences for $P \leq 0.05$, and all tests were two-tailed.

Results

Within approximately 10 min after sunrise, about 80% of the individuals of a colony appeared aboveground and similarly, around 80% of the individuals retired into their burrows in the evenings within a few minutes of one another (Fig. 1). In both seasons, there was a decrease in aboveground activity during the middle of the day, leading to a bimodal diurnal activity profile, whereas individuals were aboveground for most of the day in winter. In the evenings, before sunset, at approximately 17:00 in winter and 19:00 in summer, aboveground activity increased again before the colony retreated into their burrows for the night. Some aboveground activity was observed for approximately 30 min after sunset in winter (Figure 1).

O. s. robertsi spent significantly more time foraging in winter than in summer ($F_{1,135} = 7.35$, $p = 0.016$), but time of day ($F_{9,135} = 1.62$, $p = 0.115$) and its interaction with season ($p = 0.320$) did not influence foraging behavior (Fig. 2). In contrast, levels of basking were greater in summer than winter ($F_{1,135} = 8.39$, $p = 0.011$), but were not influenced by time of day ($p = 0.09$) or by between time of day × season ($p = 0.312$). *O. s. robertsi* spent significantly more time belowground in summer than winter ($F_{1,135} = 6.18$, $p = 0.025$), mainly in the early mornings and around midday in both seasons ($F_{9,135} = 4.59$, $p < 0.001$). The statistical interaction between time of day and season was significant ($F_{9,135} = 6.90$, $p < 0.001$), and post hoc tests showed that significantly more time was spent belowground between 11:00 and 13:00 in summer than in winter (Fig. 2).

Solar radiation and ambient temperature were significantly higher in summer than in winter ($F_{1,306} = 78.61$, $p < 0.001$), and significantly associated with time of day in both seasons ($F_{217,306} = 1.73$, $p = 0.014$), peaking during the middle of day in both seasons (post hoc tests; Fig. 3). The disappearance of *O. s. robertsi* belowground coincided with periods of high ambient temperatures and high levels of solar radiation ($F_{73,306} = 1.97$, $p < 0.001$), this effect being more pronounced in summer than in winter (post hoc tests; Fig. 4).

Heavy snowfall significantly modified the behavior of *O. s. robertsi*, with levels of basking increasing ($F_{1,70} = 76.62$, $p < 0.001$) and levels of foraging decreasing ($F_{1,70} = 9.16$, $p = 0.009$) during days with snow but time spent belowground remained unchanged ($F_{1,70} = 2.62$, $p < 0.110$; Fig. 5). None of the three

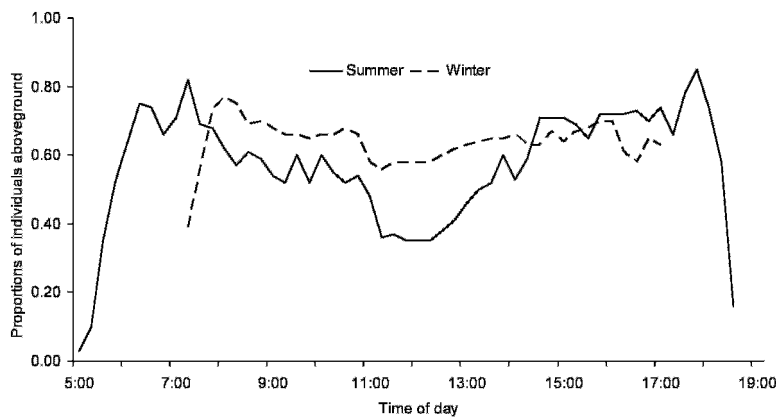


FIGURE 1. Proportion of *O. s. robertsi* aboveground in summer and winter during different times of the day. The beginning and end points of both lines indicate sunrise and sunset in each season, which coincide with the appearance of the first individuals aboveground and their withdrawal belowground, respectively.

parameters was influenced by time of day (basking: $p = 0.842$; foraging: $p = 0.859$; belowground: $p = 0.251$) nor by the statistical interaction between time of day and the presence or absence of snow (basking: $p = 0.575$; foraging: $p = 0.591$; belowground: $p = 0.395$). When the snow had melted, numerous runways that had been created beneath the snow cover could be seen and these most likely provided access routes to foraging sites. Generally, only heavy snow and rain prevented aboveground activity, but activity continued during light rain and snowfall, and basking behavior was observed occasionally under heavy cloud cover and light drizzle.

Discussion

O. s. robertsi displayed an almost unimodal diurnal activity profile during winter, spending most of its time aboveground foraging or basking before retreating into its burrow after

sundown. A bimodal profile was observed in summer, with *O. s. robertsi* disappearing belowground during the middle of the day, a period coinciding with the highest ambient temperatures and levels of solar radiation, factors which influence the activity of many other rodents (Walsberg, 1988; Vispo and Bakken, 1993; Ellison et al., 1994; Eifler and Slade, 1998; Bozinovic et al., 2000). Interestingly, whereas *O. s. robertsi* reaches its zone of thermoneutrality between 26 and 28°C (Richter et al., 1997), ambient temperatures in the Maluti Mountains rarely reach 20°C during most times of the year, suggesting a more prominent role of solar radiation in influencing activity. Temperature and solar radiation did not limit aboveground activity of *O. s. robertsi* in winter, perhaps because levels of these parameters were lower in winter than summer.

In both summer and winter, *O. s. robertsi* exhibited a peak in activity early in the morning and late in the afternoon. A similar

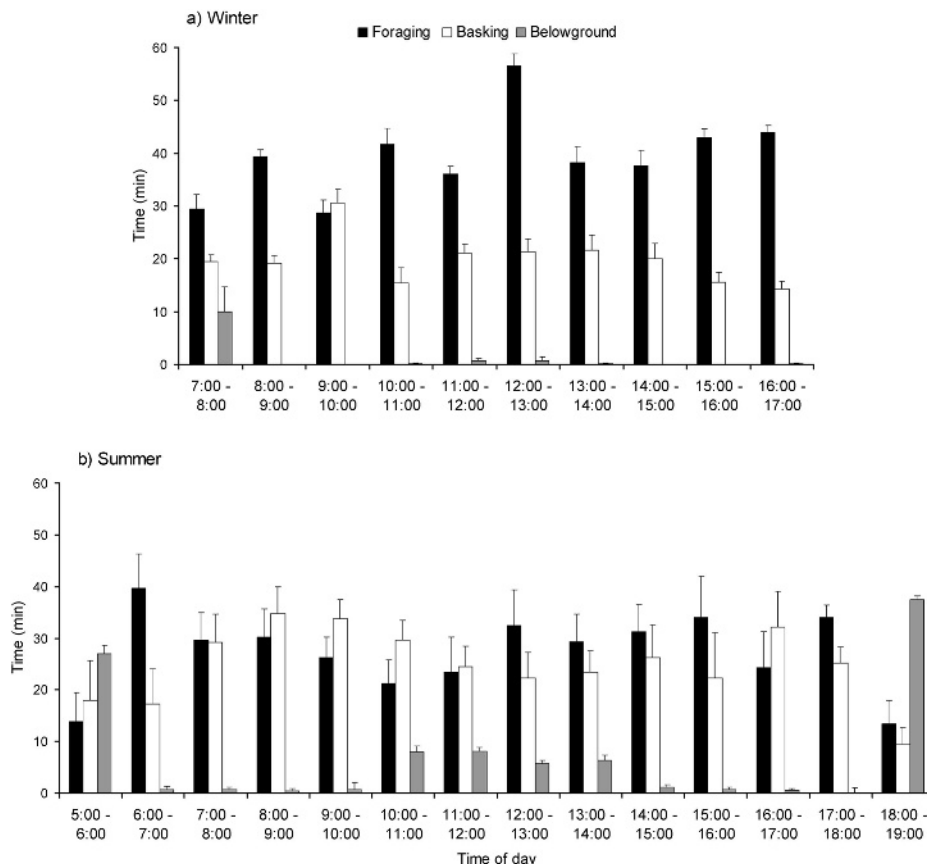


FIGURE 2. Mean time spent foraging, basking, and belowground by *O. s. robertsi* from (a) 7:00 to 17:00 during winter, and (b) 5:30 to 19:00 during summer.

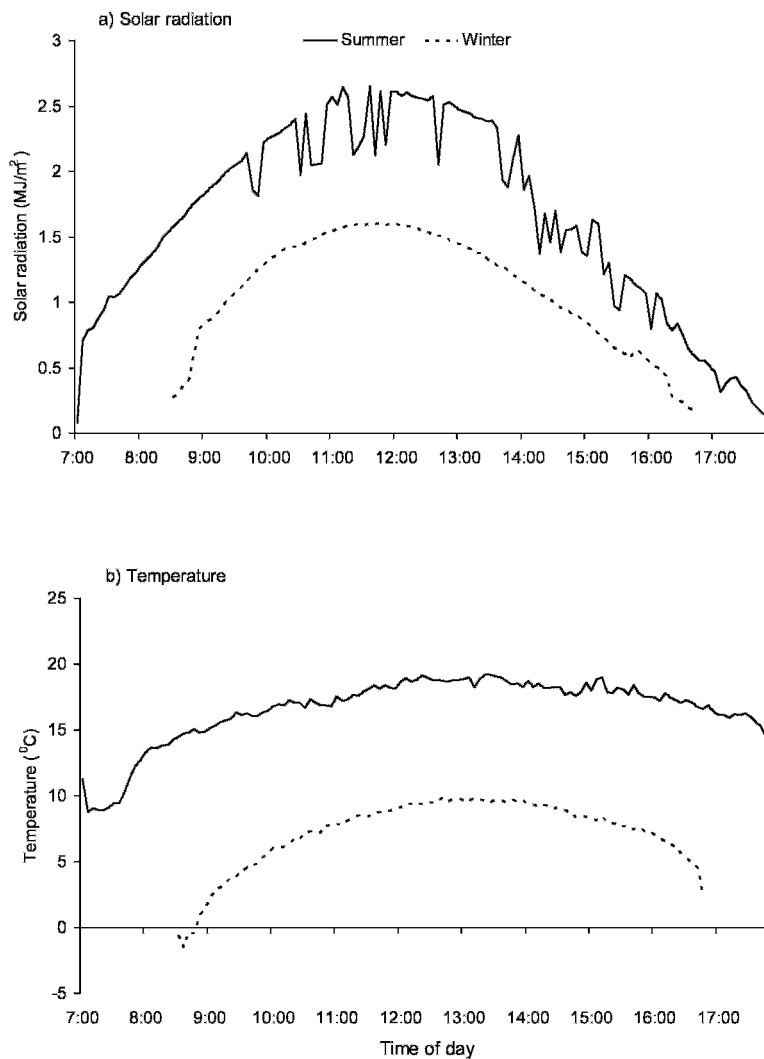


FIGURE 3. Measurements of (a) solar radiation and (b) temperature in summer and winter at the study site in the Sani Valley.

increase in activity has been observed in two close relatives of *O. s. robertsi*, the desert-living Brants' whistling rat *Parotomys brantsii* (Nel and Rautenbach, 1974) and the mesic-occurring vlei rat *O. irroratus* (Perrin, 1981). These peaks in activity probably result from a combination of factors. In summer, ambient temperatures and solar radiation levels are relatively low in the mornings and evenings and therefore do not constrain aboveground activity (Pritchard and Robbins, 1990). Another reason may be related to foraging behavior. Since *O. s. robertsi* does not hoard food, at least in the quantities that are likely to sustain it throughout the night (Hinze et al., in press), increased foraging in the mornings may replenish energy stores. In fact, foraging bouts in the mornings were unusually long compared to foraging bouts during the day (personal observation). The peak in activity in the late afternoon may likewise provide opportunities for feeding before retiring for the night, as no aboveground activity has been observed at night. In contrast, *P. brantsii* spends most of its time during afternoon foraging sessions collecting plants for consumption overnight in its burrows (Jackson, 1998). Although *O. s. robertsi* does not hoard food to the same extent as *P. brantsii*, it may compensate for this shortcoming in another way: compared to its relatives living in warmer, low-lying areas, *O. s. robertsi* has a larger gut capacity, which may increase the quantity of plant material it can consume per unit time (Schwaibold and Pillay, 2003).

Rodents inhabiting temperate environments, such as the thirteen-lined ground squirrel *Spermophilus tridecemlineatus* (Chappell, 1980; Vispo and Bakken, 1993), generally limit their activity in the cold by remaining in relatively thermoneutral refugia, by entering into bouts of torpor, or by hibernating. In contrast, *O. s. robertsi* spent most of the daylight hours in winter aboveground. Because it is poorly adapted physiologically to low temperatures, we expected that behaviors that would improve energy gain (i.e. foraging and basking) would be higher in winter than summer (Johnson and Cabanac, 1982; Schultz et al., 1999). Instead, while foraging was higher in winter than summer, basking was higher in summer. This result is unexpected since we previously observed that *O. s. robertsi* spends extended periods basking when temperatures were below 5°C (unpublished data), but indicates that foraging is a primary source of energy gain, which is traded off against basking in winter. Moreover, *O. s. robertsi* continued to forage for approximately 30 min after sunset, exposing it to potentially lethal temperatures. A major factor limiting the time spent foraging during winter in diurnal vertebrates in temperate areas is the number of daylight hours (Drew and Bissonette, 1997; Eifler and Slade, 1998). For herbivores, another limitation is food quality and quantity, both of which decrease dramatically during winter in the alpine habitats of *O. s. robertsi*. Therefore, it appears that the energy gained through foraging beyond sunset is traded off against the energy

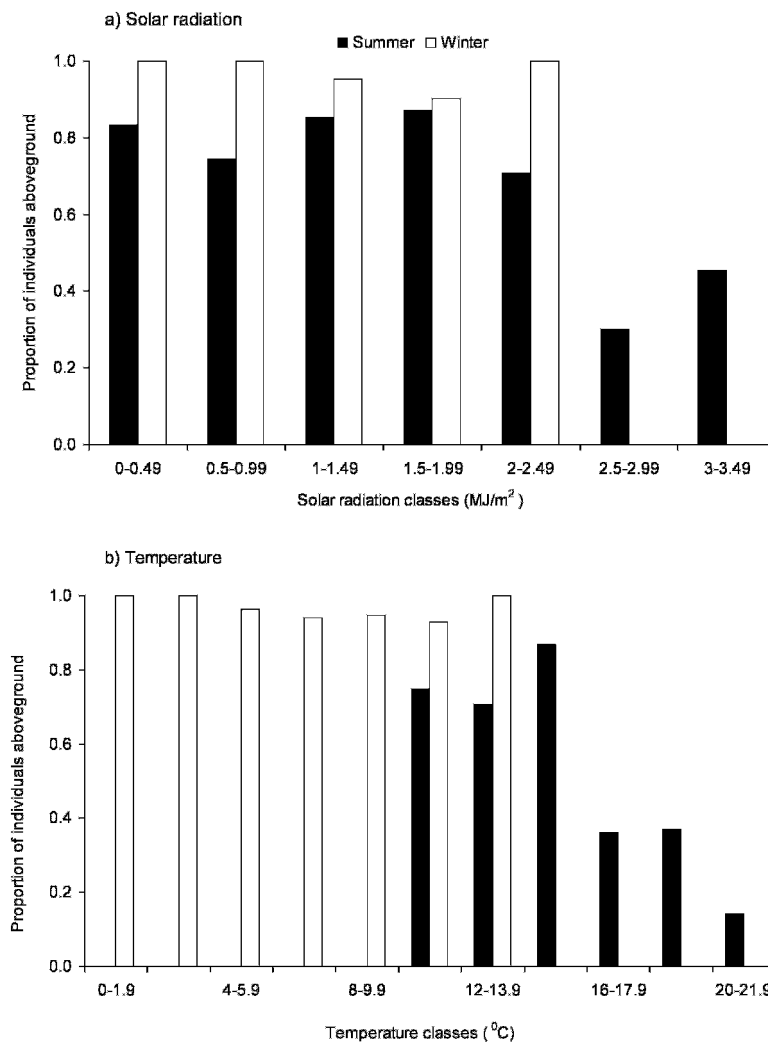


FIGURE 4. The relationship between the proportion of *O. s. robertsi* aboveground and (a) solar radiation levels and (b) ambient temperature in summer and winter.

saved by retiring into the thermoneutral nest chamber (Hinze et al., in press).

The level of aboveground activity observed in *O. s. robertsi* colonies is probably not influenced by predator risk, since most of the natural predators of *O. s. robertsi* have disappeared over the last two decades since first reported by Willan (1990). Only two instances of predation on an *O. s. robertsi* by a jackal buzzard (*Buteo rufofuscus*) were observed throughout the study period, and no terrestrial predators (snakes and small mammal carnivores) were observed at our study site. Therefore, aboveground activity is largely influenced by energy acquisition rather than predator avoidance.

In the mornings, most individuals in a colony appeared aboveground within a few minutes of each other to bask briefly before the first foraging session of the day. Similarly, at sundown, the members of a colony disappeared belowground within a short period of time. This phenomenon was also observed during the day when individuals in an entire colony retreated belowground, mainly at midday in summer, and later reappeared aboveground, all within a few minutes of one another. Such synchronization of behavior could reflect the social nature of *O. s. robertsi* (Willan, 1990), although the higher than expected incidences of aboveground aggression between colony members (Hinze and Pillay, unpublished data) suggest that the timing may be due to exploitation of favorable environmental conditions (Vispo and Bakken, 1993; Ellison et al., 1994; Eifler and Slade, 1998),

particularly following a night spent belowground with little or no food stores.

The presence of snow on the ground, and the persistence of this over a few days, changed the aboveground activity pattern of *O. s. robertsi*. Compared to periods without snow, levels of basking increased and levels of foraging decreased when snow was present. However, runways under the snow could have provided routes to foraging sites, a phenomenon also observed in voles in the Ural mountain chain (Bolshakov, 1984), which could have resulted in an underestimation of foraging behavior in our study. Even so, it is possible that prolonged snow cover, apart from lowering ambient temperatures, also decreases foraging opportunities by limiting plant growth, as well as imposing thermoregulatory constraints on *O. s. robertsi*. The combination of these factors could therefore be a major cause for mortality observed in winter in *O. s. robertsi* colonies (Willan, 1990; Lynch and Watson, 1992), as is the case with cotton rats (*Sigmodon hispidus*; Sauer, 1985; Eifler and Slade, 1998).

In conclusion, *O. s. robertsi*, a small alpine mammal, modifies its behavior according to prevailing environmental conditions, seasonally, at different times of the day, and during stochastic events like snowfall. Partitioning activity (i.e. trade-offs) into various energy-acquiring (e.g. foraging) and energy-saving (e.g. basking or disappearing underground) behaviors appears to be critical for meeting thermoregulatory requirements in rodents facing extreme environmental conditions (Cabanac and Johnson,

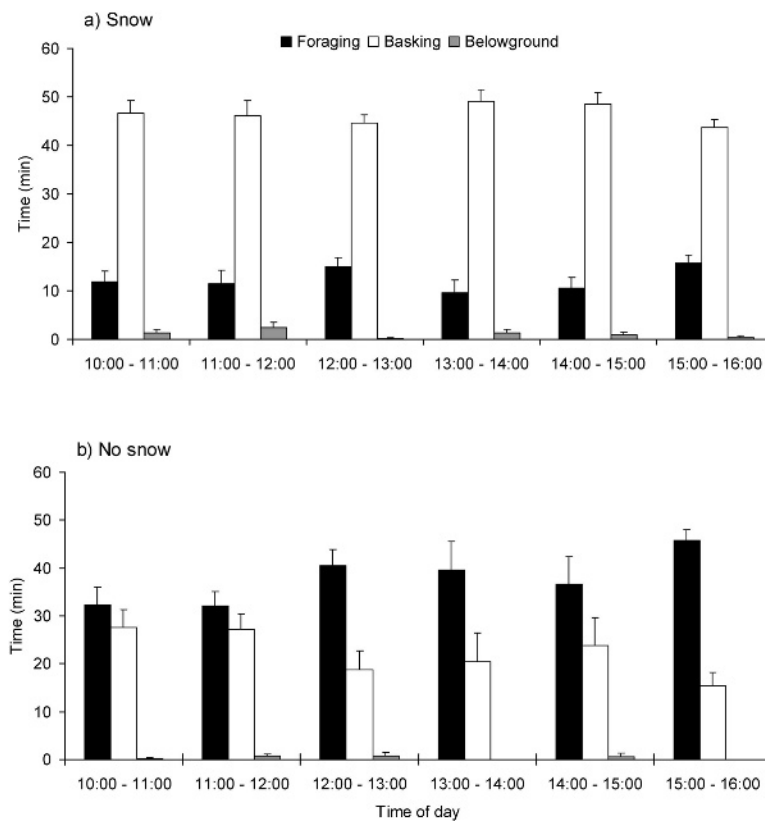


FIGURE 5. Mean (\pm SE) time spent foraging, basking, and belowground by *O. s. robertsi* during the (a) presence and (b) absence of snow cover.

1983; Collier et al., 1989; Schultz et al., 1999). The mechanisms underlying these behavioral trade-offs need to be investigated further in *O. s. robertsi*, although temperature and solar radiation appear to be important abiotic determinants of activity. The seasonal variation in activity patterns (unimodal vs. bimodal) is predictable, and occurs also in desert-living *P. brantsii*, probably indicating similar responses to harsh environments.

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