Does habitat modification and population size of ice rats (*Otomys sloggetti robertsi)* contribute to soil erosion in Lesotho?

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A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa, in fulfilment of the requirements for the degree of Master of Science

Johannesburg 2007

Declaration

I hereby declare that this dissertation is my own, unaided work. I am submitting it for a MSc in the University of the Witwatersrand (School of Animal, Plant and Environmental Sciences), Johannesburg. It has not been submitted for examination in any other university before

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August 2007

Abstract

Alpine environments are poorly studied ecosystems, largely due to their inaccessibility and severe climatic conditions. Nonetheless, a better understanding is needed of the ecological processes shaping these habitats, particularly the interactions between plants and animals. Recent studies indicate that the levels of soil erosion have increased in parts of Lesotho, possibly because of overgrazing by domestic livestock and the activities of the African ice rat *Otomys sloggetti robertsi*, whose population numbers have increased in recent times. *O. s. robertsi* is a diurnal, herbivorous, burrowdwelling, murid rodent, endemic to the southern African Drakensberg. The aim of my study was to establish whether and how the ice rat influences the vegetation and the soil characteristics in its habitat, and to determine whether ice rat population numbers have increased. I conducted three experiments. 1) Enclosures/plots were erected in the Sani Valley to measure the impact of; i) ice rats alone; ii) both ice rats and livestock on vegetation and soil loss and gain (which was used as a proxy for soil erosion). 2) I also ascertained ice rat numbers (colony sizes) at three different locations in Lesotho (Katse Dam, Oxbow and Sani Valley) by conducting monthly censuses of discrete colonies at each locality. 3) Finally, questionnaire surveys were used to ascertain the perception of, and influence on, ice rats by the local human inhabitants in Lesotho. The enclosure/plot experiments showed that the plots accessed by ice rats only had higher levels of vegetation change (loss of cover, decrease in height) and soil movement than other plots from which they were excluded or could access together with livestock, which was contrary to my prediction that the combined influence of ice rats and livestock would have a greater impact. The size of ice rat colonies showed a three-fold increase in my study compared to those a decade ago. The interviews of the local human inhabitants supported this finding, with people also claiming that ambient temperatures had increased and snowfall had decreased. The interviewees did not express any meaningful opinion about how they influenced the biology of ice rats, but claimed that ice rats were responsible for land degradation in the high Drakensberg. In conclusion, the results suggest that ice rats are responsible for large scale damage at my study sites as a result of their foraging and burrowing activities, and erosion is likely to be exacerbated by the increasing numbers of ice rats. Nonetheless, soil erosion is a complex problem involving several biotic and biotic contributing factors, and long term studies are required to fully understand the underlying determinants of erosion in the Lesotho Highlands.

Acknowledgements

I would like to express my gratitude to my supervisors Prof. Neville Pillay for his patience in teaching me scientific skills and Dr Ute Schwaibold for help in the field. Moreover, I also pass a special thank you to the Sani Top community for cooperation and assistance during fieldwork. They watched over the research material which facilitated data collection for the study.

Funding for this project was provided by the National Research Foundation and the University of the Witwatersrand.

Finally, my family supported me from the first stage of my study to the last, for which I am thankful.

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Chapter 1. Introduction

Alpine environments are among the most understudied ecosystems, largely due to their inaccessibility and inherent severe climatic conditions (Bryant, 1996). However, some research indicates that they contain unique faunal and floral species, the interactions of which are of significance for the ecology of alpine habitats. I studied the effects of a small rodent, endemic to alpine habitats in southern Africa, on the vegetation and soil characteristics in its habitat. This dissertation starts with definition a major theme of the study (soil erosion) and highlight how soil erosion is brought about by the activity of rodents generally. Thereafter, different factors underlying population dynamics in rodents are considered. I then describe the biology of the study animal, the African ice rat *Otomys sloggetti robertsi*, including a review of how people and the ice rats interact and how this relationship has developed to date. Finally, a rationale for my study together with the aims and predictions/questions of the study are presented.

1.1 Soil erosion

Soil erosion is defined as a collection of processes during which debris is loosened and removed from any part of the earth's surface and moved to another area (Goudie *et al*., 2000). It is an intrinsic, natural process but becomes a problem due to acceleration of the process through anthropogenic activities, such as deforestation and overgrazing through cattle farming (Toy *et al*., 2002).

One of the more important factors contributing to soil erosion is the loss of vegetation cover. Vegetation cover is important for regulating soil moisture content and stability as it promotes infiltration of water into the soil and reduces surface flow (Garland, 1987; Arias *et al*., 2005). The roots of plants then absorb some of the water for photosynthesis (Garland, 1987). Vegetation cover also minimises the hitting impact of raindrops, thereby reducing the breakdown and erosion of topsoil (Garland, 1987; Schmidt, 2000). Therefore, the destruction of vegetation may impact adversely on the soil moisture content and result in soil degradation. Damage to vegetation cover may be brought about by diverse factors, such as the foraging activities of herbivores (Roberts *et al*., 1972; Krebs and Kacelnik, 1991) and poor land use practices by people (Marake *et al*., 1998; Letšela *et al*., 2003).

1.2 Impact of herbivorous rodents on vegetation cover

Rodents exert a very strong influence on their environment through their activities (Kinlaw, 1999; Eldridge and Myers, 2001; Reichman and Seabloom, 2002; Hall and Lamont, 2003). In this section, I will discuss how two important rodent activities, namely foraging and burrowing, contribute to a loss of vegetation cover. Intensive foraging by herbivorous rodents in combination with their burrowing is often blamed for large-scale vegetation damage and thus erosion (Kinlaw, 1999; Zhang *et al*., 2003). However, the habitat requirements and use of some rodents may also account for large-scale vegetation damage. In a study of the European beaver *Castor fiber*, Meentemeyer *et al*. (1998) describe how the activities and habitat use of these beavers contribute to soil erosion. These beavers fell trees along steam banks, which destroy tree root systems, thereby increasing soil erosion by exposing soil to natural erosion processes. Moreover, their trampling of vegetation creates paths into the water, increasing the susceptibility of topsoil to erosion.

1.2.1 Foraging

Foraging is a process of searching and acquiring food (MacArthur and Pianka, 1966). Successful foraging involves decision making to maximise energy intake while at same time minimizes energy loss. Thus, different organisms employ different strategies during the process (Emlen, 1966).

Selective foraging by herbivorous rodents can negatively influence ground vegetation cover (Roberts *et al*., 1972; Kiehl *et al*., 1996). For instance, lemmings *Lemmus spp*. can destroy about 90% of the moss cover and crop off all monocotyledonous shoots in their habitat (Batzli, 1981). Additionally, the meadow vole *Microtus pennsylvanicus* of central Illinois mostly forages on green shoots of dicotyledonous plants and consequently create bare ground patches in areas colonised by this type of vegetation (Lindroth and Batzli, 1984). This relationship was also noted in the grasslands inhabited by vizcachas *Lagostomus maximus* and tuco-tucos *Ctenomys mendocinus* (Branch *et al*., 1999; Tort *et al*., 2004; Arias, *et al*., 2005; Spiegelberger *et al*., 2006). Ongoing grazing of the preferred species patches can lead to complete destruction of that particular plant (Ecological Society of Australia, unpublished data).

Seed predation by rodents also affects ground vegetation cover, since consumption of large numbers of seeds inhibits regeneration of plants and hence retards individual species recruitment (Roberts *et al*., 1972; Golley *et al*., 1975). For instance, seed predation by white-footed mice *Peromyscus maniculatus* and red-backed voles *Clethrionomys gapperi* reduce the recruitment and succession of annual plants and ground vegetation cover in alpine tropical grasslands (Golley *et al*., 1975).

Whereas seed predation is one of the factors indirectly influencing ground cover by limiting plant recruitment, rodents can have other indirect influences on ground cover. American pocket gophers *Scalopus aquaticus* forage underground primarily on the roots of goatbeard *Tragopogon dubius* by simply pushing the soil aside to access the roots and thereby destroying the plants (Reichman and Seabloom, 2002). Similarly, Indian crested porcupines *Hystrix indica* in the Negev desert break the soil crust to feed on ground bulbs (Yair and Rutin, 1981; Alkon, 1999). In both examples, whole plants may be killed by the formation of sediment mounds in foraging patches (gophers; Reichmann and Seabloom, 2002) or exposing the root systems of neighbouring plants systems (porcupines; Alkon, 1999). Both processes contribute to a loss of ground cover and disturb the topsoil, making it more vulnerable to erosion agents (Reichman and Seabloom, 2002).

1.3 Burrowing activity of rodents

Bioturbation is a mechanical reworking of soils and sediments caused by organisms in their different habitat environments, and include the burrowing activities of animals (Meysman *et al*., 2006). This section considers the influence of rodents' burrowing in relation to vegetation cover and soil erosion.

Typically, rodents use burrows for protection from predators and as thermal refugia from climatic extremes (Roper *et al*., 2001; Reichmann and Seabloom, 2002; Hinze *et al*. 2006). In addition, the tunnels of complex burrow systems may also serve as access routes to suitable foraging patches, as seen in the African mole rats *Georychus capensis* (Meentemeyer *et al*., 1998) and subterranean moles *Scalopus aquaticus* (Reichmann and Seabloom, 2002).

Burrowing can have tremendous impacts on the landscape integrity by accelerating soil erosion (Kinlaw, 1999). Rodents that forage underground produce vast loads of free sediments that are easily transported by shallow surface water flow and wind (Yair and Rutin, 1981; Gabet, 2000; Hunt and Wu, 2003). Approximately 22 m^3 of soil sediments measured from burrows of North American beavers *Castor canadensis* were lost into streams per year (Meentemeyer *et al*., 1998). Although different studies demonstrate that soil excavated from burrows also facilitates the formation of new landscapes such as hummocks (van Zinderen and Werger, 1974; Meentemeyer *et al*., 1998; Reichmann and Seabloom, 2002), it is argued that new landscapes (hummocks) appear to be highly prone to erosion by abiotic agents, such "needle ice" action in winter and surface water flow in summer, since they consist of an incompact soil mass (Grab, 1997).

Tunnels and soil mounds produced by burrowing rodents make the soil prone to trampling and thus erosion (Gabet, 2000; Reichman and Seabloom, 2002; Hall and Lamont, 2003; Zhang *et al*., 2003). Trampling alters structural stability of soil because of compaction (Amiaud *et al*., 1998; Hall and Lamont, 2003), which in turn reduces infiltration. Since trampling also contributes to biomass reduction, dry and bare landscape can fracture and crush easily, producing soil aggregates that are readily transported by agents of soil erosion (Garland, 1987; Tuner, 1987; Tuner, 1999; Hall and Lamont, 2003).

1.4 Population dynamics of rodents

The causes of density fluctuations in rodents continue to be debatable in the ecological literature (Yocooz *et al*., 2001). However, it is believed that population dynamics in rodents are due to dynamic environmental factors, the biology of individual species, demographic factors, and ecological processes occurring individually or/and in combination within the ecosystem (Putman, 1984; Begon *et al*., 1996; Batzli *et al*., 1999; Lima *et al*., 2002). Based on the population size (low or high) in which the effect of each factor is detectable, these factors may be categorised into density-dependent and density-independent factors (Solomon, 1969; Belovsky and Joern, 1995; Oli and Dobson, 2001). Density-dependent factors include, for instance, food availability (habitat productivity), habitat suitability and predation rates, whereas density-independent factors include stochastic climate change and other forms of catastrophic factors such as fire. Belovsky and Joern (1995) argued that density-independent factors do not directly limit population size but determine the influences of density-dependent factors on a population.

Habitat productivity is most integral to the population dynamics of rodents since it predicts a population size that can be supported by the ecosystem (Hansson, 1979; Adler and Wilson; 1998; Malizia, 1998). For instance, tuco-tuco *Ctenomys talarum* populations occurred in large numbers where habitat productivity was relatively high while low densities were recorded in low productivity patches (Malizia, 1998).

Moreover, bank vole *Clethrionomys glareolus* densities increased significantly owing to the experimental addition of extra food (Batzli, 1981; Boutin, 1990). Under favourable conditions, rodents are able to invest more energy and time in breeding because resource competition is low, and therefore population sizes grow (Putman, 1984; Akcakaya, 1992). In contrast, lack of food resources results in physiological stress, which has negative effects on the population growth through poor breeding ability (Kudo, 1991). Juveniles may also be inhibited from reaching maturity and consequently die before they reproduce (Milner *et al*., 1999). The negative effects of dietary deficiencies on body condition was also reported in feral house mice *Mus musculus* on Marion Island (Smith *et al*, 2002)

Rodent population dynamics are also influenced by suitability of habitat, which in turn affects the reproductive output (Lima *et al*., 2002; Pillay, 2003). Suitable habitats are free from human disturbance that usually lead to habitat destruction and expose organisms to predators and lethal environmental conditions (Stevens and Boness, 2003). Highly suitable habitats have a positive effect on the population densities. For example, the availability of breeding sites increases survival probability of pups in microtine rodents (Malizia, 1998). Low mortality rates as opposed to high mortality rates in the highly human-disturbed habitats, encourage population growth (Stevens and Boness, 2003).

Predation risk is one of the critical factors that influence the population size of small mammals (Delany, 1974; Lima and Dill, 1990; Wauter, 2000). In the absence of predators, prey population numbers increase while intense predation leads to a decline in the local prey species (Danilowicz and Sale, 1999). The population of the house mice increased substantially after the removal of cats on sub-Antarctic Marion Island (Matthewson *et al*., 1994). Furthermore, field vole *Microtus agrestis* numbers declined in the presence of predators whereas numbers increased and remained comparatively high when terrestrial predators were experimentally excluded (Norrdahl *et al*., 2004). A similar relationship was also observed in population size of snowshoe hares *Lepus americanus* (Hik, 1995).

Stochastic events such as unusually heavy snowfall may also lead to population crashes in rodents (Akcakaya, 1992). Extreme regional climate changes affect microclimate, thereby creating thermoregulatory challenges for animals (Körner *et al*., 1997; Merritt *et al*., 2001). The strange conditions are sometimes so harsh that they lead to increased mortality rates (Merritt *et al*., 2001; Bertolino *et al*., 2001) because the inhabitants cannot adapt rapidly to keep pace with the changes in environmental conditions (Körner *et al*., 1997). For instance, deer mice *Peromyscus maniculatus* experienced highly significant decrease in population sizes during extremely cold periods compared to normal winters, while significantly high population sizes occurred during warm summer periods (Calisher *et al*., 2005).

1.5 The ice rat *Otomys sloggetti robertsi*

1.5.1 Phylogeny and description

Otomys sloggetti robertsi is a murid rodent endemic to the southern African Drakensberg and Maluti mountains and restricted to altitudes above 2500 m (Willan, 1990). It belongs to the subfamily Otomyinae, which has representatives living in the wettest (e.g. *Otomys angoniensis*, *Otomys irroratus* and *O. s. robertsi*) and driest (e.g. *Otomys unisulcatus*, *Parotomys brantsii* and *Parotomys littledalei*) areas of southern Africa (Skinner and Smithers, 1990). Adult ice rats weigh between 121-143g (Willan, 1990) and their head-body length is approximately 150-170 mm with the males tending to be about 10% larger than the females (Willan, 1990). The pelage is reddish brown with rusty-yellow at the side of the snout while the tail and ears are relatively short compared with the body size (Willan, 1990).

1.5.2 Physiological characteristics

The ice rat is poorly adapted physiologically to the low temperatures in its habitat. Its thermoneutral zone is at about 34˚C (Richter *et al*., 1997), which is much higher than the temperatures it encounters (Hinze and Pillay, 2006). Furthermore, the ratio of the metabolic rate and percentage thermal conductance (0.87) appears to be lower than expected for its cold environment (Richter *et al*., 1997). Since ice rats face high thermoregulatory challenges in alpine areas, they are likely to invest in activities (e.g. communal huddling, sun basking, flexible decision-making) that maximise thermoregulatory benefits because they do not hibernate (Schwaibold and Pillay, 2006). Additionally, ice rats show morphological adaptations such as short ears and tails that reduce heat loss (De Graaff, 1981; Willan, 1990), and modifications of the gut to facilitate increased food uptake in the small intestine (Schwaibold and Pillay, 2003).

1.5.3 Activity pattern and diet

Otomys s. robertsi is active during daylight and its activity is strongly influenced by prevailing weather conditions (Willan, 1990; Hinze and Pillay, 2006). Ice rat's aboveground activity profile is bimodal in summer, with peaks of activity in the morning and late afternoon. The ice rat retreats into its burrows when temperature and solar radiation are highest during midday. In winter, ice rats display a unimodal activity profile and devote more time to energy acquisition activities (Hinze and Pillay, 2006). Ice rats are exclusively herbivorous, feeding on wetlands plants such as *Limosella vesiculosa*, *Haplocarpha nervosa* and *Saniella verna* and herbaceous vegetation (*Gerenium multisectum)* occurring in the habitat (Willan, 1990; Schwaibold, 2005). Ice rats are central place foragers that travel a distance of about 50cm from the burrow entrance to forage (Schwaibold, 2005). Food is commonly consumed at the foraging patch in summer, while in winter food is more frequently carried back and consumed near the burrow entrance. It is suggested that this foraging strategy minimises exposure to low temperatures (Schwaibold, 2005).

1.5.4 Habitat use

Ice rats are abundant in areas with rocky surfaces but they avoid steep slopes, deep valleys and boggy areas (Willan, 1990). They nest in rock crevices when these are available, but usually construct complex underground burrow systems, which are situated at a depth of 20-40 cm and which may have up to 25 entrance holes (Hinze *et al.*, 2006). Environmental attributes such as soil type and moisture content do not influence the location of colonies, but instead the absence of short woody vegetation (*Helichrysum* spp.) and the presence of herbaceous (food) plants were good predictors of ice rat distribution (Schwaibold, 2005). Since ice rats are exclusively herbivorous, their association with food plants is logical.

1.5.5 Social organisation and population biology

Ice rats are colonial (Willan, 1990). Recent field observations in the Sani Valley, Lesotho, indicated that a colony consists of at least 4-16 individuals (Hinze, 2005), covering an area of up to 1200 m^2 (Hinze *et al*. 2006). Colony members compete aggressively for resources aboveground, but also huddle together in their burrows indicating spatial variation in social structure: solitary aboveground and social in the burrows (Hinze, 2005). Interestingly, Willan (1990) did not record agonistic interactions among free-living members of a particular colony, and maintained that ice rats lived in small family groups. In a recent study, however, Hinze (2005) found that ice rat colonies consist of several reproductively active males and females living in a promiscuous mating system.

The breeding season of ice rats occurs between October and March. Gestation is about 38 days with a mean litter size of 1.44 in captivity (Willan, 1990) and 2.14 in nature (Hinze, 2005). Newborn ice rats weigh between 10.6g and 12.2g, are semi-precocial and nipple-cling for the first few days after birth (Willan, 1990). They are weaned at 16 days of age (Willan, 1990) and emerge aboveground 3-4 weeks after birth (Hinze, 2005). Males reach sexual maturity after 14 weeks while females mature at about nine weeks (Willan, 1990).

Previous observations by Willan (1990) and Schwaibold (2005), as well as anecdotal reports by local Basotho shepherds in the Sani Valley, indicate that predation pressure on ice rats is minimal in summer and virtually absent in winter. This may be due to excessive hunting of predators by local human inhabitants (Willan, 1990). However, Schwaibold (2005) reported that ice rat colonies near Katse Dam are exposed to significantly higher levels of predation than other ice rat populations observed to date. In the absence of natural predators in many parts of its range, ice rat population numbers are apparently regulated by density-dependent mortality owing to limited resource availability during cold winters, as well as prolonged periods of snowfall and low winter temperatures (Willan, 1990; Lynch and Watson, 1992).

1.5.6 Interaction between people and ice rats

The interaction between humans and ice rats at Sani Top[1] and other locations in Lesotho has not been investigated previously. However, reports indicate that there is pronounced hunting of wildlife in the Lesotho highlands (Willan, 1990). Hunting has always been a traditional game and life skill for African shepherds since the prey is used for human consumption (S. Mokherane pers. com.). Interviews with local human inhabitants at Phatla-ea-poho within the Sani Top region confirmed the hunting and eating of ice rats, but other community members deny eating these rodents. In addition, there is some anecdotal evidence of Basotho herdsmen hunting ice rats in areas around Katse Dam (Willan, 1990; Schwaibold, 2005).

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[1] Sani Top is a region with different sub-villages while Sani Valley is a specific area where the experiments were conducted.

1.6 Rationale for my study

Lesotho is renowned for being a heavily eroded country, and different factors have been associated with soil erosion occurring in the highlands of Lesotho. For instance, anthropogenic activities (e.g. overstocking of livestock, harvesting woody plants) in combination with drought on the rangeland appear to be major mechanisms of soil erosion (Jacot Guillarmod, 1963; Showers, 1989; Talukdar, 1994; Quinlan, 1995; Phororo and Sibolla, 1999). Drought imparts hydro-physiological stress that retards reproduction in vegetation, which in turn reduce plant community recruitment and hence, the ground cover as well (Munns, 2002). Delegate vegetation (ephemerals and annuals) are more prone to high levels of mortality during periods of extended drought, thereby reducing the ground cover (Munns, 2002). Overstocking of about 100-300% was reported in many areas in the Lesotho highlands (Marake *et al*., 1998). Local human communities keep large numbers of goats and sheep for mohair and wool production (pers. obs.). Overstocking alone or together with other factors mentioned above significantly reduce vegetation cover, thereby leading to easily eroded landscapes. Additionally, the increase in human population and prevalence of poverty in the rural communities of Lesotho encourages direct dependency on woody vegetation for fuel (Letšela *et al*., 2003), which consequently destroys vegetation cover and causes land degradation (Q. Chakela and R. Seitlheko, pers. comm.).

Whereas anthropogenic causes of soil erosion dominating in the Lesotho Drakensberg are known, little attention has been paid to the effect of non-anthropogenic ecological processes on soil erosion here. Specifically, the contribution of the endemic ice rat to erosion is not known. Nonetheless, the local human inhabitants in Lesotho have raised a concern about the damage of the pastures by ice rats (pers. comm.), and more formally, Grab and Deschamps (2004) have implicated ice rats in soil erosion through their overgrazing and burrowing in the Sani Valley and other alpine areas of the Lesotho Drakensberg, which they associate with increasing ice rat population densities.

The increase in ice rat numbers may be associated with two factors. Firstly, there is minimal predation pressure on ice rats due to low numbers of predators in many parts of Lesotho (Willan 1990; Schwaibold 2005). Secondly, since ice rat population size is primarily regulated by cold winters (Willan, 1990), the warm winters of the past decade has yielded ideal thermal conditions for ice rat survival and increase in population size (Hinze, 2005; Schwaibold, 2005). While maximum temperatures have remained constant, minimum temperatures have increased by about 3˚C in the last five years (Hinze, 2005; Lesotho Meteorological Services data). Moreover, the number of days with snow cover has also dropped (Hinze, 2005; J. Khau pers. comm.). Warm and stable winter temperatures reduce mortality rates caused by thermoregulatory stress in small mammals during periods of harsh climate (Akcakaya, 1992; Moilanen *et al.*, 1998; Putman, 1984; Richter *et al.*, 1997), which may also be the case with ice rats (Hinze, 2005). A similar scenario whereby an increase in the numbers of house mice was related to an increase in temperature in for Marion Island has been previously reported (Smith and Steenkamp in Matthewson *et al.*, 1994). Furthermore, shorter winters have ensured longer growing seasons with more food available and hence less energy stresses (Avenant and Smith, 2003, 2004).

Ice rats are said to have colonised the Lesotho Drakensberg three million years ago (Taylor *et al.*, 2004). Therefore, it is most likely that ice rats and their food plants in terms of resource demand and utilisation may have co-evolved (Begon *et al.*, 1996). Co-evolution in ecological systems occurs between two coexisting species, such as prey and its predator and herbivores and plants in the ecosystem (Malcom, 1990; Takehito *et al.*, 2003). It occurs in such a way that any shift in the balance of the relationship between two species is counterbalanced through re-adaptation, creating equilibrium (Ehrlich and Raven, 1964). Therefore, assuming that an increase in ice rat population numbers leads environmental degradation (Grab and Deschamps, 2004) suggests that there is an ecological imbalance.

One confounding issue is the assumption that ice rats are the major faunal contributor to erosion. Since domestic livestock also causes soil erosion through overgrazing and trampling (Grab and Nusser, 2001), it is perhaps short-sighted to overlook the complexity of the ecological relationship between ice rats and livestock. Instead, a combined influence of these two groups may increase the levels of soil erosion as vegetation cover is negatively affected.

1.7 Objectives and aims

The main objective of the study is to quantify whether and how ice rats influence the vegetation characteristics of their habitat and whether these activities result in soil erosion. A second objective is to study the population size of ice rats in several locations in Lesotho in order to assess population persistence and size over time.

There are three aims for my study.

1) To measure the influence of ice rats on the vegetation and soil characteristics, and to distinguish between the impacts of ice rats from that of domestic livestock. For this, exclosures/plots were erected to measure the impact of: i) ice rats alone; ii) domestic livestock alone; and iii) both ice rats and livestock on soil loss and gain (which was used as a proxy for erosion). Vegetation cover, plant species cover, vegetation height, vegetation type frequency, and burrow density (when ice rats were not excluded) were measured in each exclosure/plot to establish differences in these parameters; exclosures in which both groups were excluded served as controls. Measuring the discrete and combined influence of ice rats and domestic livestock on their habitat may establish the contribution of ice rats to soil erosion in my study site and other parts of the Lesotho Drakensberg.
2) To establish ice rat numbers (colony size) at different locations in Lesotho by conducting monthly censuses of discrete colonies at three localities: Katse Dam, Oxbow and Sani Top. In addition, I compared my monthly census data with those of previous studies by Hinze (2005) and Pillay (unpublished data). It was anticipated that such censuses would indicate whether: i) population sizes fluctuate seasonally, as postulated by Willan (1990); and ii) patterns of population fluctuations are similar across locations and years.
3) To use questionnaire surveys to ascertain the perception and influence of human inhabitants on ice rats. Such questionnaires were designed to gain a historical perspective on: i) ice rat population sizes (i.e. whether ice rat numbers are increasing); ii) whether ice rats were suspected of contributing to habitat damage; and iii) whether ice rats were exploited as a food source. Interviews are highly recommended when a researcher seeks unknown facts about a matter under investigation from a particular target group (Creswell, 1994; Kitchen and Tate, 2000).

1.8 Predictions/Questions

1) Because of the combined effects of ice rats and livestock, vegetation cover and erosion will be worse in treatments when both animal groups are present than when one or both (control) are excluded.
2) If low winter temperatures regulate ice rat mortality rates, it is predictable that ice rat numbers will remain stable or increase over the year because of the recent

milder winters. However, different ice rat populations are subject to different predation pressures, and I asked whether population sizes in such areas (Katse Dam) would vary in comparison with other locations where predation is minimal or absent (Sani Valley, Oxbow).

3) Do the local human inhabitants in Lesotho believe that ice rat numbers have increased over the last two decades? Do they believe that ice rats contribute to habitat degradation and erosion? Do local inhabitants in Lesotho eat ice rats, and if so, to what extent?

Chapter 2. Materials and methods

2.1 The study areas

Most experiments were conducted in the Sani Valley in Lesotho. Two other study sites were also used: Katse Dam and Oxbow. The Sani Valley study site (29˚ 37′ S; 29˚ 14′ E) is located in the eastern Drakensberg of Lesotho at an altitude of 2900 – 2950 m above sea level. The Katse Dam site was situated about 7km southeast of the Katse Dam (29˚ 21′ S; 29˚ 32′E) in north eastern Lesotho at an altitude of approximately 2000 m. The Oxbow site was in the vicinity of Malibamatso River valley, Northeast Lesotho (28˚ 46′ S; 29˚ 39′E) at an altitude of about 2590 m.

The Drakensberg Maluti massive consists of an ancient basaltic plateau marked by steep-sloping valleys and extensive bogs. The recorded mean temperature is about 6 ˚C in winter (Grab, 1997), with an absolute minimum of -13 ˚C. Summers are mild (mean of 12˚C and absolute maximum of 22˚C) and wet, with about 70% of the annual precipitation, while winters are cold and dry with about 10% of the annual precipitation, dominated by snowfall (Grab, 1997; Grab and Deschamps, 2004). Mean annual precipitation exceeds 1200mm, decreasing towards central Lesotho (Grab and Deschamps, 2004). The subalpine vegetation consists of *Passerina-Philippia-Widringtonia* fynbos while the alpine area is characterised by woody species of *Erica* and *Helichrysum* with slopes and grasslands dominated by *Festuca*, *Danthonia* and *Pentaschistis* (Willan, 1990; Killick, 1963 in Grab and Deschamps, 2004). The wetlands in the Sani valley are dominated in most parts by flowering plants such as *Haplocarpa nervosa, Trifolium burchellianum, Saniella verna, Limosella vesiculosa, Cotula paludosa* and *Ranunculus multifidus* (Schwaibold, 2005).

Since most of the alpine areas of the eastern Drakensberg are inaccessible, Sani Top, Katse Dam area and Oxbow were selected as study sites for their accessibility as well as the presence of several ice rat populations. Moreover, some data are already available for these ice rat populations in the Sani Valley and Oxbow (Willan, 1990; Hinze, 2005; Schwaibold, 2005) and will be used for comparison of my findings. Three experiments were conducted, as described below.

2.2 Experiment 1. Exclosure experiments

Exclosure experiments were set up in the Sani Valley from January to December 2006 to quantify the impact of ice rats and domestic livestock. Sampling was not conducted in August 2007 because of heavy snowfall. Three replicates (referred to here as sites), containing four 4 x 4 m (16 m^2) plots were marked off in the Sani Valley in three different areas with very similar geology and vegetation. The minimum distance between sites was about 150 m; and their relative positions are shown in Figure 1.

For each site, I identified a large flat and open space in Sani Valley to ensure uniform slope. Then, I ensured that the soil and vegetation composition were also uniform by recording the soil type (i.e. dark humus-rich loam soil was preferred to stony mineral soil; see Hinze *et al*., 2006) and dominant vegetation type. The minimum distance between plots was 70 m in each of the three sites respectively. The four plots in each site were assigned to one of three treatments and a control, as described below.

1) Ice rats only - domestic livestock but not ice rats were excluded from plots by erecting a 1m high wire mesh fence around the 16m^2 plot. These plots were situated in an area populated by ice rats. The wire mesh fence was raised about 20cm from the surface to ensure that ice rats could access the plot beneath the fence.

2) Livestock only – these plots were marked with corner pegs, connected with string to mark the perimeter of the plot, at 50cm above the ground. The plots were located in areas without ice rat colonies and at distances that ice rats could not cover easily (i.e. by spatially isolating the plot). To achieve this, a survey of the location of ice rat colonies was carried out in four cardinal directions, such that the four sides of the plots were at least 70m away from areas inhabited by ice rats. Ice rats are central place foragers and therefore do not travel long distances (usually <1m) to access foraging patches (Schwaibold, 2005).

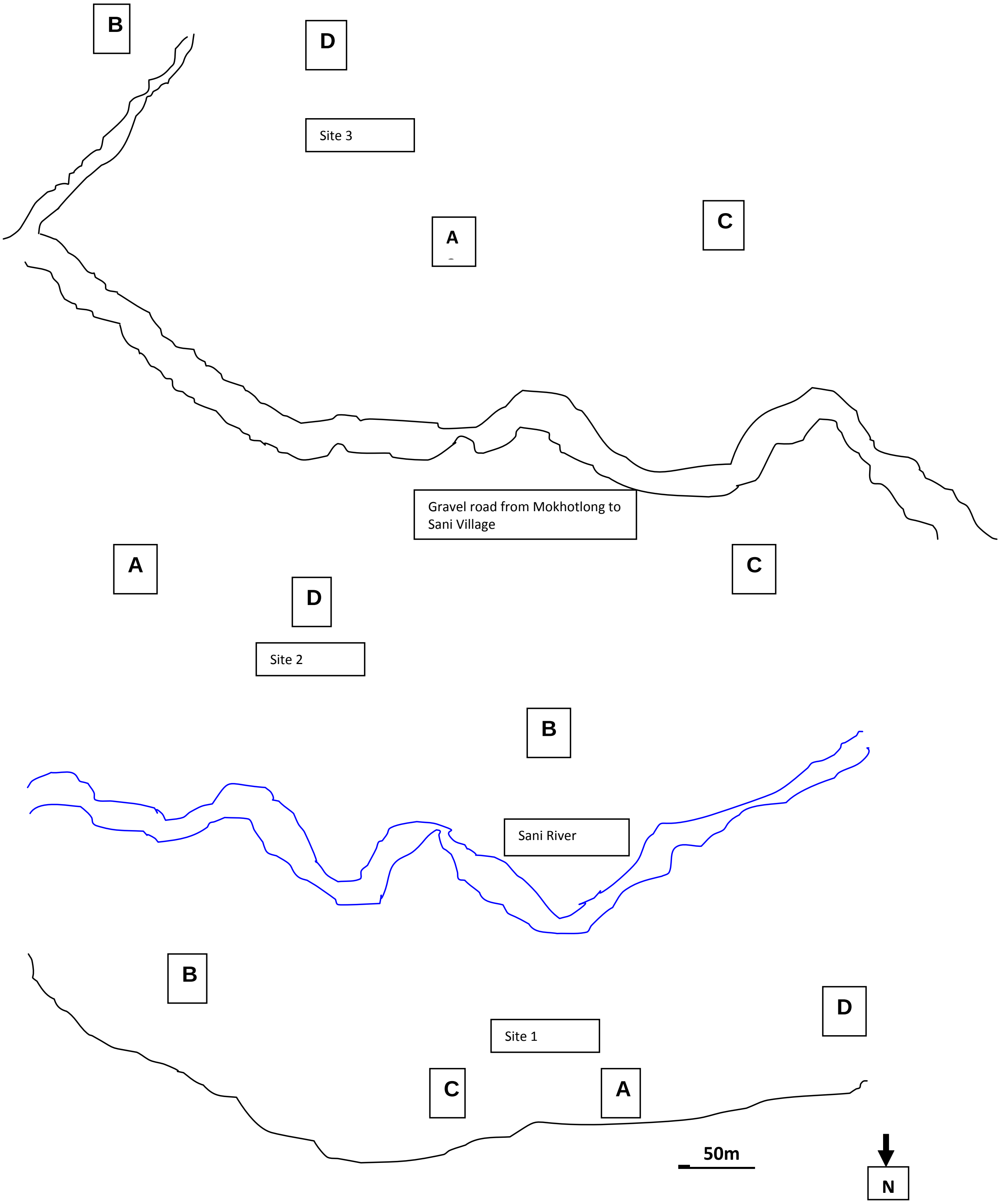


Figure 1. Map showing the position of experimental plots (A-D) in three sites in the Sani Valley, Lesotho. A=ice rats only; B=livestock only; C=ice rats and livestock; D=control.

Another criterion for the location of these plots was the absence of big rocks that may provide domiciles for ice rats (Willan, 1990). No ice rat droppings and attempted burrow diggings were detected in these plots over the year and therefore ice rats did not access these plots. These plots were accessed by domestic livestock throughout the year.

3) Ice rat and livestock present – these plots were also marked with string and pegs, but were located in an area inhabited by ice rats and was accessible to domestic livestock so that a combined impact of these animals could be established. The string was tied to corner pegs at the height of 50cm above the ground.

4) Control - ice rats and domestic livestock absent – these plots were located in areas that were not inhabited by ice rats. A 1m high wire mesh was erected to exclude domestic livestock. About 20 cm of the base of the wire fence was folded outward and held securely on the ground with rocks to prevent ice rats from accessing the plot; ice rats did not access these plots throughout the study.

2.2.1 Measurements: vegetation and burrows

The plots were not all marked in the same month due to inclement weather conditions and damage by the local inhabitants. The first and second sets of experimental plots were marked in November and December 2005 respectively, but I was able to collect the data consistently from January when the third set was also marked and guards were available. Therefore, I analysed the data that showed change from January to December 2006. A semi-random sampling method was used to sample vegetation in the plots. Using a 0.5 x 0.5 m wooden frame quadrat, I used the "over-shoulder-toss" method to position the wooden frame within the boundaries of the plot (Greig-Smith, 1964; Kent and Coker, 1996; Bullock, 1997; Hill *et al*., 2005). To ensure that the quadrats did not overlap substantially, I kept changing the position from which I threw the sampling quadrat over the plot. Ten random quadrats were sampled within each plot, in which I recorded vegetation type frequency (percentage of quadrats in which a species occurred), overall vegetation canopy cover, percentage species cover and average height (in mm, excluding roots) of all individuals of identified plant species. The percentage vegetation canopy cover was estimated using the vegetation cover classes adapted from Braun-Blanquet scale (Table 1; Kent and Coker, 1996; Hill *et al*., 2005). To obtain the percentage cover value for each quadrat, I first asked whether the cover was more or less than half of the quadrat (50%). If more, the next question was whether percentage cover was more or less than 75% and so on. If it was less, I estimated whether vegetation cover was less or equal to 25%, and so on. The percentage canopy cover of individual plant species was also estimated using the procedure mentioned above but low vegetation cover categories (i.e. 1 to 5% and less) were used (see Kent and Coker, 1996; Hill *et al.*, 2005).

Table 1. Braun-Blanquet classes (adapted) that were used to estimate vegetation canopy cover in experimental plots in the Sani Valley.

Class	**Cover**
0	**0%**
1	**5%**
2	**25%**
3	**50%**
4	**75%**
5	**100%**

The density of ice rat burrow entrances per plot was calculated in areas colonised by ice rats. For this, the number of burrow entrances was counted monthly and divided by the area of the plot (i.e. 16m^2). All vegetation measurements were taken at monthly intervals together with burrow counts.

2.2.2 Measurements of changes in soil levels

Changes in soil levels (i.e. removal and deposition of soil) in each plot were determined by measuring soil loss and gain from March 2006 to November 2006. Again, no data were collected in August 2006 due to heavy snowfall. For this, 60 cm metal droppers were used (E. Witkowski. pers. comm.). The droppers were marked at the 40 cm length by sawing to a depth of 3 mm, and taping the point above the mark with insulation tape. In each plot, five droppers were hammered into the ground up to the level of the insulating tape mark. A dropper was situated about 50 cm away from each of the four corners of a plot along the two diagonals, and a fifth dropper was positioned in the centre of the plot. This arrangement of the droppers maximised spatial variation within the plot and ensured that measurements taken from each dropper was independent of readings from the other droppers in the plot. Thus, a total of 60 droppers were used in the study (5 droppers x 4 plots x 3 sites). Thereafter, I measured changes in the gap between the bottom of the insulation tape and the ground. The increase in the gap indicated soil loss. After measuring the exposed section, the dropper was hammered into the ground to the level of the insulation tape mark, so that changes in the soil level could be detected later. If the soil level increased (i.e. covered the tape), the excess soil was removed by hand from one side of the dropper and the increase in soil was measured on the opposite side. After measuring the height, all the soil was cleared away to facilitate measuring soil levels later. Soil loss was recorded with a negative value and soil gain with a positive value.

2.2.3 Data analysis

Prior to analyses, all proportion data sets were arcsine transformed to meet the assumptions of normality. To compare the monthly changes in percentage vegetation cover within and between sites, a mixed model nested ANOVA was used, in which sites were nested within plots. Since there was no difference between particular experimental plots across sites, the data sets of the different sites for the same treatment/control were pooled. Thereafter, a repeated measures ANOVA was the used to analyse changes in vegetation parameters by plots (independent variable) over the months (repeated measures variable). Tukey post hoc tests were used to assess individual differences when $\alpha \leq 0.05$.

A General Regression Model (GRM) was used to determine the association between burrow density and vegetation cover of two plots: ice rats only and ice rat and livestock. The plot type was the independent variable in the model. I also ran a paired-t test to statistically compare the number of burrows between the plot types.

The soil loss/gain data were difficult to analyse because of the high number of zero values; no data were collected in June because of snow fall. For the analyses, I added the data for all droppers per plot per month, so as to account for zero values and also to avoid pseudoreplication. Thereafter, comparisons between sites and between plots were analysed using a Kruskall-Wallis test. Dunn's post hoc analysis was used to identify specific differences.

2.3 Experiment 2. Population census

I investigated whether ice rat population densities changed in different localities through 2006. This experiment was feasible because ice rats are known to occupy the same colonies for more than a year (Hinze, 2005). It was reported that the ice rat population near Katse Dam experiences comparatively high levels of predation while in the Sani Valley and Oxbow predation risk is negligible (Willan, 1990; Schwaibold, 2005). Therefore, my study provided an opportunity to assess how ice rat numbers change due to climatic conditions alone or in combination with predation.

The ice rat population censuses were conducted from January to December 2006 in the Sani Valley and March 2006 to December 2006 at Oxbow and Katse Dam. Populations were sampled in all the months except August 2006 when a heavy snow covered the whole Drakensberg. Three colonies were monitored in the Sani Valley and Oxbow, while only one colony was studied at Katse Dam because of the difficulty of locating ice rats there. Due to the uneven spatial distribution of ice rats in the different localities, colonies occupying different sized areas were studied. All the colonies selected for study in the Sani Valley and Oxbow occupied a surface area of approximately 30x30 m, whereas the colony studied at Katse Dam occupied a surface area of approximately 20 X 10 m.

In the Sani Valley, one colony (designated Colony A; 29˚ 34΄ S; 29˚ 16΄ E) was situated across the Sani River, about 20m northwest of Site 1 (Figure 1). The area comprised short grass species (*Festuca caprina*, *Danthonia* and *Pentaschistis*), interspersed with patches of the shrubby Karroo species, such as *Chrysocoma ciliata* (Grab and Deschamps; 2004). A second colony (designated Colony B; 29˚ 33΄ S; 29˚ 14΄ E) was located 60m from Colony A, about 4 km from Sani Village and had a similar vegetation composition to Colony A. A third colony (designated Colony C; 29˚ 33΄ S; 29˚ 16΄ E) was located 55 m from the Colony A, along Sani River. *Helichrysum* shrubs together with wetland grasses dominated the vegetation in this colony as it was situated near a bog.

The study colonies at Oxbow, Motete Valley (28˚ 54΄ S; 28˚ 47΄ E) were all located in a linear order along a streamlet emerging on the extreme left hand wall of the valley (just below a tarred road from Butha Buthe to Mokhotlong; about 5km from Letseng-la-Draai diamond mine). The first colony here (designated Colony D; 28˚ 53΄ S; 28˚ 48΄ E) was located nearest to a water source. A second colony (designated Colony E; 28˚ 54΄ S; 28˚ 48΄ E) was situated 65m downstream from Colony D. A third colony (designated Colony F; 28˚ 52΄ S; 28˚ 48΄ E) was located about 54 m from Colony E. All three colonies were located in typical valley vegetation type described above.

The colony in Katse Dam (designated Colony G; 29˚ 20΄ S; 28˚ 26΄ E) was situated about 8 km southeast of the dam. This colony was located on the right hand side of gravel road leading to Katse Bridge and at the outskirts of the Sephareng Village. Ice rats nest in the surrounding rock (basalts) and in underground burrows at the location. The presence of the bog nearby appeared to have limited dispersion of this colony (see Willan, 1990), since ice rats were not ubiquitous like in other study areas. Due to the higher moisture content in the bog, the wetland vegetation persists longer or recovers quickly in the absence of frost and therefore, ice rats are able to forage for a larger proportion of the year, even during dry seasons.

All colonies selected for study were located on a flat, open space. The boundary of each colony studied was marked off with pegs and stones in four corners to form a rectangle. The boundary was determined mainly by the presence of the active burrows and type of the vegetation preferred by ice rats (Schwaibold, 2005). Densely shrubby areas were avoided as this impeded direct observation of the ice rats.

A point count method was employed during the census of each colony (as described by Gibbons *et al*., 1997; Southwood and Henderson, 2000; Hill *et al*., 2005). Individual ice rats that were present aboveground were counted from a raised location about 5 m from a colony. Within 5-10 minutes, ice rats became habituated to the human presence, and started their normal activity thereby allowing for the counts. The counts were done once every 10 minutes for one hour during the peak activity times: in summer, from 06h30 (sunrise) to 09h30 and from 16h00 to 18h30, and between 07h30 and 10h30 and 15h30 and 17h30 in winter (Hinze, 2005). Observations were made using 10X50 binoculars. To avoid overestimating the number of animals, the average of six counts done in 1 hour was calculated to estimate the number of animals per colony. The area of an individual colony was to hectares and then the direct proportion was used to calculate the number of ice rats per hectare. During each census, I obtained measurements of ambient temperatures in each colony in order to establish a relationship between population size and temperature. Ground temperature per month was measured with a thermometer placed horizontally on the ground while another thermometer was fixed vertically to a wooden bar with rubber bands to measure air temperature at a height of about 0.5 m. However, due to damage of equipment (thermometers) ground temperature data were incomplete and therefore only air temperature, measured during the one hour census, was used.

2.3.1 Data analysis

Seasonal changes in colony size were analysed using a repeated measures ANOVA, in which locality was the independent factor and monthly census readings were the repeated measures variable; only those months for which data existed for all three localities were used in analyses. The different colonies in each locality were not considered as an independent factor because of the unbalanced design: three colonies each were observed in the Sani Valley and Oxbow and only one colony was at Katse Dam. The Tukey post hoc test was applied to detect specific differences between localities and for each month. A linear regression analysis was used to assess whether there was a relationship between the colony size and air temperature. I also compared the results for ice rat population density (per hectare) at Oxbow and Sani Valley with those of previous studies conducted in the same localities: in the late 1980's at Oxbow (Pillay, unpublished) and in the early 2000s (Hinze, 2005).

2.4 Experiment 3. Interviews with local community members

Oral interviews using questionnaires consisting of closed questions were administered randomly to different members of communities in different study sites. Interviews were conducted at Sani Village, Matsoaing, Makhapung, Thabang Village and Mapholaneng for the Sani Top region, and Ha Lejone, Khokohoba, Ha Ramokoatsi, Sephareng, Ha Seshote in Katse Dam. No human settlements were located near the Motete Valley and thus I interviewed people from areas along the road from Butha Buthe to Mokhotlong, including the Oxbow village.

The eight interview questions (Figure 2) were designed with the help of science education specialist Ms. Megan Doidge (School of Education, University of the Witwatersrand) and they were translated into Sesotho, as it is a vernacular of the target groups – rural highland communities in Lesotho. The questionnaires were administered using oral interviews because most of the interviewees were illiterate. I wrote down their responses, and graded the responses for questions which required multiple responses (e.g. Question 2; Figure 2). I sampled a wide group of people, taking into account the gender, age and length of stay in the local area. For instance, questions that related to historical changes about the climate and changes in the population size of ice rats (Questions 3 and 4; Figure 2) were directed at older people in the community.
Ice rat is ubiquitous at Sani Top and therefore, there was no need to show the interviewees a picture of an ice rat as was the case in Oxbow and Katse Dam.

2.4.1 Data analysis

Since some age classes were under-represented in my study (i.e. young and old), I used the occupation of the participants in further analyses. People were assigned to three occupation categories: herders, workers (business people) and other. Since the number of interviewees differed among localities, the count data for questions requiring multiple responses were divided by the number of people interviewed in each locality. The resulting proportions were arcsine-transformed, and a Generalized Linear Model (GLM) with an ordinal multinomial error structure and a probit link function was applied to each of the questions where a graded response was required. For the GLM, the two independent variables were locality and occupation, the number of responses for each choice in the multiple response questions was the response variable and proportion of responses was the count variable. Since there was no significant difference between the localities, occupations and locality x occupation (Wald statistics; Table 2) for the six questions tested, the data for each question were pooled and a chi-

Sex …………Age……………...Length of stay in the area……………..years

Occupation………………..Frequency of encounters with ice rats…………………

- Please tick one phrase that you believe is the right answer for each question
- Do not write your name on the questionnaire

Questions

1. **What is your occupation?**
    a) Herders b) Working c) Nothing
2. **How often do you see the ice rats?**
    a) Not seen at all b) Rarely seen c) Moderately seen d) Abundant
3. **Have ice rat numbers increased over the past years?**
    a) No increment b) Decreased c) Moderately increased d) Dramatically increased
4. **Have temperatures increased in the past years?**
    a) No change b) Decreased c) Moderately increased d) Continuously increasing
5. **Has levels of snowfall/cover decreased or increased in the past?**
    a) No change b) Decreased c) Increased d) Highly increased e) Dramatically increased
6. **Which areas in the landscape seem to be more favourable for ice rats?**
    a) Sloping area b) Flat and rocky areas c) Farming land d) Wet valley floors e) Other
7. **What is the impact of the ice rats on human life and livestock?**
    a) Destroy vegetation b) Increase drainage c) Cause soil erosion d) Compete strongly with livestock for food resource e) No impact
8. **How do people influence the life of these animals- abundance and survival?**
9. **Does the community use ice rat for any vital purpose?**

Figure 2. Specimen questionnaire used to obtain the responses of local human inhabitants in three localities in Lesotho.

square (χ^2) contingency test applied on the totals of each question; pair-wise comparisons were made to test specific differences between responses for each question.

Two of the eight items in the questionnaire did not require multiple responses (i.e. Question 8 and 9; Figure 2). To analyse these, the responses were transcribed and translated from Sesotho into English for reporting purposes. Only the relevant information was picked out and reported in prose while irrelevant information was discarded. For instance, some interviewees did not understand the concept of the mutual relationship between people and animals (e.g. Question 9) in an ecological context and therefore denied that ice rat and people interact.

Table 2. Wald statistics for six interview questions with multiple-responses.

Question		**Degrees of freedom**	**Wald**	**P-value**
a) How often do you see ice rats?	Locality	2	1.42	0.490
	Occupation	2	0.51	0.774
	Locality x Occupation	4	0.073	0.999
b) Have the ice rat numbers increased?	Locality	2	0.00	0.999
	Occupation	2	0.00	0.999
	Locality x Occupation	4	0.08	0.999
c) Have the temperatures increased in the past years?	Locality	2	0.42	0.812
	Occupation	2	0.01	0.995
	Locality x Occupation	4	0.04	0.999
d) Have the snowfall/cover level increased in the past years?	Locality	2	0.74	0.690
	Occupation	2	0.05	0.975
	Locality x Occupation	4	0.24	0.993
e) Which areas are more favourable for ice rat?	Locality	2	0.00	0.998
	Occupation	2	0.04	0.980
	Locality x Occupation	4	0.41	0.982
f) What is the impact of ice rats on human life and livestock?	Locality	2	0.94	0.954
	Occupation	2	0.21	0.901
	Locality x Occupation	4	0.53	0.970

Chapter 3. Results

3.1 Exclosure experiments

3.1.1 Changes in vegetation cover

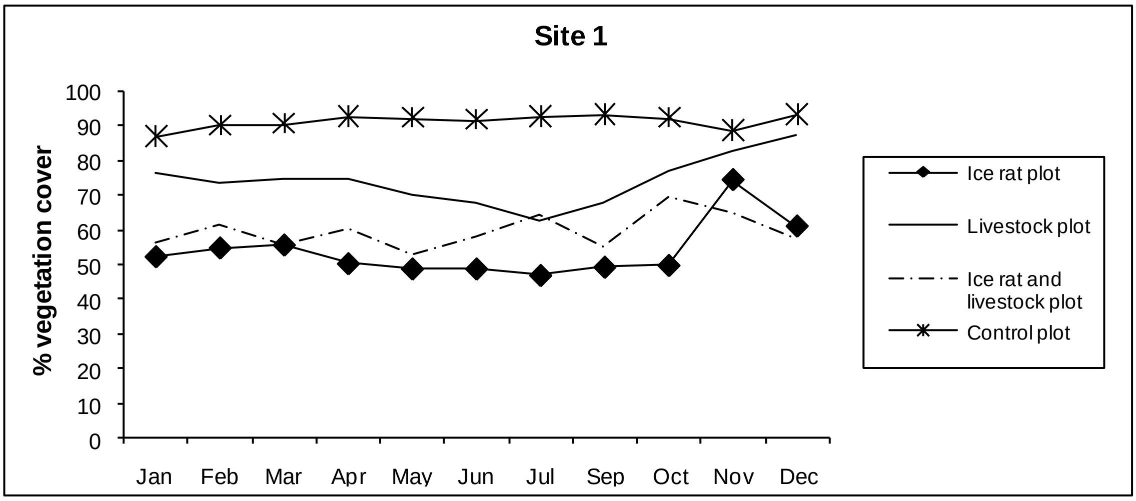
Vegetation cover was highly significantly different among the experimental plots ($F_{3,\,8} = 30.84$; $p < 0.001$). Post hoc tests revealed that control plots had the greatest amount of vegetation cover than the other plots (Figure 3). The ice rats only plots had the lowest level of cover, closely followed by the ice rat and livestock plots. The livestock only plots occupied an intermediate position. Interestingly, vegetation cover was not influenced by month ($F_{7,\,56} = 0.73$; $P=0.645$) or the interaction between month and plot ($F_{21,\,56} = 0.73$; $P=0.645$).

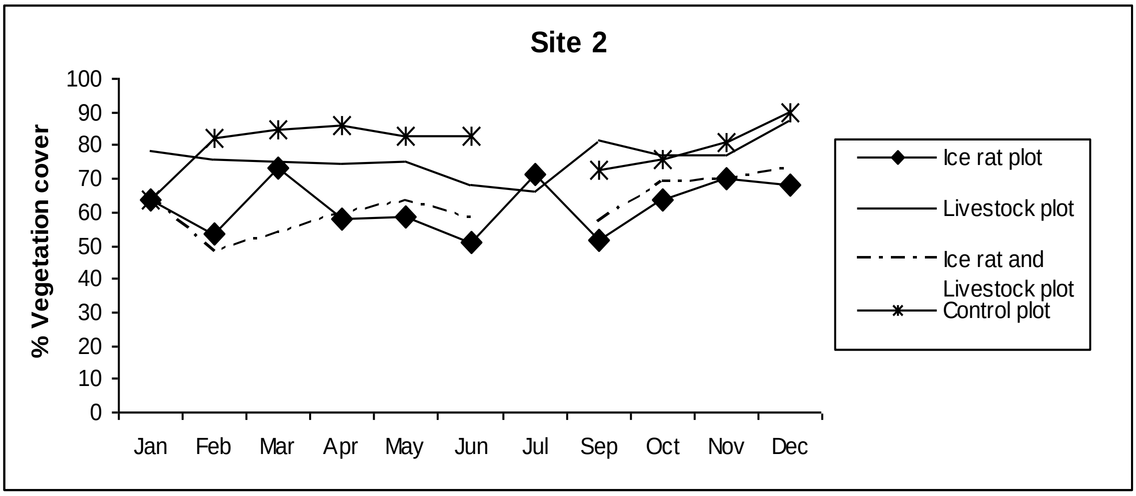
3.1.2 Vegetation type frequency

The individual plant species recorded within the plots in my study area were grouped into four categories – grasses, wetland sedges, herbaceous plants and *Helichrysum* shrubs. The frequency of grasses had very low variance within and between plots. For the remaining groups, there were no plot differences (wetland sedges: $F_{3,\,8} =1.51$; $p = 0.283$; herbaceous plants: $F_{3,\,8} =1.05$; $p = 0.422$; *Helichrysum*: $F_{3,\,8} =1.64$; $p = 0.255$). However, there were significant monthly changes in frequency (wetland sedges: $F_{10,\,80}=9.00$; $p < 0.001$; herbaceous plants: $F_{10,\,80}=10.84$; $p < 0.001$; *Helichrysum*: $F_{10,\,80}=8.49$; $p < 0.001$). The post hoc tests showed that frequency dropped off significantly in the winter months and was highest during the growing season (Table 3).

3.1.3 Vegetation height

Similarly to vegetation frequency, individual plants were grouped into four categories to analyse vegetation height. Grass height differed significantly among the plots ($F_{3,\,8} = 14.61$; $p = 0.001$), with grass being significantly taller in the control plots than the other plots (Figure 4a). There were no plot effects for wetland sedges ($F_{3,\,8} = 1.65$; $p = 0.381$; Figure 4b)**.** Highly significant plot differences were noted in the height of herbaceous plants ($F_{3,\,8} = 28.41$; $p < 0.001$) and in this case, post hoc tests revealed that herbaceous were significantly shorter in ice rats only plots compared to the other plots and significantly taller in the control plots (Figure 4c). *Helichrysum* height also significantly differed among the plots ($F_{3,\,8} = 14.61$; $p = 0.001$; Figure 4d). All four categories of plants showed significant monthly changes in height (grass: $F_{10, 80} = 41.38$; $p < 0.001$; sedges: $F_{10, 80} = 10.55$; $p < 0.001$; herbaceous plants: $F_{10, 80} = 106.70$; $p < 0.001$; *Helichrysum*: $F_{10, 80} = 39.36$; $p < 0.001$), reflecting seasonal differences: tallest in summer and shortest in winter (Figure 4).





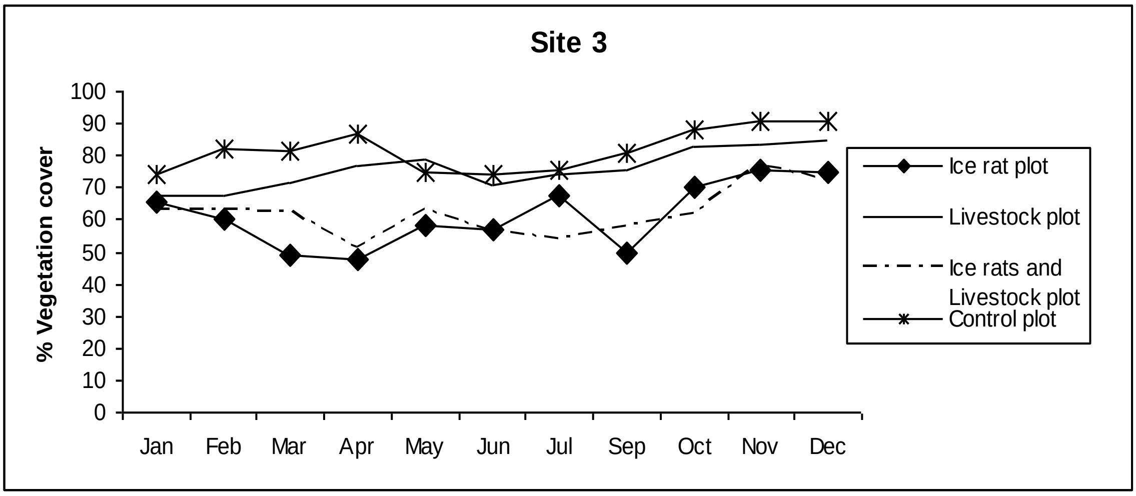


Figure 3. The mean percentage vegetation cover in three four experimental plots in three sites Sani Valley, 2006. Vegetation cover was not sampled in the ice rats only and control plots of site 2 in July due to heavy snow cover.

Table 3. Mean (±SE) frequency of four plant types in four experimental plots in the Sani Valley, 2006. Frequency is expressed as the percentage of quadrats in which the plants appeared. Sites are distinguished because of a lack of statistical differences (see text).

Plot	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Sep**	**Oct**	**Nov**	**Dec**
a) Grass											
Ice rats only	90 (0)	90 (0)	50 (0)	90 (0)	83 (6)	56 (0)	90 (0)	90 (0)	90 (0)	90 (0)	90 (0)
Livestock only	90 (0)	90 (0)	50 (0)	90 (0)	90 (0)	56 (0)	90 (0)	90 (0)	90 (0)	90 (0)	90 (0)
Ice rats &Livestock	90 (0)	90 (0)	50 (0)	90 (0)	90 (0)	37 (18)	90 (0)	90 (0)	90 (0)	90 (0)	83 (5)
Control	90 (0)	90 (0)	50 (0)	83 (6)	90 (0)	37 (14)	90 (0)	90 (0)	90 (0)	90 (0)	90 (0)
b) Sedges											
Ice rats only	36 (6)	35 (3)	29 (4)	42 (9)	35 (7)	31 (9)	22 (3)	27 (8)	32 (6)	31 (3)	27 (5)
Livestock only	39 (2)	37 (3)	31 (1)	40 (3)	37 (2)	33 (2)	25 (0)	38 (2)	35 (2)	38 (4)	37 (4)
Ice rats &Livestock	35 (8)	40 (9)	22 (2)	42 (4)	19 (11)	8 (8)	0 (0)	8 (8)	31 (6)	29 (1)	33 (5)
Control	29 (5)	29 (6)	19 (1)	30 (4)	25 (5)	25 (5)	13 (8)	21 (6)	25 (5)	22 (11)	36 (4)
c) Herbaceous											
Ice rats only	29 (7)	33 (1)	24 (3)	3 (1)	28 (4)	24 (2)	22 (2)	29 (5)	36 (5)	35 (1)	34 (1)
Livestock only	34 (7)	31 (5)	25 (5)	4 (3)	33 (4)	33 (2)	31 (1)	34 (3)	33 (5)	32 (2)	38 (1)
Ice rats &Livestock	33 (2)	31 (0)	25 (1)	3 (0)	25 (3)	22 (2)	15 (7)	31 (1)	31 (0)	33 (2)	33 (2)
Control	41 (1)	40 (2)	29 (1)	3 (3)	36 (2)	35 (2)	19 (9)	34 (2)	38 (3)	36 (1)	38 (1)
d) *Helichrysum*											
Ice rats only	66 (14)	65 (15)	44 (5)	73 (16)	74 (15)	65 (13)	49 (6)	64 (14)	66 (14)	62 (8)	61 (9)
Livestock only	60 (14)	54 (8)	41 (6)	52 (9)	60 (15)	52 (9)	47 (4)	49 (3)	52 (9)	52 (5)	49 (7)
Ice rats &Livestock	77 (6)	75 (7)	50 (0)	83 (6)	90 (0)	90 (0)	37 (18)	90 (0)	83 (6)	75 (7)	78 9 (11)
Control	60 (15)	60 (15)	39 (5)	57 (16)	60 (14)	53 (8)	24 (12)	58 (16)	50 (10)	48 (8)	52 (9)

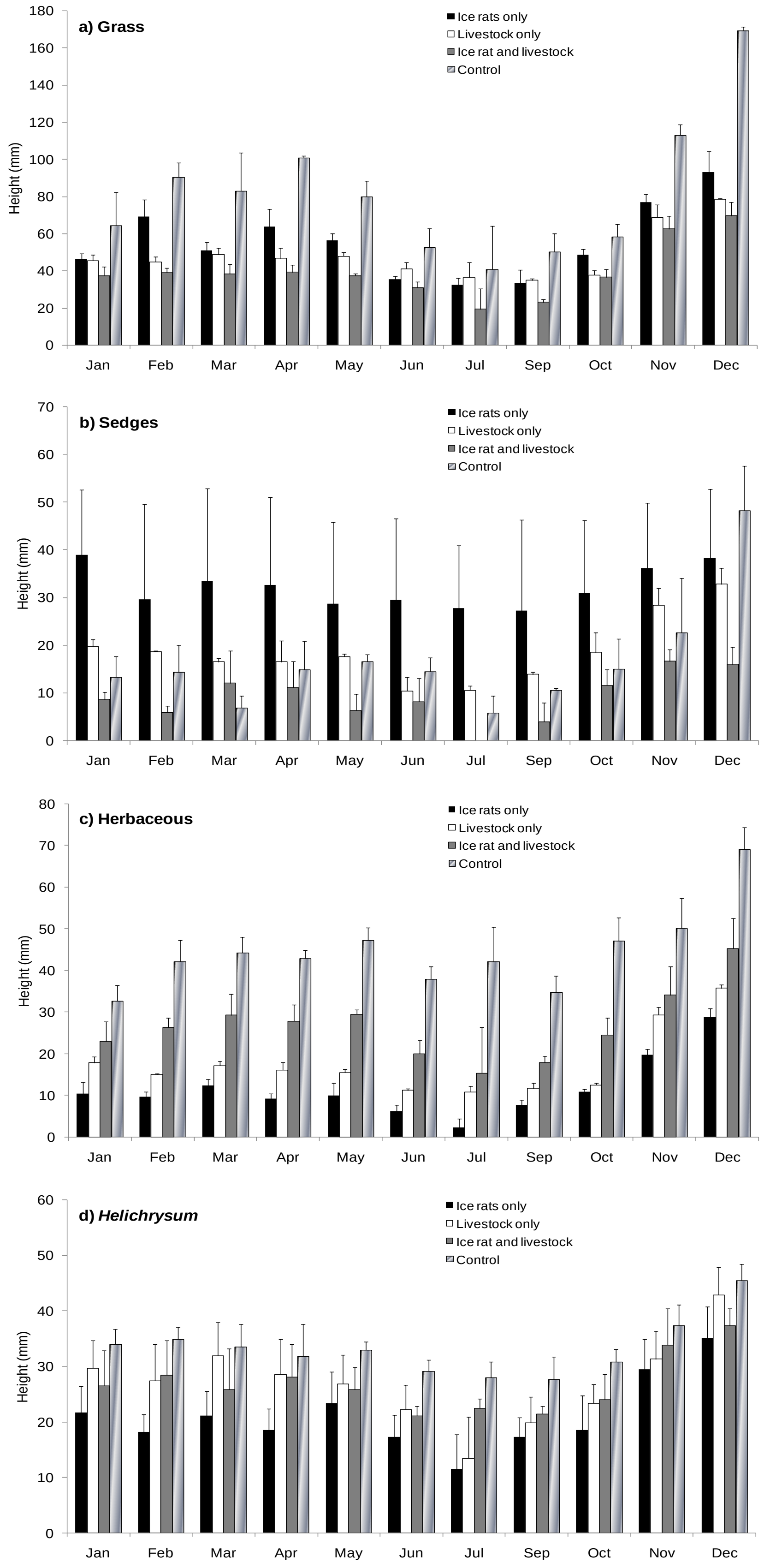
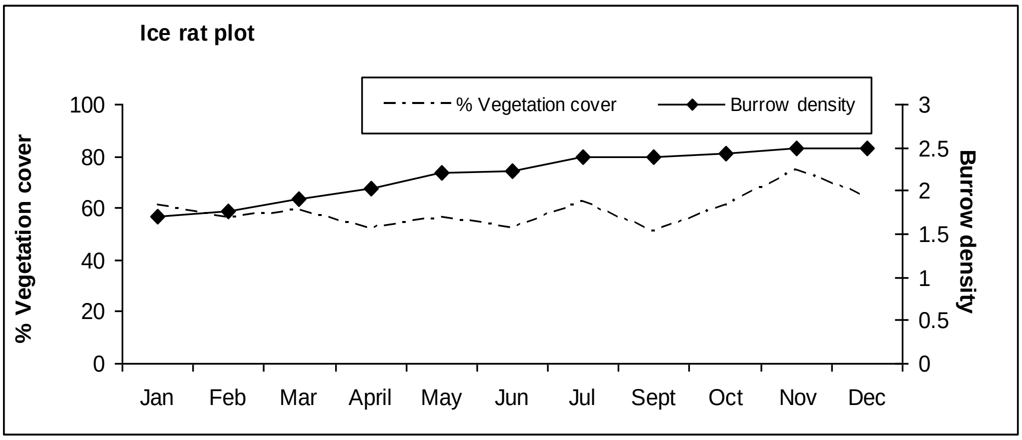


Figure 4. Mean (±SE) heights of a) grass, b) sedges, c) herbaceous vegetation and d) *Helichrysum* in four experiment plots from three sites in Sani Valley, 2006.

3.1.4 Burrow density

There were significantly more burrows in the ice rat plots than in the ice rat and livestock plots ($t_{10} = 42.61$; $P<0.001$; Figure 5). In addition, there was a significantly stronger relationship between the number of burrows and vegetation cover in the ice rat only plots ($F_{2,\,19} = 130.0$; $p < 0.001$) than in the ice rat and livestock plots ($F_{2,\,19} = 1.55$; $p = 0.238$). Generally, the increase in ice rat burrows was associated with a decrease in vegetation cover in the ice rats only plots ($r = -0.77$; $p<0.05$), but there was no significant association between these parameters in the ice rat and livestock plots ($r = 0.34$; $p>0.05$).



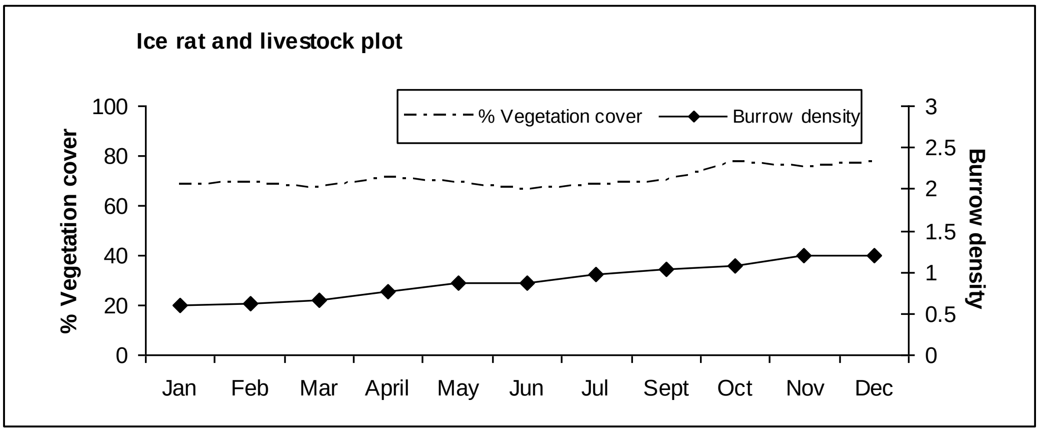


Figure 5. The relationship between the burrow density and % vegetation cover in the ice rat plot and the ice rat and livestock plot at Sani Valley, 2006.

3.1.5 Measurement of soil loss/gain the plots

My results indicated no significant differences between sites in the levels of soil gain and loss ($H_{2,\,60} = 1.50$; $p = 0.473$). However, there was a significant plot effect ($H_{3,\,60} = 15.30$; $p = 0.001$; Figure 6), with the ice rat only plots showing the greatest variation in soil loss and gain. There was almost no soil gain or loss in the control plots.

3.2 Population census

There was no significant difference in colony size between the localities ($F_{2, 4}$ = 0.90; p= 0.474; Figure 7). However, there was a significant difference in colony size between months of the year ($F_{8, 32}$ = 6.02; p <0.001), with colony sizes in colder months (June, July) and early breeding season (September, October) being significantly reduced compared to the warmer months (March - May). There was no significant relationship between air temperature and colony size: Sani Valley (colony A: R=0.139, p=0.721; colony B: R=0.237, p=0.539; colony C: R=0.124, p=0.751); Oxbow (colony D: R=0.287, p=0.0.541; colony E: R=-0.042, p=0.914; colony F: R=0.240, p=0.535); and Katse Dam (colony G: R=0.437, p=0.239).

I compared the results for ice rat population density (per hectare) at Oxbow and Sani Valley with those of previous studied conducted in the same localities in the late 1980's at Oxbow (Pillay, unpublished) and in the early 2000's (Hinze, 2005). It is apparent that ice population density has increased substantially over the last decade or so. While Pillay (unpublished) and Hinze (2005) recorded a maximum of 110 ice rats per hectare, my study indicates a threefold increase in ice rats per hectare in summer (Table 4). Even during winter, my data collected at Oxbow indicates a four-fold increase in ice rat population density since Pillay's study in the 1980's, although there was little difference between population sizes in my study and that of Hinze (2005) at Sani Top.

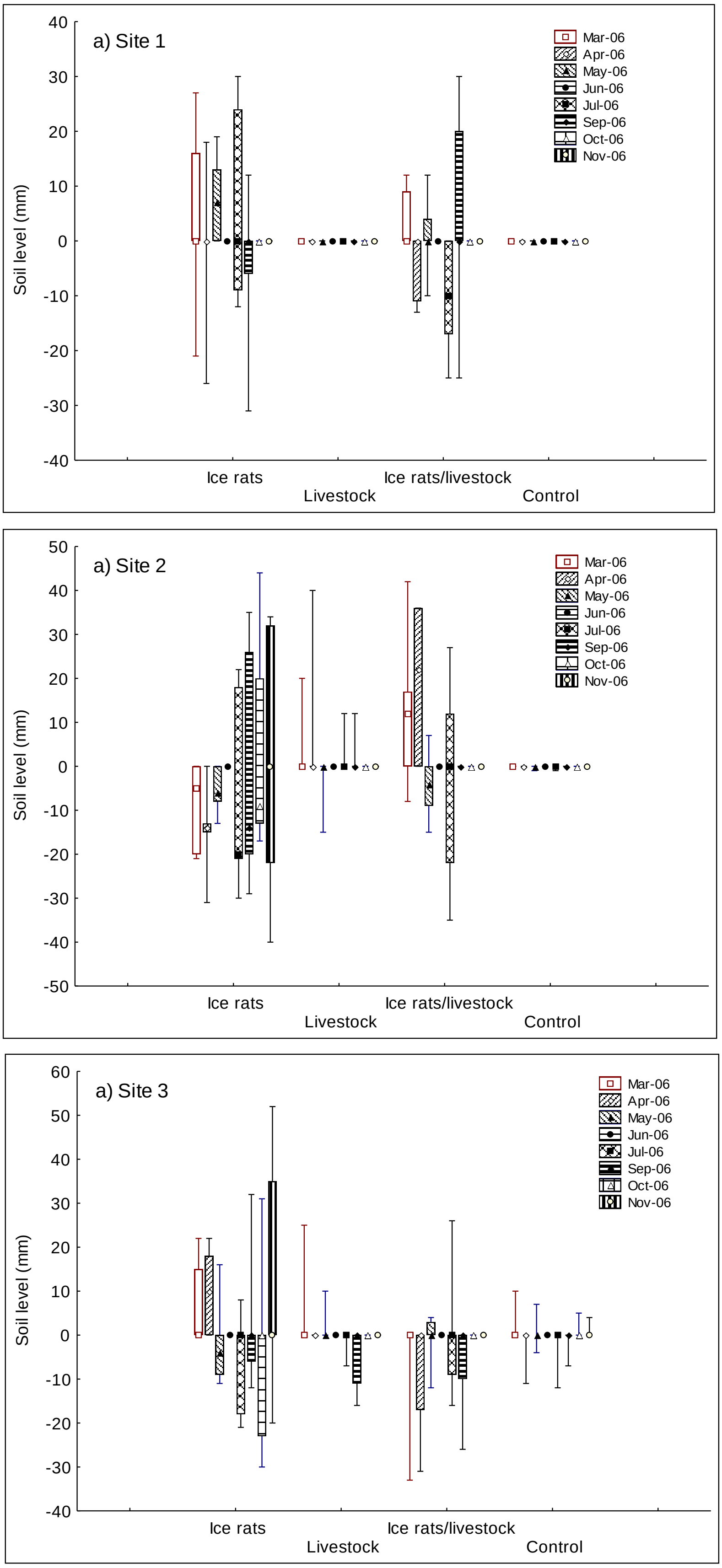


Figure 6. Monthly variation in the soil loss (negative) and gain (positive) measured using droppers in four plots per site in the Sani Valley, 2006. Markers = median values; bars = 25th and 75th percentiles, and whiskers = range.

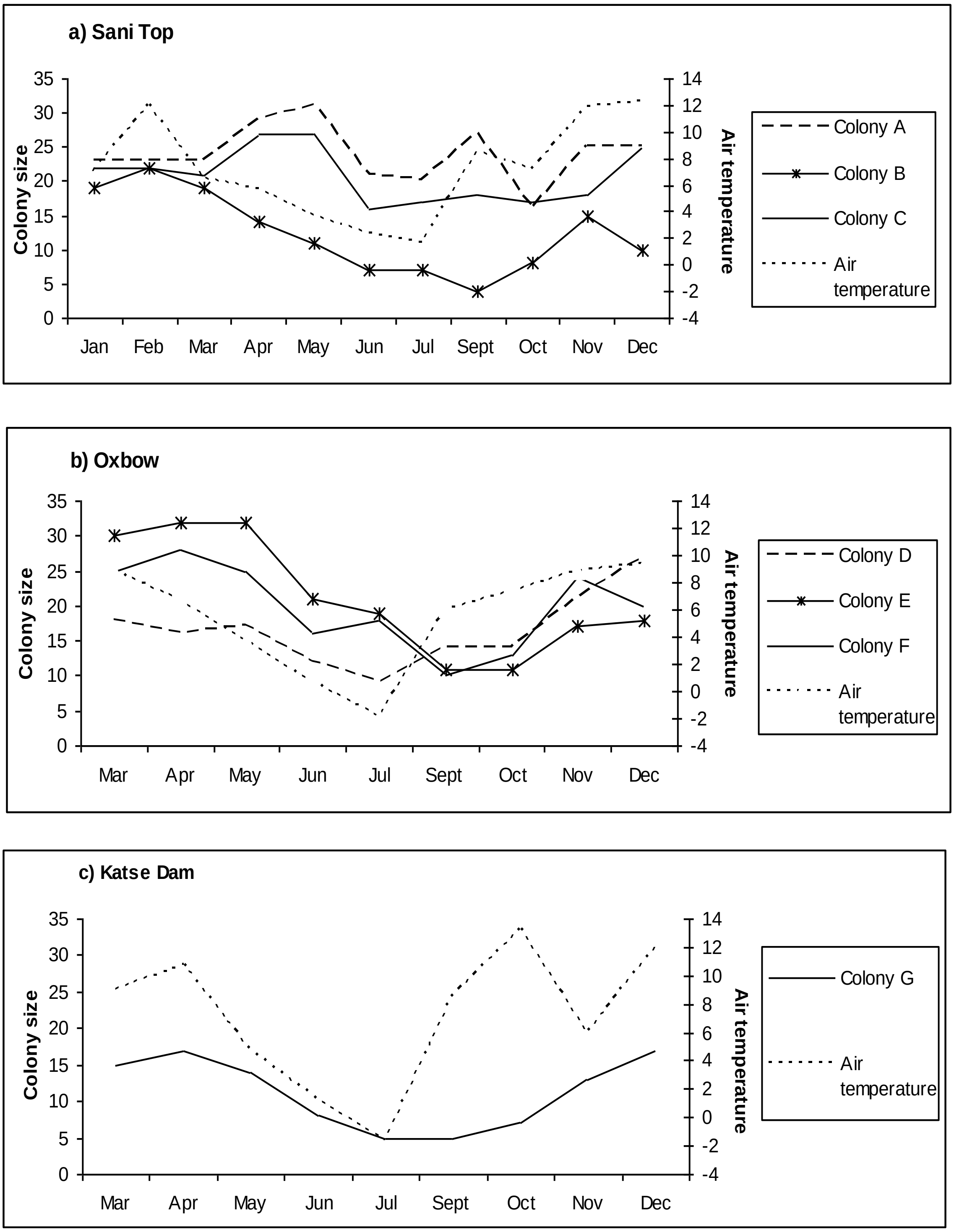


Figure 7. Monthly variation in colony size of ice rats in three colonies at Oxbow and Sani Valley and one colony at Katse Dam in 2006. Air temperatures collected during censuses are also presented. No data are provided for August 2006 heavy snowfall prevented field work.

Table 4. A comparison of the highest and the lowest density of ice rats per hectare at two localities (Oxbow and Sani Top) between my study (2006) and those in the late 1980's (Pillay, unpublished) and early 2000's (Hinze, 2005).

Parameters	Locality and source			
	Oxbow (Pillay, unpublished)	Oxbow (this study, 2006)	Sani Valley (Hinze, 2005)	Sani Valley (this study, 2006)
Highest density	110	352	110	319
Months with highest density	October to April	November to April	September to April	December to April
Lowest density	25	99	38	44
Months with lowest density	May to September	May to October	May to August	May to November

3.3 Interviews with local community members

A total of 92 people were interviewed, comprising 53 at Sani Top, 19 at Oxbow and 20 at Katse Dam. The population comprised about 90% adults, 5% old people and 5% young people. (Individuals above 15 years of age were considered to be adult, and those 45years and older were categorised as old.) Based on occupation, these age groups were categorised as herders, workers and other. More people were interviewed at Sani Top than in other two localities, since I spent more time at Sani Top (conducting exclosures experiments) than at Oxbow and Katse Dam. Moreover, Oxbow had a lower human population density than the other localities.

The combined responses by people (herders, workers, other) at three sites (Sani Top, Katse, Oxbow) to six questions about ice rats and the environment is depicted in Figure 8. From the questionnaires, it is apparent that most interviewees frequently observed ice rats ($\chi^2_{0.05,\,3}$ =16.0; p = 0.001; Figure 8a): 88% of the interviewees observed ice rats while only 22% had never seen the ice rat at all.

Approximately 73% of the people in Lesotho believe that ice numbers have increased whereas 27% of the people did not agree with this statement ($\chi^2_{0.05,\,3} = 12.6$; $p = 0.006$; Figure 8b). A significant number of people also believed that temperatures have increased or are continuously increasing ($\chi^2_{0.05,\,3} = 6.2$; $p = 0.0258$; Figure 8c).

It is important to note that similar numbers of interviewees maintained that temperatures have increased and decreased. This could be due to the inability of interviewees to distinguish between the concepts of decreasing and increasing temperature.

A highly significant number of people claimed that snowfall/cover has decreased, while fewer interviewees refuted this statement ($\chi^2_{0.05,\,4} = 38.5$; $p < 0.001$; Figure 8d).

It was surprising that a highly significant number of people maintained that ice rats prefer vegetated area and sloping areas to wetlands ($\chi^2_{0.05,\,1} = 28.3$; $p < 0.001$; Figure 8e). Finally, a highly significant number of people (70%) associated ice rats with environmental damage, whereas 44% complained about vegetation degradation and 26% complained soil erosion ($\chi^2_{0.05,\,4} = 25.7$; $p < 0.001$; Figure 8f).

The interviewees did not express any opinion on how people influence the life of ice rats. Hunting of ice rats for consumption was insignificant because few people (about 9% from Kate Dam and 4% from Sani Top) acknowledged eating ice rats.

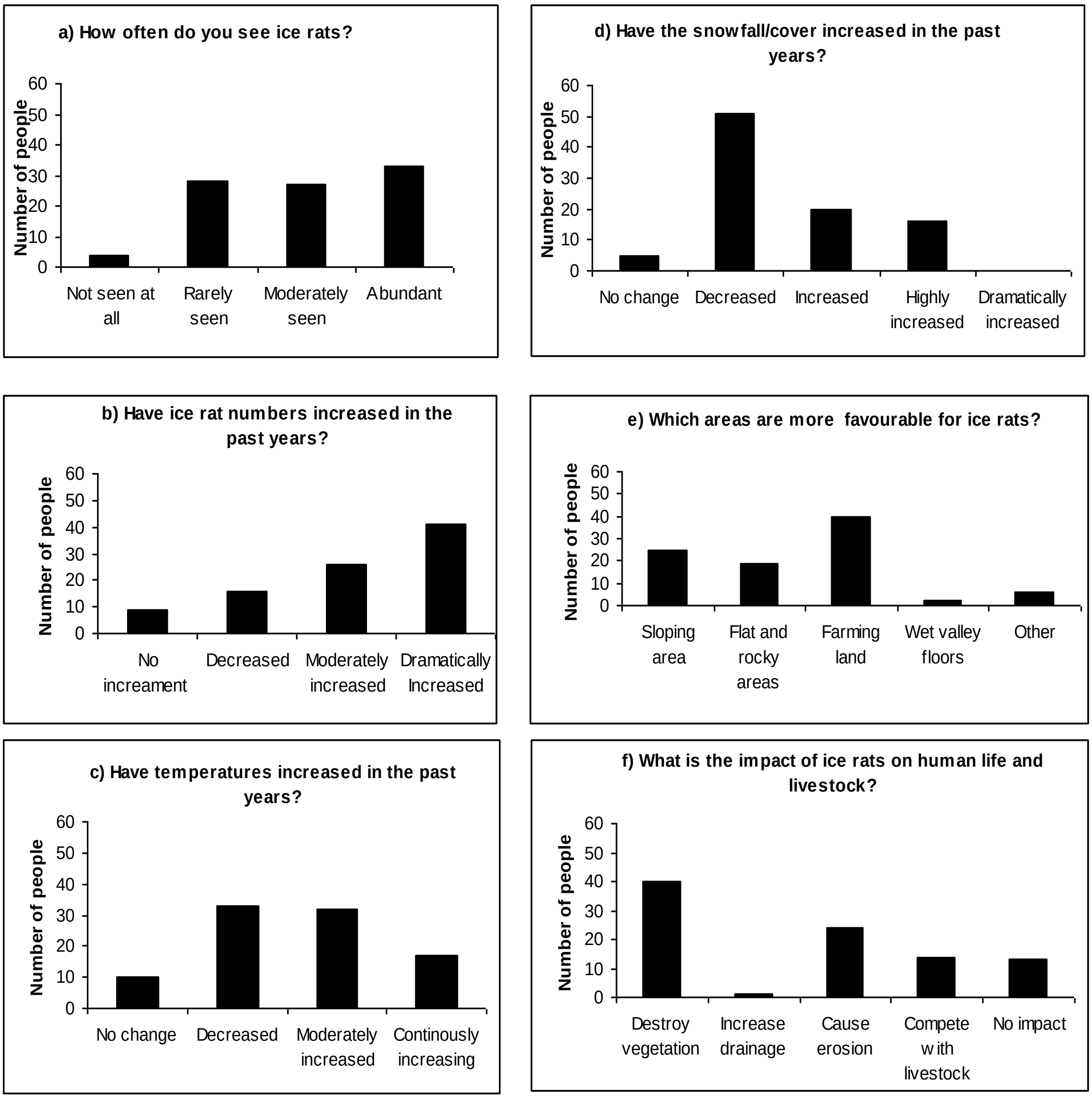


Figure 8. The combined responses by people (herders, workers, other) at three sites (Sani Top, Katse, Oxbow) to six questions about ice rats and the environment.

Chapter 4. Discussion

4.1 Vegetation sampling and soil erosion

I predicted that vegetation loss as well as soil erosion would be worse in the experimental plots which were accessed by both ice rats and domestic livestock, than in the other plots, since both these groups consume plants and because of the burrowing of ice rats (Hinze *et al*., 2006) and the trampling by livestock (Garland, 1987; Hall *et al*., 1999; Grab and Nusser, 2001). This prediction is evaluated below, first for vegetation cover and then soil erosion

4.1.1 Vegetation cover

The control plots together with the livestock only plots had significantly higher vegetation cover compared to the ice rats only plots and ice rat and livestock plots. Greater vegetation cover increases the soil resistance to erosion (Tyson, 1998); since it regulates soil moisture content and stability by promoting water infiltration to the ground surface (Garland, 1987; Arias *et al*., 2005). Vegetation cover also minimises the hitting impact of raindrops, thereby reducing the breakdown and erosion of topsoil (Quinlan, 1995; Tyson, 1998; Schmidt, 2000). Adequate vegetation cover also decreases wind erosion as vegetation impedes the movement of free debris (Garland, 1997; Schmidt, 2000). Therefore, areas with high vegetation cover are less prone to environmental stress than those with low vegetation cover.

The presence of ice rats significantly reduced vegetation cover. During foraging, ice rats do not only consume plant shoots and dig up the roots of plants, but also destroy vegetation when digging burrows for their refugia (Schwaibold, 2005). Selective browsing reduces the abundance as well as the cover of palatable vegetation (Focardi and Tinelli, 2005). However, underground foraging also destroys non-palatable plant species because of attrition of root systems, resulting in bare-ground patches aboveground (Yair and Rutin, 1981; Alkon, 1999; Reichman and Seabloom, 2002). During winter, food plants (herbs) become scarce due to extremely cold and dry conditions in the high Drakensberg (Willan, 1990; Quinlan, 1995; Hall *et al*., 1999; Schwaibold, 2005). Consequently, ice rats switch their diet to include roots of the shrubby vegetation (Schwaibold, 2005), as these are hydrated and rich in carbohydrates (Quinlan, 1995). Since shrubs provide extensive ground cover, their destruction left the bare patches (Roques *et al*., 2001). More bare patches were observed in the ice rats only plots, which were greater than in patches the plots that were subjected to the combined influence of ice rats and livestock, indicating that ice rats are responsible for more vegetation cover loss than livestock. Bare sediment mounds and ground patches are vulnerable to erosion, as described in previous studies of overgrazing in other alpine areas (Kirkpatrick *et al*., 2002).

4.1.1.1 Livestock grazing

Vegetation cover was significantly higher in the plots that were grazed by domestic livestock alone in the Sani Valley. Livestock grazing and trampling are known to compact the soil, thereby incurring large scale damage of vegetation cover in alpine habitats (Wimbush and Costin 1979; Jensen, 1995; Kiehl *et al*., 1996; Austrheim and Eriksson, 2001; Bridle and Kirkpatrick, 2001; Kirkpatrick *et al*., 2002). Vegetation loss due to livestock trampling in the high Drakensberg was reported by Garland (1987) and Grab (1997). Field observations revealed that trampling significantly reduces vegetation cover when it occurs in a specific area and/or when there is serious animal overstocking (Tuner, 1987; Tuner, 1999; Hall and Lamont, 2003, Marake *et al*., 1998). Nevertheless, this was not the case in my study area. This finding is intriguing because, historically, livestock grazing was blamed for the loss of vegetation cover associated with soil erosion in the high Drakensberg (Showers, 1989; Talukdar, 1994; Quinlan, 1995; Phororo and Sibolla, 1999).

4.1.1.2 Vegetation type frequency

There was no between-plot variation in the species frequency for all four vegetation types (grasses, wetland sedges, herbaceous plants and *Helichrysum* group) in my study area. This observation was partly due to individual species resistance to grazing and trampling, and seasonal changes in climate. The absence of plot differences may also imply that alpine vegetation is resistant/adapted to the physical disturbance from domestic livestock and ice rats in the high Drakensberg. This argument is based on the theory of species co-evolution (Ehrlich and Raven, 1964; Malcom, 1990; Begon, *et al*., 1996; Takehito *et al*., 2003). Alternatively, it is interesting that all species categories showed a significant frequency variation in all the sampling months. Vegetation dynamics are linked with strong seasonality in the alpine zones (Wimbush and Costin, 1979; Tyson, 1998; Grab and Nusser, 2001). Regular frosts may destroy poorly adapted plant species, resulting in low species frequency (Bryant, 1996; Körner *et al.*, 1997). Additionally, spring drought causes a fatal hydro-physiological stress in plants (Quinlan, 1995; Munns, 2002).

4.1.1.3 Vegetation height

Grass height was tallest in the control plots, largely because there were no physical disturbances such as browsing and trampling, and may represent optimum growth in my study site. There was no significant difference between the three experimental plots, although it was anticipated that the ice rats only plots would have taller grass in the absence of livestock grazing, since grazing by livestock is known to impact severely on grass (Landsberg *et al.*, 2002). Regular grazing keeps the vegetation short and retards maturity, which affects the reproduction and development of protective plant cover due to slow recovery in alpine environments (Roberts *et al.*, 1972; Wimbush and Costin, 1979; Mathew *et al.*, 1992; Tyson, 1998; Bridle and Kirkpatrick, 2001; Sundra and Noy-Meir, 2001). Ice rats do not consume large quantities of grass (Schwaibold, 2005) but it is possible that they could influence grass height in other ways. For instance, burrowing around the base of grasses could weaken the root structure and hence retard growth (Alkon, 1999; Reichmann and Seabloom, 2002). Furthermore, the observed shorter grass in the experimental plots could be related to physical disturbance (e.g. trampling) in combination with strong seasonal variation in climate in the alpine habitats (Mathew *et al.*, 1992).

The height of the herbaceous plants also showed significant between-plot differences. These differences indicate differences in forage preferences between ice rats and livestock. Ice rats are known to be associated with and feed on herbaceous plants (Schwaibold, 2005), which supports the finding of my study. In contrast, the livestock only plots had taller herbaceous plants, indicting a decreased selection for these plants by livestock. It is interesting that the height of herbaceous plants in the ice rat and livestock plots was less affected than in ice rats only plots, a pattern that is also seen in the vegetation cover and soil gain/loss. This finding is related to the fact that there were fewer burrows in the livestock and ice rats plots than in the ice rat only pots. Furthermore, overgrazing of herbs creates the risk loss of protective ground cover and soil (Ehrlen, 1995; Katoh *et al.*, 1998), which may be one factor contributing to the greater soil exposure in the ice rats only plots..

The heights of wetland sedges and *Helichrysum* did not differ among the plots, despite the fact that livestock trampling together with growth-limiting climatic conditions are known to limit *Helichrysum* growth in the high Drakensberg (Wimbush and Costin, 1979; Garland, 1987; Mathew *et al*., 1992; Tyson, 1998; Orr et al., 2004). However, from my observations, ice rats consume the roots of shrubby *Helichrysum* in winter when hydrated and softer food plants have withered. Moreover, ice rat use *Helichrysum* shoots for nesting in their underground burrows (Hinze *et al*., 2006), and expectedly, *Helichrysum* may be affected during periods of high ice rat population densities (personal observation). In addition, ice rats are known to be abundant in the wetlands where they preferentially forage on sedges (Schwaibold, 2005). It appears that both *Helichrysum* and wetland sedges are more resilient to ice rat use, and to livestock grazing and climatic disturbances. This is consistent with the findings of other studies which showed that forbs maintained high fecundity and constant height even under continuous cattle grazing in Australian arid rangelands (Landsberg *et al*., 2002) and southern Finland (Pykala, 2005).

4.1.2 Burrow density

Ice rats only plots had significantly more burrows than ice rat and livestock plots, indicating greater ice rat presence and activity in the former plots; the relationship between ice rat burrows and activity has been reported previously (Hinze *et al*., 2006). In addition, there was a strong negative relationship between burrow density and vegetation cover in the ice rats only plots; there was no relation between these parameters in the ice rat and livestock plots.

The results also suggest that livestock has a strong influence on the activity of ice rats, since more ice rat burrows where found in the absence than presence of livestock. Taken together, the high numbers of burrows and the lower levels of vegetation cover strongly suggest that the foraging and burrowing activity of ice rats may contribute to the soil erosion problems in Lesotho. This finding contradicts both the prediction of this study and assumptions made by Grab and Deschamps (2004) that the collective impact of ice rats and livestock exacerbate soil erosion processes in high Drakensberg.

4.1.3 Soil loss/gain

Severe browsing reduces the abundance as well as the cover of the palatable vegetation, which also affects the soil stability (Kinlaw, 1999; Kirkpatrick *et al*., 2002; Focardi and Tinelli, 2005). Specifically, the activity of burrowing rodents and the foraging habits of herbivorous rodents results in soil disturbance/movement, potentially facilitating erosion (Eldridge and Myers, 2001; Reichman and Seabloom, 2002; Hall and Lamont, 2003). My study indicates that ice rats (herbivorous, burrowers) significantly reduce vegetation cover which, in turn, influenced changes in soil levels (i.e. loss and gain), which is used here as a surrogate measure of soil erosion. Significantly high soil level changes were recorded in the ice rats only plots and the ice rat and livestock plots in all three sites. The large variations in soil levels in these plots are most certainly associated with a high level of ice rat activity in these plots although ice rat activity appeared to be lower in the ice rat and livestock plot. The aboveground ice rat activity peaked during warm and sunny days towards end of summer (April and May) when population densities and competition levels for food are high. The topsoil disturbed during foraging and trampling together underground removal of soil during burrowing account for soil level fluctuation observed in the plots. The livestock only plots had comparatively less soil level changes than the other experimental plots while changes in soil level were negligible in the control plots. Soil movement, through a multitude of agents (e.g. wind, water) contributes to soil erosion (Wimbush and Costin; 1979; Garland, 1987; Showers, 1989; Boelhouwer, 1997; Tyson, 1998; Goudie *et al*., 2000; Schmidt, 2000; Toy *et al*., 2002; Arias *et al*., 2005). If so, the ice rats only plots are more prone to soil erosion than the other plots. If the data from soil gain/loss are examined in association with vegetation cover, it is clear that the level of soil movement is directly related to the vegetation cover, as has been reported elsewhere (Yair and Rutin, 1981; Garland, 1987; Gabet, 2000; Schmidt, 2000; Arias *et al.*, 2005). In support, in the presence of adequate vegetation cover (i.e. control plots), soil movement was minimal while reduction of the vegetation cover led to higher soil movement.

4.1.4 Bio-interactions in the high Drakensberg (ice rat, livestock and vegetation)

I predicted that loss of the vegetation cover and erosion would be worse in the ice rat and livestock plots, but my results indicate that vegetation cover remained significantly high in these plots. It appears that the differences between the plots accessed by both animal types in relation to the other experimental plots may be the result of a form of interference competition, which occurs when one species aggressively excludes another species, by denying it access to a limiting resource (e.g. vegetation; Case and Gilpin, 1974; Vance, 1985). However, the results of my study suggest there is mutual interaction between the aboveground activity of ice rats and that of domestic livestock, so that the interference is not uni-directional. A possible scenario is that ice rats spend more time below ground in their burrows when livestock are present to minimise the risk of physical injury due to trampling. At the same time, livestock are likely to spend less time foraging on ground that has become unstable due to the burrowing by ice rats. If so, this form of mutual interference will restrict the activity of ice rats and livestock, effectively minimising the impact on vegetation and soil characteristics, rather than being additive as predicted at the outset of my study.

4.2 Ice rat population census

Since low winter temperatures apparently regulate ice rat numbers (Willan, 1990; Lynch and Watson, 1992), I predicted that colony sizes would remain constant or increase during my study because of the recent milder winters in Lesotho (Lesotho weather services). In support, Hinze (2005) found that colony sizes were stable over 2002-2004, with very little fluctuation over each year. In contrast, the results of my study do not support my prediction, since colony sizes changed significantly over the course of the sampling period (January to December 2006). There was a seasonal pattern in the change in ice rat colony size, being highest during the warmer months (March, November and December), and lowest the colder during winter months (June, July). There were some exceptions, however. For instance, in April and May, population density remained high while temperatures began to drop, which probably reflects a lag in the response to population increases following summer reproduction. For September and October, population density was low while temperatures started increasing, which coincides with period before the first young of the year are produced (Willan, 1990; Hinze, 2005). This pattern of population changes, summer peak densities was also previously described for in house mice on Marion Island (Matthewson *et al.*, 1994).

There was a non-significant relationship between air temperature and colony size. This is surprising given that temperature was previously reported to regulate ice rat population density (Willan, 1990; Lynch and Watson, 1992). It is possible that the temperature data that I collected during the hours of days I conducted the colony censuses (i.e. one hour per day monthly) did not reflect the overall temperature profile of the three localities selected for study. A more inclusive data set, comprising monthly minimum and maximum temperatures, would have perhaps provided a better basis for comparison with population density; such data were not available during my study. Moreover, the micrcoclimate of the Sani Valley is different to that of the location of the weather station and using climate statistics from the weather station may not have been representative of the situation in the valley.

Willan (1990) postulated that ice rats are more susceptible to snow cover on the ground which persists for a few days rather than snow fall *per se*, since snow cover would reduce foraging opportunities by decreasing food availability. Furthermore, formation of ice on the foraging patches in winter had a similar effect on feral house mice in Marion Island (Matthewson *et al*.,1994). Snow was more frequent in my study (preventing data collection in August 2006) than in the very recent past, which could explain the larger decrease in population size in my study compared to the study by Hinze (2005).

Harsh winters also influence primary productivity and hence food availability in the high Drakensberg (Hansson, 1979; Hall *et al*., 1999; Grab and Nusser, 2001). Food availability is most integral to the population dynamics of rodents since it influences the population size that can be supported by the ecosystem (Hansen and Beck, 1968; Hansson, 1979; Matthewson *et al*., 1994; Adler and Wilson; 1998; Malizia, 1998). Grab and Nusser (2001) reported a significant decrease in vegetation quantity in winter in the Drakensberg due to freezing, thereby reducing food for the herbivorous ice rat. Loss of vegetation influences the survival of herbivores and energy flow through the ecosystem (Hall *et al*., 1999; Milton, 2004). Since ice rats are exclusively herbivorous, feeding on green, hydrated vegetation (Schwaibold, 2005), they are adversely influenced by a decrease in food availability in winter (Kudo, 1991; Hinze, 2005). Moreover, ice rats were shown to compete aggressively with colony members for experimentally introduced good quality food during winter but not in summer (Hinze, 2005). Such intraspecific resource competition during periods of low food availability would favour stronger competitors (Vance, 1985; Ostfeld and Canham, 1995; Begon *et al*., 1996; Oli and Dobson, 2001). Together with the thermoregulatory stress, low food availability would contribute to an increase in mortality rate in the high Drakensberg.

During periods of high population density, it becomes a challenge for all individuals to access food equally (Matthewson *et al*., 1994; Begon *et al*., 1996). Consequently, in search of better unexploited foraging patches, animals disperse to areas where food is available. Such movements affect the local population dynamics (Emlen, 1966, Krebs and Kacelnik, 1991; Denno and Peterson, 1995; Begon *et al*., 1996). Local population size declines when individuals emigrate and/or when number of deaths outweighs the number of births and immigrations (Roland and Taylor, 1995; Begon *et al*., 1996). Since the cold winter climate destroys vegetation in the high Drakenbserg, it is most likely that many animals leave their colonies in search of food. Furthermore, winter temperatures also impacted on rodent numbers through its influence on breeding (Avenant and Smith, 2003, 2004; van Aarde and Jackson, 2006). At the onset of winter, young and old mice experience higher levels of thermoregulatory stress that make them reproductively inactive and also lead to deaths. Therefore, it could be argued that the ice rat population decline in winter is associated with dispersal due to reduced abundance of food, mortality alone and retarded breeding capacity in winter (Matthewson *et al*., 1994; Denno and Peterson, 1995; Avanant and Smith, 2003, 2004). However, dispersal may pose an additional challenge for ice rats because of high levels of aggression between members of different colonies (Hinze, 2005). This finding is interesting and needs further research because recent studies reported that food availability does appear to limit population numbers of house mice in winter on Marion Island (van Aarde and Jackson, 2006). However, one possible explanation may be the difference in altitude and environmental conditions between Marion Island (low lying and oceanic climate) and my study site (high altitude and alpine climate).

Despite the steep decline in colony size in winter, my study generally suggests that conditions for the survival of ice rats have improved in the high Drakensberg during summer. Ferreira *et al*. (2006) contend that current temperature increases seem to improve the ecosystem conditions for house mice on Marion Island and therefore the situation may be true for ice rats in the high Drakensberg. The highest density of ice rats recorded was 352 animals per hectare (observed at Oxbow) at the start of my study, which may reflect better survival during the past winter. In contrast, Pillay (unpublished) and Hinze (2005) previously recorded a maximum of 110 ice rats per hectare at Oxbow and in the Sani Valley respectively. In consensus with the study of Mathewson *et al.* (1994) on Marion Island house mice, my results indicate that the current summer peak densities are larger than those recorded in previous studies. Previous studies reported that predation pressure on ice rats located at Sani Top (Hinze, 2005) and Oxbow (Willan,

1990) is negligible. Since ice rats are physiologically poorly adapted to cold temperatures (Richter *et al*., 1997), my findings suggest the possibility that the recent milder winters (Lesotho Meteorological Services) may have contributed positively to ice rat population growth and persistence. Since warm temperatures result in an increase in primary productivity (Whittaker, 1975; Adler and Wilson, 1998; Malizia, 1998; Ferreira *et al*., 2006), more food would become available to support a larger population of the herbivorous ice rat. The results of this study also support the finding of Matthewson *et al*. (1994) and Avanant and Smith (2003, 2004) that the length of breeding season has increased because it started earlier and stopped later than in the 1980s. Population increase is therefore feasible for organisms such as ice rats that breed seasonally.

Furthermore, I expected that there would be between-locality differences in the seasonal fluctuation of ice rat populations, since, in addition to cold winters, the Katse Dam population experiences high predation pressure. This was not the case, however, since colony sizes varied similarly in all the study sites through 2006. Instead, what was striking was that Katse Dam had a very low population density compared to Sani Valley and Oxbow, resulting in only one colony being used for the study. A combination of factors appeared to account for scarcity of free-living ice rat colonies at Katse Dam. For instance, the Katse Village and surrounding native villages are located on the banks of the dam, mostly around the dam tributaries, resulting in a higher human population density than the other two study localities. People would compete with ice rats for space or they may be hunting ice rats (Willan, 1990). Furthermore, seasonal flooding of dam banks seemed to limit the space available for ice rats. Finally, Schwaibold (2005) reported high predation pressure for ice rats at Katse Dam, mainly by jackal buzzards *Buteo rufofuscus* and barn owls *Tyto alba*.

My study indicates that the ice rat population dynamics still show a strong density-dependent seasonal pattern, as reported by Willan (1990) and Lynch and Watson (1992). With further increase in population densities, Ferreira *et al*. (2006) predicted that density-dependent factors that regulate mouse population are likely to intensify and further control mice numbers. However, the relationship between snow cover, air temperature and primary productivity on the population biology of ice rats requires further investigation because Aarde and Jackson (2006) argue that food availability is not a limiting factor for mice on Marion Island. Rather, it is believed that low winter temperatures retard the breeding capacity and that high mortalities, that are density-dependent, reduce population densities.

4.3 Interviews with local community members

The interview results revealed no significant variation in the responses by people to ice rats and their environment in the three study localities, indicating similar perceptions across people over a wide geographic area. These results also confirm that ice rat numbers increased together with temperatures while snowfall events decreased. It also appears that ice rats indirectly affect human life through environmental damage-vegetation degradation and soil erosion. In contrast, human beings indirectly influence aboveground activity of ice rats through overstocking since the vegetation cover sampling analysis above indicates that ice rats' activity level was comparatively lower in the ice rat and domestic livestock plot than in ice rat only plot. Few people indicated that they hunt ice rats, which, if true, means that the hunting may not influence the survival and abundance of ice rats.

Perceptions are that ice rat population numbers have increased in the past decade (Grab and Nusser, 2001; Grab and Deschamps, 2004). The interview results also confirm that the frequency of seeing ice rats has increased significantly, with 73% of interviewees reporting that ice rat numbers have increased. This finding is interesting because our census study also recorded a significantly higher maximum number of animals per hectare than in the past (352 ice rats per hectare against 110 ice rats per hectare).

While most interviewees mentioned that temperatures have increased, many also mentioned that temperatures had decreased. This was most likely because the question was not well understood (e.g. high frequency of snowfall but melting after a very short time meant ground and air temperature increased). Although interviews were conducted in Sesotho (the local language), the interviewees were unable to distinguish between the concepts of decreasing and increasing temperature perhaps to due illiteracy.

About 56% of the people interviewed suggested that snowfall/cover, has significantly decreased. However, this question confused some people because snowfall is still common in winter but melts in a shorter time than in the past, so that human activity returns to normal quicker (personal observation). Therefore, the apparent contradiction is still revealing of the decrease in the persistence of snow cover, which may result in improved survival rates during winter (Willan, 1990).

It was surprising that significantly large proportions of people mentioned that they have seen ice rat in the sloping areas and farming land, because ice rats appeared to be abundant in the wetlands during my fieldwork, and are reported to generally avoid steeply slopes (Willan, 1990). This is possible since herders spend most of their time at higher positions for inspection of the flock as they are grazing in the valley. Moreover, peasant farms of green vegetation attract ice rats, increasing the encounter rate between farmers and ice rats.

A significantly large number of people (70%) associated ice rats with environmental damage through grazing and burrowing. Out of the 70%, 44% emphasized vegetation degradation, whereas the other 26% percent pointed out that ice rats contribute to soil erosion mainly. This difference in responses could reflect the occupation of the residents in my study areas. A large number of the residents are livestock farmers who would recognise the effect of ice rats on vegetation more than on the soil. The alpine climate is not very conducive for crop farming because of the very short growing season (Garland, 1987; Showers, 1989; Grab and Nusser 2001), and therefore a small number of people practise crop farming, and hence fewer of the interviewees recognised ice rats as a cause of soil erosion.

Finally, the human communities did not mention any other utility of ice rats except a few people (<10%) who acknowledged hunting of rats for consumption. Socio-cultural conservativeness of the interviewees may have prohibited me obtaining more information about utility of ice rats. Nevertheless, my findings support those of the previous study by Schwaibold (2005). A larger percentage of ice rat hunters (7%) were recorded at Katse Dam than at Sani Top (4%), although I believe hunting is minimal nowadays. Since the number of ice rats has increased, the impact of hunting appears to be insignificant in regulating ice rat population size

4.4 Concluding remarks

Initially, the emergent soil erosion problems in Lesotho were associated with overstocking of livestock in summer (Showers, 1989; Talukdar, 1994; Quinlan, 1995; Showers, 1996; Marake *et al*., 1998; Grab and Deschamps, 2004), while the contribution of ice rats was unknown maybe because ice rat numbers were low. More recently, ice rats have been hypothesised to be responsible for large scale soil erosion and land degradation in many parts of Lesotho because of their foraging and burrowing habits (Grab and Deschamps, 2004). Ice rats are thought to have colonised the high Drakensberg some three million years ago (Taylor *et al*., 2004), while livestock farming started in the region a little before 1900 (Quinlan, 1995). The ice rats and their plant food must have co-existed for many generations, and therefore, if ice rats are responsible for habitat degradation, there is likely to be some form of ecological imbalance.

One reason for the imbalance may be the large and increasing population sizes of ice rats, which was shown in my study from direct observations and interviews of local Basotho people. These large population sizes, which were also shown previously, apparently reflect the better survival of ice rats because of favorable climatic conditions (Hinze, 2005). This potential for the population increase of ice rats had been predicted many years ago by Willan (1990).

What was unclear was the role of ice rats in habitat degradation, and my primary aim was to assess this relationship and separate the impact by ice rats from that of livestock. On this basis, I predicted that the combined influence of ice rats and livestock would have a greater impact on vegetation cover and soil erosion. However, the exclosure/plot experiments showed that the ice rats alone contributed to greater levels of vegetation change (loss of cover, decrease in height) and soil movement. In contrast, the impact of plots accessed by both ice rats and livestock was not as severe as predicted, possibly due to some form of interference (Case and Gilpin, 1974), which may have decreased livestock and ice rat activity. In fact, more burrows were recorded in the ice rats only plot than in the ice rats and livestock plots.

The greater loss of ground cover with concomitant higher levels of soil movement in the ice rats only plots compared to the livestock only plots is surprising given the lack of interspecific competition, and contradicts assumptions made by others (Showers, 1989; Quinlan, 1995; Hall *et al*., 1999; Grab, 2002; Grab and Deschamps, 2004). On the one hand, these results are consistent with several previous studies which emphasised that intensive herbivory together with burrowing impacts vegetation cover negatively, thereby encouraging soil erosion (Yair and Rutin, 1981; Alkon, 1999; Reichman and Seabloom, 2002). On the other hand, these results illustrate important species-typical use of grazing land in Lesotho. Livestock feed mainly on grass (Roberts *et al*., 1972; Wimbush and Costin, 1979; Tyson, 1998) and are herded from one pasture to another by their human minders. In contrast, ice rats feed on herbaceous plants mainly and are confined to particular habitats where these plants occur (Schwaibold, 2005), to some extent because of aggression between conspecifics from neighbouring colonies (Hinze, 2005). These differences most likely influence the impact by each animal species on experimental plots they alone could access.

My plots provided evidence of the impact of mammalian fauna at a small scale. However, if livestock is herded to areas of better grazing, the true impact of livestock may not have been revealed in my study. Clearly, long term data sets are needed to establish how species frequency and other vegetation parameters respond to the individual and combined influences of ice rats and livestock. From a biodiversity/management perspective, it is important to investigate the threshold population sizes necessary for a stable equilibrium in order to manage vegetation loss and soil erosion without compromising any of the organisms and human inhabitants in the High Drakensberg (Menges, 2000).

Soil erosion is a complex, multifaceted process which starts with the loss of vegetation cover (Hall and Lamont, 2003). While ice rats appear to be a major contributor to land degradation in Lesotho, there are likely to be many other contributing factors. Therefore, future studies should consider the interplay between the biotic components considered in my study, other biotic factors (e.g. drainage of wetlands and fires by people) and abiotic components to soil erosion in the high Drakensberg. Examples of these abiotic contributors include geo-morphological aspects (e.g. slope, type of soil substrate) and climatic factors (e.g. ice formation) (Kirkby, 1980; Grab, 1997; Hall *et al*., 1999; Schmidt, 2000; Grab and Deschamps, 2004).

In conclusion, the results of my study strongly suggest that the ice rat is a major mammalian contributor to the soil erosion problem in the Lesotho highlands through their foraging and burrowing. The erosion problem is likely to be exacerbated by the increasing numbers of ice rats.

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