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THE DISTRIBUTION AND BEHAVIOUR OF SMALL MAMMALS IN RELATION TO NATURAL AND MODIFIED SNOW IN THE AUSTRALIAN ALPS



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A thesis submitted for the degree of Doctor of Philosophy of
The Australian National University
March 2005



THE AUSTRALIAN NATIONAL UNIVERSITY

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DECLARATION

This thesis is my own work except where otherwise acknowledged.

A handwritten signature in black ink, appearing to read 'Glenn Sanecki', written over a horizontal line.

Glenn Sanecki
March 2005

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ABSTRACT

Snow is an important factor in the lives of flora and fauna in those regions where it occurs. Despite this, there is a relative lack of information about the ecological role of snow. In addition, on a global scale the majority of the research on snow ecology has been based in the boreal regions of North America and Eurasia. Insights from these areas may not extrapolate well to Australia.

The distribution and physical characteristics of snow are highly variable both temporally and spatially. Its occurrence is affected by a range of factors acting at multiple scales. Working in snow covered areas, however, presents considerable practical problems, particularly for researchers attempting to sample organisms in the subnivean space between the base of the snowpack and the ground surface. As a result, most research has focused on small-scale projects because of logistical and animal-welfare issues.

A technique was developed for this study for sampling small mammals beneath the snow using hairtubes fitted with bait and a removable adhesive surface that could be inserted into the subnivean space through a vertical PVC pipe. The technique provided a 39% detection rate with only 0.2% of tubes visited but not collecting hair samples. Using this technique, it was possible to expand systematic sampling of small mammals in the subnivean space to larger scales at which snow cover can vary spatially and temporally particularly at the landscape scale.

The main part of this research was conducted over two winters (2002-2003) at sites established in a series of valleys close to the Summit Road in Kosciuszko National Park, south-eastern Australia. Selection of sites was based on factors considered important in influencing the distribution of snow in the landscape and representative of the key vegetation types occurring in the subalpine zone. The resulting design consisted of 72 sites stratified by elevation (1501-1600 m, 1601-1700 m, 1701-1800 m), aspect (accumulating, ablating) and vegetation type (woodland, wet heath, dry heath, grassland) with each combination replicated three times. Each site consisted of three hairtube plots approximately 10 metres apart, at which small mammals were sampled. In addition, a range of biotic and abiotic factors including snow cover characteristics were measured throughout the winter at these same sites.

In January 2003, a major bushfire burned 70% of the subalpine area of Kosciuszko National Park and damaged 83% of the sites established in 2002. As a result sampling during winter 2003 was limited to high elevation sites, along with a fifth habitat type (boulderfields).

The snow cover that occurs in the main alpine and subalpine region of the Snowy Mountains is primarily maritime in areas where there is sufficient accumulation, and ephemeral at lower elevations and on higher ablating aspects. Maritime snow is generally deep (> 100cm), with a density >0.30gcm⁻³, as a result of destructive metamorphism throughout the winter. The formation of depth hoar, which is considered to be important in facilitating the development of the subnivean space, does not occur under these conditions. Ephemeral snow is characterised by warm shallow snow that often melts before new snow is deposited.

When snow was present, detections of dusky antechinus, *Antechinus swainsonii* and the bush rat, *Rattus fuscipes* were negatively correlated with snow depth and duration, and positively correlated with the complexity of structures and microtopography. At high elevations, detections were largely confined to boulderfields, and at mid- and low elevations, small mammals were detected primarily in habitats where the subnivean space was most extensive. *Antechinus swainsonii* and *R. fuscipes* responded differently to snow cover with the latter seeming better able to overwinter where snow cover was shallow and patchy. In contrast, *A. swainsonii* occurrence was correlated with the size of the subnivean space.

The development of the subnivean space in the Snowy Mountains is dependent on the presence of structures such as shrubs, boulders and microtopographic features that are capable of supporting a snow layer above ground level.

The temperature in the subnivean space was virtually constant beneath the snowpack, ranging between 0 and +1°C. When snow was patchy or absent, temperatures at ground level were highly variable with a minimum as low as -13°C and maximum as high as +47.5°C. *Antechinus swainsonii* and *R. fuscipes* were detected more regularly at sites that were thermally variable. At sites with deep and persistent snow cover (maritime snow), subnivean temperatures were

stable, but small mammals were detected at low frequencies. At high elevations, boulderfields were favoured by small mammals during the nival period but were no different thermally from other habitats.

The limitations imposed by snow cover on small mammals were further verified by a radio tracking study conducted during 2003 at Perisher Creek. That study investigated the home range size and activity patterns of *R. fuscipes* and *A. swainsonii* in relation to snow cover. Once continuous snow cover became established, the home range of both species contracted dramatically and there was an increase in home range overlap. Neither species showed any change in diurnal activity patterns. *Rattus fuscipes* showed signs of social interaction during both seasons in contrast to *A. swainsonii*, which appeared to remain solitary. In winter, *R. fuscipes* nested communally at a single location, while during autumn the species appeared to use a number of nest sites. There was no significant change in daily activity patterns between autumn and winter in either species. *R. fuscipes* remained primarily nocturnal during both pre-nival and nival periods while *A. swainsonii* continued to be active throughout the diel cycle, although there was a slight shift in its peak activity time.

Human activities can have significant effects on the subnivean space and its residents. The physical characteristics of a range of modified snow types were investigated in the vicinity of several ski resorts in Kosciuszko National Park. Human activities associated with snow-based recreation, such as the creation of ski pistes, surface ski lifts and over-snow routes, involve compression of the snowpack and resulted in small or absent subnivean spaces and high snow cover densities compared to unmodified snow cover.

To test the effects of the loss of the subnivean space on small mammals, the snowpack was experimentally compressed in high quality subnivean habitats. Detections of *R. fuscipes* and *A. swainsonii* declined by 75-80%. Burnt sites from the 2002 study were used in 2003 to investigate the effect of removing vegetation on the subnivean space, to simulate the loss of structure associated with ski slope preparation. There was a significant reduction ($p < 0.0001$) in the size of the subnivean space compared to unburnt sites regardless of habitat type.

The key conclusions of the work reported in this thesis are listed below:

- Snow conditions in the Australian Alps are markedly different from those of higher northern latitudes and altitudes. As a result, conclusions about snow/fauna interactions based on research in regions with particular snow cover types need to be carefully considered before attempting to extrapolate generalisations to other parts of the world.
- The subnivean space can be formed either by passive or active processes. The former occurs when there are sufficient competent structures to permit the support of the snow pack above the ground surface, while the latter refers to the ability of small mammals to actively tunnel through relatively low density snow (depth hoar) and thus create their own subnivean space. In Australia the passive process dominates.
- The widely held assumption that small mammals are dependent on the thermally stable conditions in the subnivean space was not confirmed. *Rattus fuscipes* and *A. swainsonii* survive in the Australian Alps because they are able to exploit thermally variable environments.
- Management of human activities in nival areas should focus on avoiding disturbance in areas where a subnivean space forms, particularly in high quality winter habitats such as boulderfields.
- Global warming resulting from climate change is likely to provide conditions in the Australian Alps that favour an expansion of the distribution and population of *R. fuscipes* and *A. swainsonii*, but nival endemics such as *Burramys parvus* and possibly *Mastacomys fuscus* may be at a disadvantage.
- The extent of alpine and subalpine environments in Australia will decrease in future, imposing greater pressure on a shrinking resource and raising the possibility of conflict between user groups and conservation imperatives.

1 GENERAL INTRODUCTION

1.1 Background

In nival areas, the presence of snow in the landscape is an important environmental factor. For the fauna of these areas, snow plays an important role in their ecology. Despite this, the investigation of snow and its relationship to fauna remains underdeveloped. This is of particular concern as many areas that are subject to the accumulation of snow are under increasing pressure from human interference such as winter recreation and associated activities, and will experience additional impacts in future as a result of climate change due to enhanced greenhouse effect (IPCC 2001).

One particular area of interest is the role of snow in the ecology of fauna that reside in the subnivean space. To date, snow ecology has been explored using indirect or interpolative methods due to the difficulties of sampling in snow covered environments. Consequently, few studies have directly investigated the winter ecology of fauna in general, and small mammals in particular.

Four small mammal species are known to remain active throughout the winter in the Snowy Mountains of south-eastern Australia, including two dasyurid marsupials, the dusky antechinus, *Antechinus swainsonii* and agile antechinus *A. agilis* and two murid rodents, the bush rat *Rattus fuscipes* and broad-toothed rat *Mastacomys fuscus*. Of these species, *M. fuscus* is listed as a threatened species. The winter ecology of small mammals in the Australian Alps has received limited attention to date, especially in relation to the role of snow cover and the development of the subnivean space.

In January and February 2003, the Snowy Mountains were subject to a significant wildfire that burned 69% of the area above 1500 m. As a result of this event, 85% of the sites used in this study in 2002 were damaged, along with the Smiggin Holes trapping grid which is the longest monitored site in the Snowy Mountains. Key elements of this work were undertaken before the wildfire. However, the fire significantly impaired my ability to complete this study as originally planned. It did, however, create additional opportunities for research which have been integrated into this study. Data collected in this study is being used as the basis of a long term project by the Department of Environment and

Conservation (formerly National Parks and Wildlife Service) to monitor post-fire recovery in Kosciuszko National Park.

1.2 Aims

The aims of this study were to:

- develop techniques to enable the monitoring of small mammals in the subnivean space;
- ascertain the characteristics of snow cover under Australian climatic conditions;
- investigate the role of snow in the distribution of winter-active small mammals;
- explore the interaction between small mammals and their thermal environment during winter;
- determine the effects of snow cover on home range size and diurnal activity patterns of winter active small mammals; and
- assess the impacts of snow modification by human activities on snow characteristics and small mammals.

Thesis structure

This thesis consists of three main parts, the first of which comprises two introductory chapters. Chapter 2 provides a review of snow and its role in the ecology of wildlife that inhabit nival areas. It then considers some of the implications of human activity and conservation in nival areas. In Chapter 3, I provide an overview of the Australian Alps, review what is known about the winter active small mammals, and describe the history of human activity in the Australian Alps.

The second part of the thesis consists of a series of papers that have either been accepted or have been submitted for publication. Chapter 4 provides a characterisation and classification of Australian snow and highlights the differences between Australian snow conditions and those in other parts of the world, in particular, those areas from which we have drawn much of our understanding of nival ecology. Chapter 5 describes a new technique for

sampling small mammals in the subnivean space using hairtubes. Previously, small mammals were only able to be sampled at trapping grid-scales. The new technique developed for this thesis permitted systematic sampling of small mammals over landscape-scales in nival environments. Chapter 6 investigated the relationship between snow cover and environmental factors such as elevation, aspect and vegetation structure. This chapter also addresses the distribution of *R. fuscipes* and *A. swainsonii* in relation to natural snow cover and the factors that affect the development of the subnivean space. The effect of the thermal environment experienced by *R. fuscipes* and *A. swainsonii* on their distribution patterns during the winter was investigated in Chapter 7. The home range and activity patterns of *R. fuscipes* and *A. swainsonii* in response to snow cover are investigated in Chapter 8. Chapter 9 considers the potential impacts of human activities on the subnivean ecology of *R. fuscipes* and *A. swainsonii*.

The third part of the thesis (Chapter 10) summarises the findings of previous chapters.

1.4 References

IPCC (2001) Climate change 2001: *The scientific basis. Technical summary from Working Group I*. Intergovernmental Panel on Climate Change, Geneva.

2 SNOW ECOLOGY

2.1 Introduction

In his seminal work on the snow ecology in high northern latitudes of Eurasia, Formozov (1946) began by noting that, "*the presence of this [snow] cover with its markedly peculiar physical characteristics sharply changes the conditions of existence for plants and particularly animals where [it] falls and stays*". This observation is equally applicable to other areas that are subject to the accumulation of snow (Halfpenny & Ozanne 1989; Green & Osborne 1994; Körner 1999; Pruitt & Baskin 2004). Due to its complexity and multi-faceted nature, snow is the subject of investigation by a range of disciplines including climatology, geology, geomorphology, hydrology and agronomy to name a few.

Interactions between biota and snow are unusual because snow is a physical entity as well as a climatic phenomenon. Formozov (1946) described snow as a "periodic mineral" (i.e. combining features of climatic and edaphic factors), and suggested that snow be referred to as the chionic or nival (snow) factor to recognise its unique role in the biosphere.

Before considering how snow cover influences small mammals it was necessary to consider snow itself, and in particular its physical characteristics and the factors that influence its distribution in the landscape.

2.2 Snow

Snow is initiated in the atmosphere as ice crystals when supercooled water vapour freezes around particulate matter which acts as a nucleating agent. Ice crystal formation depends on a number of factors, including the nature of the nucleating agent, atmospheric temperature and the availability of water vapour, all of which affect the type of ice crystal that forms (Mason 1971; Davis 1998). Once formed, ice crystals grow and aggregate to form snowflakes, finally becoming too heavy to withstand the effect of gravity. The accumulation of snow on the ground depends on the conditions which snowflakes encounter after formation; for example, snowflakes may melt to form raindrops if exposed to warm air as they fall, or may melt on contact with the ground if surface temperatures are above 0°C (Seligman 1962; Halfpenny & Ozanne 1989; Davis 1998).

Snow is a catch-all term that has been applied to various forms of solid precipitation as it falls, to its agglomeration on the ground or other surfaces, as well as to various surface generated features (Halfpenny & Ozanne 1989). The term 'snow' is thus not very informative from an ecological perspective, and as a consequence it is easy to lose sight of the diversity of snow forms, each of which can have unique ecological implications (Formozov 1946; Pruitt 1958, 1970). Native peoples who have lived in snow-covered areas for hundreds of years have developed more intricate languages to describe the various forms of snow (Table 2.1), some of which are used by snow ecologists in the absence of suitable English alternatives (Pruitt 1984; Pruitt & Baskin 2004). Some of these have even found their way into more common vernacular, for example the Siberian term *sastrugi* which refers to the aeolian sculpturing of the snow surface.

Table 2.1 Inuit and native American terms for various types of snow conditions and their English meanings. Reproduced from Pruitt (1960)

ENGLISH	INUIT KOBUK VALLEY ALASKA	DINDYE FORT YUKON ALASKA	CHIPEWYAN NORTHERN ALBERTA
FALLING SNOW	ANNÍU	ŽA	SIL(CH)
SNOW THAT COLLECTS ON TREES	QALÍ	DÉ-ŽA	DE-CHÉN-KAY- SÍL(CH)
SNOW ON THE GROUND	APÍ	NON-KÓT-ZA	SIL(CH)-DE-TRÁN
DEPTH HOAR	PUKAK	ŽAI-YA	YATH(K)ÓNA
WIND-BEATEN SNOW	UPSIK	SETH(CH)	SIL(CH)-T(CH)RÁN- AL
FLUFFY TAIGA SNOW		THEN-NÍ-ZEE	YATH-THEY-YÉ- REE-LAY
DRIFTING SNOW	SĪQÓQ	ZA-HE-ÁH-TREE	NIL(CH)-SEE-NI- (K)OTH
SMOOTH SNOW SURFACE	SALUMÁ ROAQ		
ROUGH SNOW SURFACE	NATATGÓNAQ		
SUN CRUST	SIQIQTIAQ	ŽA-ES-(ČH)A	NA-HÓ-T(CH)RAN
DRIFT	KIMOAQRUK	ZA-KÉ-AN-É-HAE	YATH-NÉE-ZUS
SPACE FORMED BETWEEN DRIFT AND OBSTRUCTION CAUSING IT	AŃMANA		
SHARPLY ETCHED WIND ERODED SNOW SURFACE (SASTRUGI OF SKAVLER)	KAIQGLAQ		
IRREGULAR SURFACE CAUSED BY DIFFERENTIAL EROSION OF HARD AND SOFT LAYERS	TUMARÍNIQ		
BOWL SHAPED DEPRESSION IN SNOW AROUND BASE OF TREES	QÁMANÍQ	(ZH)E-QUÍN-ZEE	DAY-CHEN-YATH- DÓ-DEE
SNOW DEEP ENOUGH TO NEED SNOWSHOES		DET-THLO(K)	YATH-THAY-T(R) ÁN-AI(CH)-HÁ
SPOT BLOWN BARE OF SNOW		SI(CH)	OH-BÉH
AREA OF DEEP SNOW THAT PERSISTS PERHAPS ALL SUMMER		ZA-KAY-TAK-KOK	YATH-THAY-(ÁN)

2.2.1 Distribution and extent

Antarctica and parts of Greenland are permanently covered with snow and ice; the ecology of these regions is characterised by a virtual absence of vascular plants and consequent low primary productivity, resulting in the dependence by endemic animal species on marine food sources.

The boreal zones of North America and Europe, and the alpine and subalpine zones of mountains at various latitudes across the globe, experience snow-free conditions for part of the year. The alpine zone occurs above the limit of tree growth while the subalpine zone extends below the tree-line to the winter snowline.

The distribution and extent of snow cover is determined by interactions between climate, physical geography and vegetation (Mckay & Gray 1981). Macroclimatic conditions are responsible for landscape-scale patterns of vegetation, such as the occurrence of a distinct tree-line between the alpine and subalpine zones, and the corresponding but less dramatic forest-taiga boundary in the boreal zone; in turn, the distribution of alpine/subalpine or taiga/forest vegetation formations influences the pattern of snow deposition and its subsequent changes (Pruitt 1978; Körner 1999).

In boreal zones where the terrain is relatively flat, uniform snow conditions may occur over broad areas as a result of synoptic weather systems (Schemenauer *et al.* 1981; BOM 1993). By contrast, snow distribution in alpine environments is far from uniform due to the effects of wind and topography, and in alpine regions supercooling may result from localised orographic uplift (Schemenauer *et al.* 1981; Davis 1998). Despite these differences between boreal and mountain regions, it could be argued that, for example, arctic tundra represents in some ways an extensive area of alpine environment at low altitude but high latitude (Figure 2.1).

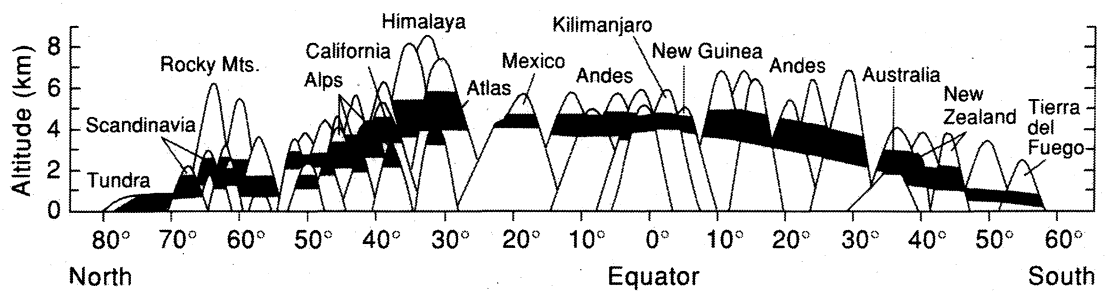


Figure 2.1 Alpine life zones across different latitudes. From Körner (1999)

In snow-covered environments, irregular snow conditions form a mosaic of habitats (Fuller *et al.* 1969) that, like heterogeneous habitats in non-snow covered environments, will mean the distribution of flora and fauna is not spatially or temporally uniform.








































2.2.2 Snow characteristics and classification










































Scientists have become more aware of the need to distinguish different forms of snow and have developed generic systems of classification and characterisation.

The International Snow Classification System (CSI 1954; Mason 1971) and the more detailed systems devised by Nakaya (1954) and Magono and Lee (1966) (Figure 2.2) distinguish types of falling snow based on the shape of ice crystals. The nature of the falling snow to some extent determines the fate of snow once it accumulates. For example, the formation of qali (snow collecting on tree branches) is dependent on the nature of the snow crystals and the conditions under which they are deposited (Pruitt 1958; Halfpenny & Ozanne 1989). Snow composed of needle-shaped flakes is more likely to avalanche, as indeed is any snow which settles with little internal cohesion (LaChapelle 1985; Halfpenny & Ozanne 1989).

To date, there is no entirely satisfactory system for describing or classifying the surface features of deposited snow, because they are produced by a number of distinct processes. Halfpenny & Ozanne (1989) recognised nine categories including hoar frost, needle ice and several types of surface crust.

Figure 2.2 Classification of snow crystals (Magono & Lee 1966).

	N1a Elementary needle		C1f Hollow column		P2b Stellar crystal with sectorlike ends
	N1b Bundle of elementary needles		C1g Solid thick plate		P2c Dendritic crystal with plates of ends
	N1c Elementary sheath		C1h Thick plate of skeleton form		P2d Dendritic crystal with sectorlike ends
	N1d Bundle of elementary sheaths		C1i Scroll		P2e Plate with simple extensions
	N1e Long solid needle		C2a Combination of bullets		P2f Plate with sectorlike extensions
	N2a Combination of needles		C2b Combination of columns		P2g Plate with dendritic extensions
	N2b Combination of sheaths		P1a Hexagon plate		P3a Two branched crystal
	N2c Combination of long solid columns		P1b Crystal with sectorlike branches		P3b Three branched crystal
	C1a Pyramid		P1c Crystal with broad branches		P3c Four-branched crystal
	C1b Cup		P1d Stellar crystal		P4a Broad branch crystal with 12 branches
	C1c Solid bullet		P1e Ordinary dendritic crystal		P4b Dendritic crystal with 12 branches
	C1d Hollow bullet		P1f Femlike crystal		P5 Malformed crystal
	C1e Solid column		P2a Stellar crystal with plates at ends		P6a Plate with spatial plates

	P6b Plate with spatial dendrites		CP3d Plate with scrolls at ends		R3c Groupel-like snow with nonrimed extensions
	P6c Stellar crystal with spatial dendrites		S1 Side planes		R4a Hexagonal groupel
	P6d Stellar crystal with spatial dendrites		S2 Scalelike side planes		R4b Lump groupel
	P7a Radiating assemblage of plates		S3 Combination of side planes, bullets, and columns		R4c Conelike groupel
	P7b Radiating assemblage of dendrites		R1a Rimed needle crystal		I1 Ice particle
	CP1a Column with plates		R1b Rimed columnar crystal		I2 Rimed particle
	CP1b Column with dendrites		R1c Rimed plate or sector		I3a Broken branch
	CP1c Multiple capped column		R1d Rimed stellar crystal		I3b Rimed broken branch
	CP2a Bullet with plates		R2a Densely rimed plate or sector		I4 Miscellaneous
	CP2b Bullet with dendrites		R2b Densely rimed stellar crystal		G1 Minute column
	CP3a Stellar crystal with needles		R2c Stellar crystal with rimed spatial branches		G2 Germ of skeletal form
	CP3b Stellar crystal with columns		R3a Groupel-like snow of hexagonal types		G3 Minute hexagonal plate
	CP3c Stellar crystal with scrolls at ends		R3b Groupel-like snow of lump type		G4 Minute stellar crystal
					G5 Minute assemblage of plates
					G6 Irregular germ

Once on the ground, snow becomes an even more complex phenomenon, varying in depth, density and internal structure as well as interacting with the ground surface and other features of the landscape. Because the type of snow depends on the climatic conditions prevailing at the time of deposition, the snowpack may consist of layers with different characteristics. Consequently, describing characteristics of snow on the ground is difficult. A classification system aimed at providing an international standard for describing snow on the ground has been devised (Colbeck *et al.* 1992); this system requires eight physical characteristics to be recorded for each layer within the snowpack (Table 2.2), so its application is laborious and requires considerable specialist expertise. To complicate the situation further, snow on the ground is not a static phenomenon, but rather is in a constant state of change, so classification using this system is only relevant for the time at which it was conducted.

Table 2.2 Primary physical characteristics of deposited snow. After Colbeck *et al.* (1992)

Feature	Unit
Density	g/cm ³
Grain shape	Visual key
Grain size, greatest extension	mm
Liquid water content	% by volume
Impurities	% by weight
Strength (compressive, tensile, shear)	Pa
Hardness index	Depends on instrument (e.g. Rammsonde)
Snow temperature	°C

An alternative approach by Sturm *et al.* (1995) describes snow on the ground at larger spatial and temporal scales taking into account the climatic conditions as well as its physical, thermal and stratigraphic characteristics derived from seasonal averages (Table 2.3). Although providing a coarser classification than the system of Colbeck *et al.* (1992), its application does not require specialised skills or equipment, nor is it as labour intensive.

Table 2.3 Snow cover classes and characteristics. From Sturm *et al.* (1995)

Snow Class	Description	Depth Range (cm)	Density (g cm⁻³)	Number of Layers	Temp Gradient (°C cm⁻¹)
Tundra	Thin windblown snow. Basal layer of depth hoar, overlain by multiple layers of wind slab. Surface sastrugi common, melt features rare.	10~75	0.38	0~4	-0.59 ~ -0.39
Taiga	Thin to moderately deep snow cover, in cold forested regions, relatively unaffected by wind. Depth hoar 50- 80% by late winter.	30~120	0.26	>15	-0.38 ~ -0.28
Alpine	Moderate to thick snow cover, with alternating thick and thin layers. Basal depth hoar common, melt features insignificant.	75~250	0.25	>15	-0.22 ~ -0.12
Maritime	Warm deep snow cover, melt features very common, coarse grained snow due to wetting. No depth hoar.	75~500	0.35	>15	-0.18 ~ -0.07
Ephemeral	Thin, extremely warm, short lived snow cover. Melt features common. Often melts between snowfalls.	0~50	-	1~3	-
Prairie	A thin moderately cold snow cover. Substantial wind drifting. Wind slabs common.	0~50	-	<5	-
Mountain	Highly variable snow, depending on wind and insolation factors.	-	-	Variable	-

When snow is deposited under cold, and still conditions, its structure can be maintained for some time, but even under ideal conditions snow begins to change greatly (Halfpenny & Ozanne 1989). Once snow reaches the ground and begins to aggregate, bonding between and intertwining of snow crystals changes its nature. Wind readily redistributes snow and is able to mechanically change snow crystals (Seligman 1962; McKay & Gray 1981; Halfpenny & Ozanne 1989).

2.2.3 Metamorphism

Metamorphism refers to the changes that occur within the snowpack following deposition. Three processes are involved: disintegration of individual snow crystals and reformation of larger grains (destructive or equitemperature (ET) metamorphism), sublimation of water vapour in one stratum and recrystallisation in another (constructive or temperature-gradient (TG) metamorphism) and melting followed by refreezing (melt-freeze (MF) metamorphism) (de Quervain 1963; Sommerfeld & LaChapelle 1970; Ruddell 1998). All three processes are related to the thermal properties of the snow and the consequent movement of water molecules.

MF metamorphism is characteristic of late winter and early spring when temperatures in the snowpack permit melting and subsequent refreezing, resulting in an increase in grain size and changes in grain shape and bonding (de Quervain 1963). Under suitable conditions and when combined with pressure due to the weight of snow, MF metamorphism can produce *névé* and *firn*, forms of consolidated snow intermediate between snow and ice (Seligman 1962).

ET and TG metamorphism occur throughout the winter and can occur simultaneously. Which of these processes predominates will depend on the vapour pressure gradient in the snowpack, that in turn depends on the vertical temperature gradient (Prowse & Owens 1984; Ruddell 1998). ET metamorphism occurs when the vapour pressure gradient is low (temperature gradient less than $10^{\circ}\text{C m}^{-1}$) resulting in destruction of snow crystals and the creation of rounded ice grains. These then continue to grow as sintering occurs, increasing snow density and strength (de Quervain 1963; Ruddell 1998). ET metamorphism slows at low temperatures and stops below -40°C (Halfpenny & Ozanne 1989).

The critical vapour pressure for TG metamorphism is 5 hPa m^{-1} (Prowse & Owens 1984) which occurs when vertical temperature gradients within the snowpack in the range of $10\text{-}25^\circ\text{C m}^{-1}$ are sustained for about one week (Akitaya 1974; Colbeck 1983; Zhang *et al.* 1996; Ruddell 1998). Water vapour sublimates from the warmer layer and recrystallises in the colder layer, producing the characteristic cup-shaped snow crystals that form depth hoar. The size of depth hoar crystals is positively correlated to temperature gradients and vapour pressures. At the base of the snowpack, greater vapour pressure gradients occur at higher temperatures, thus the largest crystals are found there (Halfpenny & Ozanne 1989; Sturm & Benson 1997). Depth hoar also may occur at other locations in the snowpack, especially if there are ice layers in the snowpack, hence the term 'depth hoar' can be somewhat misleading (Seligman 1962). Due to their shape, depth hoar crystals do not coalesce, forming a layer with poor cohesion and low density. Depth hoar has been thought to play an important role in the development of the subnivean space, between the base of the snowpack and the ground surface (Pruitt 1960, 1970, 1984; Halfpenny & Ozanne 1989; Auerbach & Halfpenny 1991).

2.3 Ecological relationships

Ecology is the study of organisms and how they interact with other organisms and the environment (Halfpenny & Ozanne 1989; Krebs 1994). The ecology of organisms in snow-covered environments has received little research attention compared with more temperate regions. One reason is that access to these environments can be difficult and perilous for researchers with climatic conditions often harsh and highly variable. In addition, snow itself can directly or indirectly hinder the detection or observation of both fauna and flora. The presence of snow does, however, have a significant effect on both the flora and fauna of nival areas.

2.3.1 Flora

In environments subject to regular snow falls, the important macroclimatic factors are temperature and light. Temperature varies with latitude and altitude (Figure 2.3); intensity of solar radiation does not vary with elevation *per se* (Körner 1999) but is affected by the depth and duration of snow cover. In terms

of plant ecology, snow plays a dual role; it limits primary production by preventing solar energy from reaching photosynthetic tissue, but also insulates plants from extremely low air temperatures.

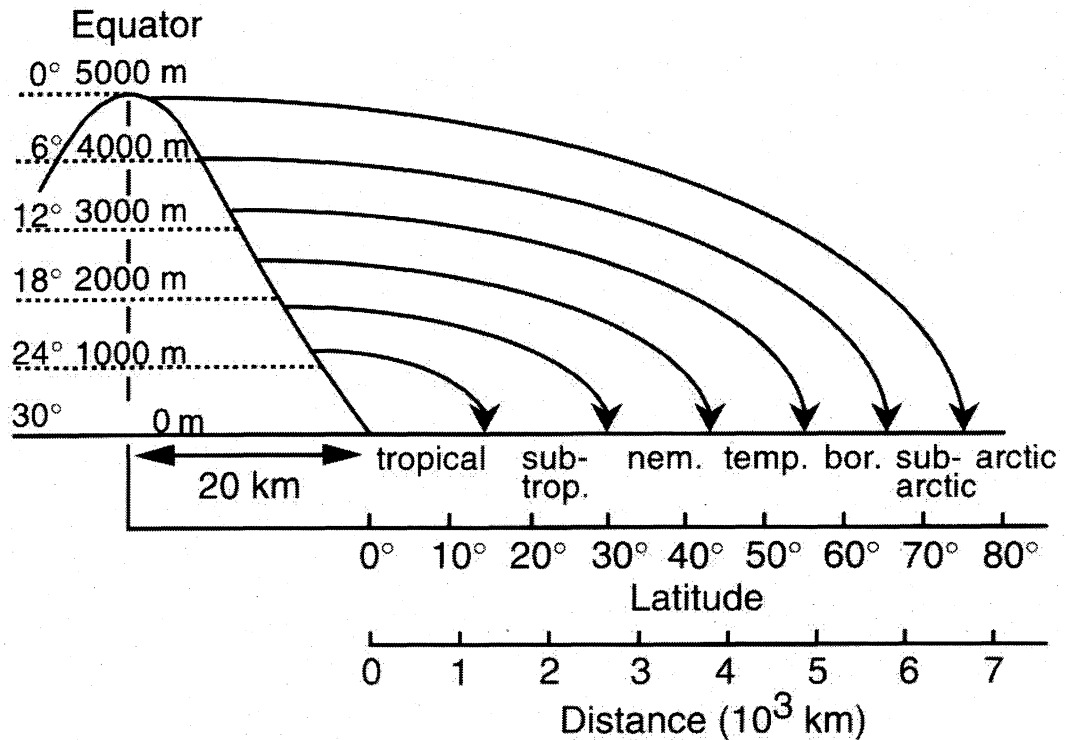


Figure 2.3 The relationship between altitude and latitude with respect to temperature, using as an example a hypothetical mountain located on the equator. From Körner (1999).

Light is critical for providing energy for photosynthesis and, in some cases, provides cues for plant reproduction. Light extinction beneath the snow varies in response to the physical properties of the snow, in particular depth and density, with 40 cm of low density snow able to prevent almost all light penetration. As density increases initially, light penetration is reduced further, however once it exceeds 0.50 g cm⁻³ light transmission increases (Marchand 1984). Irrespective of light transmission levels, differential transmission through the snow reduces the amount of longer wavelengths, including red light used for photosynthesis (Evernden & Fuller 1972; Halfpenny & Ozanne 1989).

Alpine floras are relatively depauperate; individual mountain regions of the world have about 300 species of higher plants each, although the actual species number differs from region to region (Körner 1999). Tundra and alpine plants,

beyond the physiographic limit of tree growth, display a range of morphological and physiological adaptations that assist in avoiding the extreme macroclimatic conditions in the supranivean environment and compensating for the restricted growing season (Körner 1999). Plants are typically compact and low growing perennials; characteristic growth forms include dwarf shrubs, cushion plants, tussock grasses and plants with prostrate or creeping stems (Pruitt 1978; Körner 1999; Costin *et al.* 2000). Many tundra and alpine plants can survive freezing of tissues and start growing under snow or at subzero temperatures, and may produce flower buds in autumn for the following spring, using carbohydrates stored in underground organs, to enable rapid spring growth (Pruitt 1978; Körner 1999).

Similar, but less extreme, adaptations are likely to occur in subalpine plant species which also experience periods of snow cover and low winter temperatures. Non-uniform snow distribution in alpine and subalpine areas can have significant localised effects upon the development of vegetation and its productivity (Billings & Bliss 1959; Good 1998; Wardlaw 1998; Körner 1999).

2.3.2 Fauna

The presence of snow on the landscape has a significant effect upon the ecology of animals that exist under these conditions and has exerted a strong influence on the nature of their adaptations (Hoffman 1984). Formozov (1946) provided a three-category classification for animals in relation to their responses to snow cover. Chionophobes are animals which are not well adapted to snow and have little to no ability to exist in its presence, including those animals which either do not occur in areas that are subject to seasonal snow cover, or migrate away from nival areas during the winter months (Hoffman 1974). Examples include small cats *Felis* spp., sand grouse *Pterocles* spp. and black partridge *Francolinus francolinus*. Chionophiles, in contrast, are those species that inhabit extreme snow covered environments and have specific physical, physiological or behavioural adaptations that permit them to over winter successfully (Pruitt 1978). These include species such as the arctic fox *Alopex lagopus*, ptarmigan *Lagopus* spp., arctic hare *Lepus timidus* and collared lemming *Dicrostonyx torquatus*. Between these lie the chionophores which, although not specifically adapted to snow environments, are able to tolerate and survive moderate nival

conditions. Such species include the fox *Vulpes vulpes*, moose *Alces alces*, reindeer *Rangifer tarandus*, wolf *Canis lupus*, many voles such as *Microtus* spp., *Clethrionomys* spp. and others, moles *Talpa europaea*, and shrews *Sorex* spp.

While Formozov's (1946) classification scheme provides a useful paradigm for considering the interactions between animals and snow, it is important to appreciate that snow cover itself is variable in space and time. In a particularly hard winter, conditions may be so harsh that even the best adapted chionophile is at risk (Formozov 1946; Pruitt 1960).

For chionophiles and chionophores, snow becomes an integral part of their habitat, thus any factor which affects snow conditions and characteristics is likely to have an effect on them as well. This can be seen in the response of barren ground caribou *Rangifer arcticus* to snow cover conditions (Pruitt 1959). This species occurs in arctic and subarctic regions of North America which may be subject to the presence of snow for up to eight months of the year. Snow represents a substrate that, depending on its density, depth and ability to support weight, can influence the distribution of caribou and its ability to obtain forage located beneath the snow (Pruitt 1959). Typically this species will occur in areas with relatively shallow, soft snow of low density, with areas of harder snow acting as "fences" that govern their activities (Pruitt 1960). Over the course of winter, herds of caribou move about in response to changing positions of the unsuitable snow fences (Pruitt 1959; 1960).

The snow fence effect also influences the geographic distribution of Canadian lynx *Lynx canadensis* by affecting its ability to hunt its main prey species, the snowshoe hare *Lepus americanus* (Stenseth *et al.* 2004). In regions with few warm spells during winter, snow remains fluffy and soft, conferring an advantage on the hare which has a lower ratio of mass to foot surface area – or foot load – than the lynx (Halfpenny & Ozanne 1989) and thus is more difficult for the latter to catch. Snow cover characteristics interact with other factors which, when combined, can influence the behaviour and distribution of fauna. For example, the interaction of falling snow with tree branches produces qali which affects the arboreal activity of red squirrels *Tamiasciurus hudsonicus*, chickadees *Parus atricapillus* and *P. hudsonicus* (Pruitt 1958) and marten *Martes martes* (Formozov 1946).

The presence of snow creates two distinct environments, supranivean (above the snow) and subnivean (below the snow). Large animals are confined to the supranivean environment unless they have morphological adaptations that enable them to access subnivean resources, for example the ability of caribou and other large herbivores to use their hooves to excavate feeding craters. A more extreme example is the American marten *Martes americana* and related mustelids which spend a considerable portion of their time on the snow surface but are also able to hunt in the subnivean space by virtue of their elongated body shape. As a result marten and other mustelids are less energy-efficient and have high metabolic rates compared to similar sized mammals (Iversen 1972), requiring them to be active predators if they are to maintain energy balance (Buskirk & Harlow 1989).

2.3.3 Small mammals

Small mammals have become dependent upon the formation and existence of a subnivean space during the winter, spending virtually the entire winter beneath the snow (Formozov 1946; Pruitt 1984; Halfpenny & Ozanne 1989; Happold 1989; Green & Osborne 1994). The subnivean space provides ready access to the food supply on which they depend, in contrast to larger mammals which must excavate food sources covered by snow, rely on snow-free patches or change diet to utilise more accessible items (Pruitt 1978).

It is widely accepted that the presence of depth hoar is important in the development of the subnivean space, because the low density of this layer allows small mammals to dig a network of tunnels and runways through the snow at surface level (Pruitt 1960, 1970, 1984; Halfpenny & Ozanne 1989; Auerbach & Halfpenny 1991). Boreal small mammals that inhabit underground burrows during the snow-free period transfer their activities to the ground surface once snow depth reaches 5-10 cm (Formozov 1946).

The size of the subnivean cavity is dependent upon variations in snow depth and the height, density and strength of the underlying vegetation. Even a pasture of grass and clover can support the snow about 3 to 8 cm above the ground (Coulianos & Johnels 1962). Small mammal distribution and activity can be influenced by this, for example the home ranges of long-tailed voles *Microtus*

longicaudus were related to the characteristics of vegetation especially mechanical strength that in turn influenced the amount of snow-free space available (Spencer 1984). The mortality rates and density of red-backed voles *Clethrionomys rutilus* were related to vegetation structure with higher survival rates over winter found in forested areas apparently due to better subnivean conditions (Whitney & Feist 1984), and red-backed voles also tend to avoid areas of shallow snow (Pruitt 1960). In addition to the presence of suitable structure, the ability for small mammals to remain active in the subnivean space has also been attributed to the presence of depth hoar or pukak. This low density layer of snow occurring at the snow/ground interface is believed to permit small mammals to burrow more freely through the snow and thus facilitate the formation of the subnivean space (Pruitt 1984; Halfpenny & Ozanne 1989).

The subnivean space provides a habitat that is climatically quite distinct from the surface environment (Pruitt 1957; Coulianos & Johnels 1962; Happold 1998). Snow is a good insulator, so once snow cover is sufficiently thick, the temperature in the subnivean space is decoupled from the supranivean environment. This point, the hiemal threshold, is achieved in freshly fallen snow when the cover is 15-50 cm deep (Coulianos & Johnels 1962; Pruitt 1970; Halfpenny & Ozanne 1989; Courtin *et al.* 1991). The temperature in the subnivean space remains virtually constant regardless of air temperature, staying within a few degrees of freezing in the subalpine zone but possibly falling somewhat lower in the boreal zone (Pruitt 1957; Happold 1998). The deeper and less dense the snowpack, the greater the difference between the supranivean and subnivean environments (Penny & Pruitt 1984). If snow cover is not complete, however, cold air may enter the subnivean space and thus cause substantial temperature variation (Pruitt 1957; Green & Osborne 1994; Green 1998).

Snow density plays a critical role in the subnivean environment. As snow density increases, its ability to insulate is reduced (Marchand 1982; Pruitt 1984). With reduced insulation, whether as a result of snow compression or a depauperate snow cover, the risk of mortality for small mammals is increased. This is due to the ground freezing, making it difficult for animals to forage (Formozov 1946). Snowpack with little temperature buffering capacity discourages the use of certain locations by mobile animals, and also affects the

composition and distribution of plant species (Auerbach & Halfpenny 1991). Small mammals are reluctant to burrow through dense snow, thus its presence is likely to restrict their distribution (Pruitt 1984). Long-tailed voles *Microtus longicaudus*, for example, are deterred from burrowing through snow when density is above 0.15 g cm^{-3} (Spencer 1984).

2.4 Impacts and threats

As in other biomes, humans have an effect on the characteristics and integrity of snow-covered areas that, in turn, can affect the flora and fauna of these areas. Activities such as the movement of oversnow vehicles and the modification of snow for winter-based recreation such as skiing are known to have effects on the biota beneath the snow (Fahey & Wardle 1998). These activities can have more severe impacts in alpine environments than in the boreal zone. This is because most snow-based recreational pursuits (in particular downhill skiing) are associated with topographically variable terrain.

With increasing interest in snow-based recreation, the modification of snow conditions within alpine areas could have implications for the long-term preservation of native fauna, some of which are only known to occur in these areas (Mansergh & Broome 1994). The development of oversnow transport routes and the grooming of ski trails has meant that in many alpine areas of the world, networks of compressed snow tracks are regularly developed during the winter months, particularly in the vicinity of ski resorts (Schmid 1971; Young & Boyce 1971; Maysk 1973; Foreman *et al.* 1976; Keddy *et al.* 1979; Rixen *et al.* 2003).

Regular compaction of snow can destroy the subnivean space, causing the snowpack to rest directly on the ground, and can prevent it from re-forming (Green 1998). However, compaction can occur with a single pass of a snowmobile, which may compress snow by up to 75% of the total possible by subsequent passes of the same machine (Keddy *et al.* 1979), especially when applied to freshly fallen snow with low physical strength (Seligman 1962; McKay & Gray 1981). The end result is a layer of snowpack that seasonally modifies the subnivean environment in a manner analogous to the division of non-snow

habitat by roads or other linear artefacts, separating otherwise contiguous habitats and further dividing already fragmented habitat patches (Sanecki 1999).

The compressive force applied to the snow is a function of the downward force and the area over which it is applied. As such, a skier may compress the snow to a greater extent than a snowmobile because the latter has less weight per unit area due to its wide track (Halfpenny & Ozanne 1989), for example large snow-grooming machines exert a relatively low ground pressure of 0.05 kg cm^{-2} (Fahey & Wardle 1998). However, when a subnivean space is present, vehicles with large mass can cause the snowpack to collapse and destroy the subnivean space (Schmid 1971), whereas the impact of a single skier is highly localised.

The ability of the snowpack to resist compression increases over time since ET and MF metamorphism result in increased snowpack density and strength (Seligman 1962; de Quervain 1963) and sintering processes add further strength (Adam 1981; Langham 1981). Therefore, activities that may destroy the subnivean space early in the season could have less severe impacts in later winter or early spring.

The compaction of snow has been implicated in the disturbance of subnivean thermal conditions (Schmid 1971; Kattelman 1985; Singh 1999) as a result of the increased thermal conductivity of dense snow (Halfpenny & Ozanne 1989) and consequent increase in thermal variability in the subnivean space. The loss of thermal stability can lead to a wide range of changes that impact on subnivean small mammals, both directly (Green 1988; Halfpenny & Ozanne 1989; Sanecki 1999) and indirectly through effects on plant physiology and vegetation communities (Maysk 1973; Greller *et al.* 1974; Emers *et al.* 1995; Pickering & Hill 2003), the duration of the growing season (Knight *et al.* 1979; Price 1985; Rixen *et al.* 2003), the physical properties of soil (Kattelman 1985; Pesant 1987) and soil fauna and microflora (Neumann & Merriam 1972; Meyer 1993).

Physical damage to vegetation can be caused in a number of ways by snow modification. Where snow is shallow and vegetation protrudes through the snow surface, exposed stems can be broken by oversnow vehicles and skiers (Forbes 1992; Emers *et al.* 1995); shrubs with erect growth habits are particularly vulnerable due to the brittle nature of their woody tissues (Neumann & Merriam

1972; Emers *et al.* 1995). Long-term changes in species composition have been noted in a range of vegetation types as a result of crushing of the snow as well as the changes in thermal conditions if the overlying snowpack is compressed (Greller *et al.* 1974; Foreman *et al.* 1976; Keddy *et al.* 1979; Mosimann 1985; Forbes 1992).

Snow modification is not restricted to grooming and compression. Supergrooming, which is designed to extend the ski season by enabling skiing on shallow snow, involves clearing of vegetation from ski slopes during the non-snow period and grading the exposed surface to remove boulders and other irregularities (Perisher 2000). Snow farming, where snow is moved from sites of accumulation to augment locations with poor snow cover, can cause considerable damage to vegetation and alter snow cover regimes (G. Sanecki pers. obs).

Artificial snow is being increasingly used to augment snow cover in ski resorts (Kocak & van Gemert 1988; Konig 1998; Rixen *et al.* 2003). A number of issues have emerged regarding the environmental consequences of its widespread use. Artificial snow making increases the depth and duration of snow cover which can have implications for the phenology of vegetation (Rixen *et al.* 2003). The addition of sterilised bacteria as ice nucleating agents (Kocak & van Gemert 1988) has raised concerns about potential pathogenic effects on plants (Rixen *et al.* 2003) and other biota (Goodnow *et al.* 1990).

At a broader scale, the use of cloud seeding to enhance precipitation either as rain or in the form of snow (Bigg 1995) is being applied in various regions (Ryan & King 1997). The potential implications of cloud seeding activities are for the most part unknown and its use remains controversial (Ryan & King 1997).

Winter-based activities are not the only possible impacts that may occur in snow covered ecosystems. Human activities that serve to modify the environment during non-nival periods also may have an impact on the ability of small mammals to over winter in the subnivean space, for example, as a result of the removal of habitat structure (Mansergh & Broome 1994). Such modifications also may occur without human intervention, and may result from changes in faunal or floral assemblages. Changes in grazing pressure for example by the introduction of exotic herbivores such as rabbits which are not well adapted to

nival environments may have an impact on local floristic composition (Green & Pickering 2002), as may the invasion of weed species (Sanecki *et al.* 2003).

Climate change may exacerbate such impacts (Green & Pickering 2002) as snow cover declines in mountain regions (Whetton *et al.* 1996; Whetton 1998; IPCC 2001; Hennessy *et al.* 2003) Hennessy *et al.* 2003).

The factors that affect the physical characteristics of snow and its distribution are largely universal. Likewise, snow can have a range of generic effects on flora and fauna. However, snow cover characteristics and distribution are dependant on prevailing climatic conditions in association with a range of other factors. In addition, the fauna and flora of the Australian Alps is very different from those of other nival areas. This is the subject of the next chapter.

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3 THE AUSTRALIAN ALPS

3.1 Introduction

The Australian Alps occur at the south-eastern end of the Great Dividing Range and consist of a series of disjunct peaks and plateaux extending from the Australian Capital Territory in a generally south-westerly direction through southern New South Wales to Victoria. The term “Snowy Mountains” refers to the portion of the Australian Alps in New South Wales, which is for the most part contained within the Kosciuszko National Park. The Snowy Mountains contain the largest portion of contiguous nival area on the Australian mainland. What follows is mainly relevant to the Snowy Mountains area, but some aspects are also relevant to other parts of the alps.

The limit of tree growth (the treeline) marks the lower elevational boundary of the alpine zone, and lies at about 1800-1900 m in the Snowy Mountains (Costin 1975; Costin *et al.* 2000), but gradually descends southwards through the Victorian Alps where it lies at about 1750 m (Green & Osborne 1994) and is as low as 800 m in south-west Tasmania (Kirkpatrick 1997). Most of the highest peaks on the Australian mainland, including Mt Kosciuszko (2228m asl) and Mt Townsend (2208m asl), occur within the alpine zone of the Snowy Mountains.

The subalpine zone extends below the treeline to the snowline where typically snow remains on the ground for about one month per year (Costin *et al.* 2000). Its lower boundary, at about 1400 m in the Snowy Mountains, is generally characterised by a change from woodland to tall montane forest (Costin *et al.* 2000). The subalpine zone surrounds the alpine zone in the Snowy Mountains, in the Victorian Alps but in Tasmania, the maritime climate means that an alpine zone can exist without the necessity of snow and hence the “subalpine” zone is less well defined. There are also small areas of subalpine habitats in the vicinity of the Barrington Tops north-west of Newcastle that may be subject to the occasional accumulation of snow for short periods of time.

For the purpose of this thesis, I use the term “nival area” to describe the combined alpine and subalpine areas in the Snowy Mountains that are subject to the accumulation of snow cover for at least one month per year.

3.1.1 Geology and geomorphology

The Snowy Mountains consist of a heavily dissected uplifted peneplain, which has been tilted so that it rises steeply in the west and descends gradually to the tablelands in the east. The current landforms reflect the geological and geomorphic history of the area and consist primarily of Silurian/Devonian granites that were intruded into older Ordovician sedimentary strata, and underwent a number of periods of uplift and erosion, most prominently during the Tertiary period in which the area reached approximately its present elevation (Brown *et al.* 1969). Erosion of the peneplain was encouraged by fracturing and faulting, which resulted in the incision of the long straight stream patterns which are evident today (Good 1992; Costin *et al.* 2000).

During the Pleistocene period, the eastern highlands were subject to extensive periglacial activity while only the highest parts of the ranges were significantly affected by glacial ice (Galloway 1963). Some periglacial processes such as diurnal frost heave and some solifluction are still evident today, while other features such as solifluction terraces, earth hummocks and boulderfields are now inactive remnants of earlier more dynamic periglacial processes (Good 1992).

Soils in the Snowy Mountains are as diverse as the vegetation that they support. About 15 great soil groups are now recognised and, although some reflect their parent material, soils in higher elevations are independent of rock types (Costin 1954) and have accumulated through aeolian processes (Good 1992) and have been mainly influenced by climatic changes since the Pleistocene (Good 1992). Alpine soils are typically dominated by organic matter and include alpine humus and associated soils. In subalpine areas, transitional alpine humus soils predominate in woodland, grassland and heath. Below these levels, podsoles dominate (Good 1992).

3.1.2 Climate

The climate of the Snowy Mountains is characterised by cool to mild summers and cold to very cold winters. Precipitation is relatively even throughout the year, and falls as snow predominantly during the colder months, although falls can occur throughout the year (Good 1992; Davis 1998).

Temperatures vary across the altitudinal range such that while the lowest winter minimum temperature recorded in the alpine area (Charlotte Pass, 1759m asl) was -23.8°C , summer maximum temperatures in lower areas may be 35°C or more (Good 1992; Happold 1998). The north-south orientation of the ranges intersects the prevailing west to east weather patterns. The resulting orographic effect produces heavy precipitation in the order of about 2800 mm in the alpine zone declining towards the east to about 750 to 1800 mm in the subalpine zone (Costin 1975; Good 1992). Climate averages for Crackenback (alpine zone, 1957m asl) and Perisher Valley (subalpine zone, 1735m asl) are shown in Table 3.1 and Table 3.2.

Table 3.1 Climate averages for Crackenback. (Source: Bureau of Meteorology).

	<i>Jan</i>	<i>Feb</i>	<i>Mar</i>	<i>Apr</i>	<i>May</i>	<i>Jun</i>	<i>Jul</i>	<i>Aug</i>	<i>Sep</i>	<i>Oct</i>	<i>Nov</i>	<i>Dec</i>
Mean Daily Max Temp (C°)	15.7	16.4	13.5	9.6	4.7	1.9	0.1	0.5	2.9	6.7	10.1	14.1
Mean No. Days >= 30 C°	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Highest Max Temp (C°)	26.4	27.0	25.5	24.8	15.8	12.5	12.4	10.5	15.0	17.0	24.0	26.3
Mean Daily Min Temp (C°)	6.2	7.1	4.9	1.7	-1.5	-3.5	-5.4	-4.9	-3.2	-0.7	1.9	4.8
Mean No. Days <= 0 C°	2.7	1.1	2.8	8.9	20.1	24.0	28.6	29.0	25.2	16.6	9.8	4.4
Lowest Min Temp (C°)	-7.7	-4.2	-6.7	-9.0	-11.0	-12.5	-14.7	-15.0	-13.4	-8.8	-8.5	-9.0
Mean 9am Wind Speed (km/hr)	22.8	20.1	20.2	23.4	25.5	25.4	31.3	33.2	31.4	28.1	23.2	25.2
Mean 3pm Wind Speed (km/hr)	20.0	17.7	18.4	21.5	24.2	25.4	30.8	32.9	30.1	27.7	21.4	22.3
Mean rainfall (mm)	103.0	91.9	124.1	118.3	141.2	85.8	130.2	134.0	150.8	168.3	162.4	111.1
Mean No. Raindays	12.3	11.4	13.2	12.5	15.5	13.9	15.2	16.2	15.6	16.7	15.0	11.3
Highest Monthly Rainfall (mm)	200.6	246.5	246.5	349.5	283.2	269.5	368.4	318.2	362.0	316.0	312.6	240.3
Lowest Monthly Rainfall (mm)	36.1	7.3	40.7	10.9	42.3	9.9	8.7	14.8	21.9	55.5	37.6	9.4

Table 3.2 Climates averages for Perisher Valley. (Source: Bureau of Meteorology).

	<i>Jan</i>	<i>Feb</i>	<i>Mar</i>	<i>Apr</i>	<i>May</i>	<i>Jun</i>	<i>Jul</i>	<i>Aug</i>	<i>Sep</i>	<i>Oct</i>	<i>Nov</i>	<i>Dec</i>
Mean Daily Max Temp (C°)	18.2	18.3	15.3	11.3	7.8	3.9	2.4	3.3	5.7	9.3	13.3	15.1
Mean No. Days >= 30 C°	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Highest Max Temp (C°)	30.0	27.2	25.4	22.0	18.0	19.0	10.5	13.0	16.0	21.0	25.5	25.0
Mean Daily Min Temp (C°)	5.7	5.8	3.6	1.0	-1.3	-3.5	-5.0	-4.3	-2.1	0.2	2.1	4.2
Mean No. Days <= 0 C°	2.7	2.4	5.6	13.3	18.7	25.1	28.8	27.0	21.7	15.4	8.8	3.3
Lowest Min Temp (C°)	-5.0	-7.0	-5.5	-11.3	-9.5	-18.0	-19.5	-15.0	-12.5	-10.8	-8.5	-5.9
Mean 9am Wind Speed (km/hr)	10.9	9.0	9.0	9.9	10.1	12.6	14.5	15.6	14.9	13.6	11.2	11.2
Mean 3pm Wind Speed (km/hr)	11.2	9.6	9.6	9.3	10.6	13.0	13.8	15.1	14.6	13.0	11.2	11.4
Mean rainfall (mm)	98.4	65.3	124.4	121.1	161.3	195.3	204.1	256.9	245.4	214.1	139.9	121.9
Mean No. Raindays	8.9	7.7	10.2	11.5	12.8	14.8	14.8	15.5	15.5	14.0	12.9	10.1
Highest Monthly Rainfall (mm)	182.5	158.6	446.8	278.4	331.0	580.0	445.0	699.0	489.0	411.2	292.0	238.0
Lowest Monthly Rainfall (mm)	23.0	5.0	26.9	17.1	33.9	54.0	37.0	20.3	82.7	65.0	22.0	26.1

3.1.3 Snow cover extent and duration

In Australia, snowpack is rare with the snow covered landscape comprising only about one fortieth of the snow covered area of Switzerland (Slatyer *et al.* 1984).

In the Snowy Mountains, the distribution of snow is dependent upon a range of variables including, most prominently precipitation and temperature but also topography, including elevation, aspect and slope (Good 1992; Davis 1998; Osborne *et al.* 1998; Ruddell 1998). Snow accumulates differentially as a result of the snow fence effect in which wind-blown snow is deposited in the calmer conditions on the leeward side of slopes causing a greater build up of snow. These areas are also subject to lower isolation due to their south-easterly aspect and thus have lower rates of ablation (Good 1992). As a result, snowpack becomes established in these areas earlier and often persists much longer than snowpack in more exposed locations. In some cases, snow patches have been known to persist throughout the summer until the following winter (Good 1992; Costin *et al.* 2000). In contrast, locations that receive less snow are more exposed to wind and receive more solar energy and therefore higher rates of ablation, generally have poorer snow conditions throughout the year.

Because of the low relief of the Snowy Mountains compared to mountain ranges in other parts of the world, small perturbations in atmospheric conditions can have a dramatic effect on the extent and duration of snow cover from one year to the next (Davis 1998). During the period 1954-1996, persistent snow cover at Spencers Creek (1830m asl) had an average duration of 22.5 weeks and maximum snow depth ranged from 39 to 270 cm (Osborne *et al.* 1998). At elevations down to 1528 m, snow cover lasts about 60 days (Slatyer *et al.* 1984), while many areas at even lower elevations are subject to marginal snow conditions with thin and patchy snowpack, which in some years may fail to form altogether.

3.2 Flora and Fauna

3.2.1 Flora

The flora of the Snowy Mountains has been the subject of detailed investigation, much of which is beyond the scope of this thesis. The following brief descriptions are based on Costin (1954); Read (1987); NPWS (1988); Costin *et al.* (2000); Mitchell (2002).

The alpine area above about 1850 m is dominated by snow grass *Poa spp.* – snow daisy *Celmisia spp.* herbfield and oxlyobium *Oxylobium ellipticum* – mountain plum-pine *Podocarpus lawrencei* heathland communities. A number of communities such as bogs, fens, feldmarks and sod tussock grasslands occur in areas where conditions prove favourable. Twenty-one locally endemic species are known to occur in this area (Costin *et al.* 2000).

The subalpine area between about 1500 and 1850 m is dominated by snow gum *Eucalyptus pauciflora* – *E. niphophila* woodland with a dense shrub understorey dominated by species of the *Oxylobium ellipticum* – *Podocarpus lawrencei* alliance of which leafy bossiaea *Bossiaea foliosa* is the most common shrub species. Woodland is interspersed with heathland and tussock grassland communities of similar floristic composition to those in the alpine zone. At its lower extremity, the subalpine zone grades into montane forests and woodlands dominated by snowgum alliances including *E. pauciflora*, mountain gum *E. dalrympleana*, manna gum *E. viminalis* and black sallee *E. stellulata*, with alpine ash *E. delegatensis* dominating wetter south-east aspects.

3.2.2 Fauna

Compared to snow-covered areas in other parts of the world, particularly in the northern hemisphere, most of the vertebrate taxa of the nival areas of the Australian Alps are quite depauperate. The Snowy Mountains are home to a range of fauna including a number of snow-adapted species whose ranges have contracted since the Pleistocene and which are now only found in the alpine and subalpine areas.

Larger vertebrate species such as the eastern grey kangaroo *Macropus giganteus*, red-necked wallaby *Macropus rufogriesus*, swamp wallaby *Wallabia bicolor* and common wombat *Vombatus ursinus*, as well as the larger possums, are common

in lower areas. At higher altitudes, where snowfall becomes a predominant feature of the landscape during winter, most of these larger species that are ill adapted to snow conditions are absent or only occur sporadically (Green & Osborne 1994).

Species adapted to snow conditions are either those which hibernate, such as bats, the echidna *Tachyglossus aculeatus* and mountain pygmy-possum *Burramys parvus*, or those which remain active throughout the year but are either small enough to continue to forage beneath the snow or have other biological or ecological adaptations to deal with life above the snow (Green & Osborne 1994). Common species of year-round residents include the broad-toothed rat *Mastacomys fuscus*, bush rat *Rattus fuscipes*, dusky antechinus *Antechinus swainsonii* and agile antechinus *A. agilis*. All are known to remain active throughout the winter in the subnivean space (Carron 1985; Happold 1989; Green 1998; Happold 1998).

There are no endemic bird species in the Snowy Mountains, most being common or widespread species found in lower areas or long distance migrants which return to the mountains during spring and summer as food becomes more abundant (NPWS 1988; Green & Osborne 1994). In the treeless alpine zone the most common birds are the little raven *Corvus mellori* and Richard's pipit *Anthus novaeseelandiae*.

A range of reptile and amphibian species has been recorded, but the number of species decreases with altitude. Only three families of reptiles and two frog species are known to occur above the snowline (Green & Osborne 1994). Apart from the native galaxias *Galaxias olidus* the stream fish fauna in the mountains is dominated by the introduced salmonid species in many areas.

Like their vertebrate counterparts, many invertebrates in the Snowy Mountains are physically adapted to, or have life cycles that suit, the prevailing conditions in the mountains. Although little is known about the invertebrate fauna of the Snowy Mountains (NPWS 1988), some 979 species in 75 families have been recorded in the alpine area (Green 1987).

A number of threatened or uncommon species occur in the Snowy Mountains and include the broad-toothed rat *Mastacomys fuscus*, smoky mouse *Pseudomys*

fumeus, mountain pygmy-possum *Burramys parvus*, spotted-tailed quoll *Dasyurus maculatus*, olive whistler *Pachycephala olivacea*, Latham's snipe *Gallinago hardwicki* and the corroboree frog *Pseudophryne corroboree*.

Introduced species include the house mouse *Mus musculus*, black rat *Rattus rattus*, rabbit *Oryctolagus cuniculus*, hare *Lepus europaeus*, fox *Vulpes vulpes*, dog *Canis familiaris* and cat *Felis catus*.

3.3 Small mammal fauna

The alpine and subalpine areas of Australia have relatively few species of small mammals when compared with other parts of south-eastern Australia (Carron 1985; Green & Osborne 1994). Only the mountain pygmy-possum *Burramys parvus* is endemic to the alpine and subalpine areas of Australia, while in the Snowy Mountains the broad-toothed rat *Mastacomys fuscus* can be found down to 1000 m while the other small mammal fauna are also found extensively at lower elevations. The following species represent the main species known to remain active in the subnivean space.

3.3.1 Bush rat

The bush rat *Rattus fuscipes assimilis* is a "new endemic" murid rodent with a relatively wide distribution across south-eastern Australia. It is one of several subspecies that occur in Australia from northern Queensland to the south-west of Western Australia (Lunney 1995). It occurs throughout the alpine and subalpine zones and is perhaps the most common small mammal in nival areas of the Snowy Mountains (Green & Osborne 1994). For males, head/body length and tail length average 165 and 158 mm respectively, and they have an average weight of about 125g. Females weigh 10-20 percent less (Lunney 1995).

This species is omnivorous and its diet can vary considerably between populations and over time (Watts 1977; Woodside 1983). In the nival area, its diet is diverse, and includes fungi and invertebrates as well as a range of plant material from both monocotyledons and dicotyledons including seeds, flowers, fruit, bark and leaves (Carron *et al.* 1990). This species is actually the most insectivorous of all the native rats in Australia (Lunney 1995). Because of its catholic diet, it can readily adapt to changing food abundance and while during

the warmer months fungi make up the bulk of the diet, monocotyledons predominate during the winter (Carron *et al.* 1990).

In nival areas, breeding occurs in spring and summer during which several litters may be produced (Carron 1985; Green & Osborne 1994), but in other parts of its range breeding can occur throughout the year (Lunney 1995). Adults generally live for about one year, but some may survive to breed over two seasons. Throughout its range, *R. fuscipes* is mainly nocturnal and mostly found in structurally complex habitats including heathlands, woodland and boulderfields that provide adequate cover (Hall & Lee 1982; Woodside 1983; Carron 1985). Bush rats generally inhabit burrows throughout the year; just before winter an increased level of burrow excavation is observed which is thought to be an attempt to increase the depth of the burrow in preparation for the onset of colder wet weather (Green & Osborne 1994).

3.3.2 Broad-toothed Rat

The broad-toothed rat *Mastacomys fuscus* is an "old endemic" murid rodent whose name refers to the relative size of its molars which are larger than its palate. It has a head and body length of about 161 mm, a tail length of 116 mm and an average weight of 122g (Happold 1995). Its distribution is confined to areas above 1000 m in New South Wales, but occurs down to sea level in Victoria and Tasmania (Finlayson 1933; Happold 1995; Green & Osborne 2003).

The diet of *M. fuscus* consists primarily of grasses with occasional contributions of seeds and the leaves of shrubs and does not vary significantly in the nival period (Carron *et al.* 1990; Happold 1995). Large grass nests are constructed under shrubs or logs and several individuals nest communally during winter; a system of runways leads from the nest to preferred feeding grounds (Carron 1985). Although occurring throughout the nival areas in a range of habitat types including woodland and heathlands its largest concentrations are observed in tall wet heaths in proximity to watercourses and suitable forage (Carron 1985; Green & Osborne 1994).

Breeding occurs between December and March and usually two litters of young can be produced in a season. The young do not reproduce until the following year (Happold 1995).

A key indicator of the occurrence of this species is the presence of characteristic runways and distinctive droppings, which are especially apparent after the disappearance of snow and often occur in association with the above-ground grass nests used during the winter (Green & Osborne 1994). The nesting above ground during winter is thought to predispose them to increased predation by foxes *Vulpes vulpes* that may excavate down to the nests through the snowpack. This, combined with the fact that, compared to *R. fuscipes* this species is quite docile, has led to broad-toothed rats making a disproportionate contribution of the diet of foxes (Green 2002).

3.3.3 Dusky Antechinus

The dusky antechinus *Antechinus swainsonii* is the larger of the two small dasyurid marsupials to inhabit the Snowy Mountains. Like *R. fuscipes* it is relatively widespread in south-eastern Australia, occurring from sea level through to the summit of Mt Kosciuszko at 2228 m. Head and body length averages 120 mm for males and 110 mm for females (Dickman *et al.* 1983). Tail length averages 107 mm and 92 mm for males and females respectively and males are characteristically heavier than females but converging at higher altitudes (averaging 45g and 40g respectively) (Dickman *et al.* 1983). Females that survive into their second year will also grow to about 60g (Green & Osborne 1994).

This species is fossorial and its diet primarily consists of invertebrates including Coleoptera, Lepidoptera, Hemiptera, Orthoptera and Blattodea, but it will also take small vertebrates such as lizards (Green 1989). This species has been described variously as crepuscular or nocturnal (Green & Osborne 1994) and diurnal (Carron 1985; Dickman 1995). Habitat preference is similar to that of *R. fuscipes* in that it is generally associated with complex understorey vegetation and litter in which it forages for most of its invertebrate food. It is a solitary animal, nesting in leaf- and bark-lined burrows under rocks, in logs and in tree hollows (Dickman *et al.* 1983; Green & Crowley 1989).

Populations of this species, and indeed the smaller *A. agilis*, fluctuate greatly across seasons, due in part to the unique life history of this species. Breeding is highly synchronised, with mating occurring in early to mid September in the

Snowy Mountains, often while the ground is still covered in snow (Green & Crowley 1989; Green & Osborne 1994). Within about 2 to 3 weeks of mating all of the males die (Dickman 1982). The capture of a few very large male *A. swainsonii* during summer in recent years (G. Sanecki and K. Green, unpublished data) suggest that this fate may not befall some males who appear to survive into a second year.

3.3.4 Agile Antechinus

The agile antechinus *A. agilis* was originally considered to be the brown antechinus *A. stuartii* until distinguished by electrophoretic methods (Dickman *et al.* 1988). Head and body length averages about 95 mm for males and 88 mm for females, and males are characteristically heavier than females, averaging about 25g and 18g respectively (Dickman *et al.* 1983). The distribution of *A. agilis* is widespread in south-eastern New South Wales and Victoria, overlapping with the range of *A. stuartii* in the vicinity of Jervis Bay (Dickman *et al.* 1988).

Unlike *A. swainsonii*, *A. agilis* is scansorial, but at higher elevations and in the absence of trees, (and when snow cover is present), it will forage on the ground. It is thought that this places *A. agilis* at a disadvantage as it is unable to compete successfully with *A. swainsonii* in the absence of sufficient vertical strata, as occurs above the treeline or during winter when it is restricted to the subnivean space (Dickman *et al.* 1983). *A. agilis* has been recorded at altitudes over 2000 m but above the treeline it is almost restricted to rocky habitats (Green & Osborne 1979). This species is mainly nocturnal throughout the year, and its main food consist of a range of invertebrates most of which are derived from trees. At higher elevations once restricted to ground level its diet more closely resembles that of *A. swainsonii* (Dickman *et al.* 1983; Green 1989)

Mating takes place around the same time as for *A. swainsonii* and, like its larger counterpart, males die within a few weeks of mating, and only about 20% of females survive until the following year (Wood 1970). Unlike *A. swainsonii*, *A. agilis* nests communally in leaf-lined nests in tree hollows, logs or underground (Green & Crowley 1989; Green & Osborne 1994) which is thought to substantially reduce their energy needs.

3.3.5 Mountain Pygmy-possum

The mountain pygmy-possum *Burramys parvus* (Marsupialia: Burramyidae) is a true endemic of the alpine and subalpine zone of the Australian Alps and is the only species of small mammal in Australia whose known range is entirely contained within the nival area (Mansergh & Broome 1994). The distribution of *B. parvus* is extremely limited, occurring within a total area of no more than 500 km² above about 1400 m; specimens have been found at the summit of Mt Kosciuszko at 2228m (Calaby 1995). It is most commonly found in boulderfields of periglacial origin, and the total habitat available to *B. parvus* is estimated at approximately 10 km².

Originally described from fossil fragments in 1895, it was considered to be extinct until a live specimen was captured in a ski lodge in the Victorian Alps in 1966 but first found in the wild in the Snowy Mountains. Fossil evidence indicates that this species was once more widespread, particularly during periods of glacial advance when the snowline was considerably lower than it is today. It is thought that its current limited distribution is due in part to the contraction of the snowline to its present level (Mansergh & Broome 1994). Males are slightly larger than their female counterparts, with a head and body length of 115 mm, tail length of 148 mm and weighing about 43g, compared to 100 mm, 140 mm and 40g for females (Calaby 1995).

During the non-nival period, *B. parvus* is omnivorous with insects comprising the largest component of the diet, especially in the breeding season (Mansergh *et al.* 1990). Unlike the other small mammal species of the nival areas that remain active throughout the year, *B. parvus* is a true hibernator and therefore all but inactive throughout the winter months, except during short bouts of waking when it may feed from cached food reserves or forage in the vicinity of its nest (Broome 1989; Mansergh & Broome 1994). Their presence of *B. Parvus* remains in fox scats collected during winter suggests that winter activity may be greater than generally thought (Green & Osborne 1981). Its favoured habitats are in rocky areas such as boulderfields, but it has been occasionally found in other habitats including heath and woodland (Mansergh 1984; Mansergh & Broome 1994).

Breeding occurs during spring as pouch young are present during November and December, and litters of four are usual (Calaby 1995). *B. parvus* is relatively long-lived compared to other small mammals, with some females surviving up to four years in the wild (Mansergh 1984).

3.3.6 Other species

Other species of small mammals are known to occur in the nival zones but remain uncommon. The introduced black rat *Rattus rattus* and common house mouse *Mus musculus* have been noted to occur in both the subalpine and alpine zones but their occurrence is generally associated with man-made structures. *Mus musculus* has been recorded in mountain huts, whilst *R. rattus* is more likely to be found in the vicinity of ski resorts (Green & Osborne 1994). Native species, including the eastern pygmy-possum *Ceratetus nanus*, water rat *Hydromys chrysogaster* and the smoky mouse *Pseudomys fumeus*, occur sporadically at the lower margins of the subalpine zone although the water rat has been observed at locations above 1700 m (G. Sanecki pers obs). The distribution of the smoky mouse is poorly known and although it may occur more widely, it is only known from a few sites in Victoria and the Australian Capital Territory. Although these species are not major components of nival ecosystems in Australia, their presence is of particular interest especially when considering the possible implications of changing snow cover regimes, and the possibility that with decreasing snow cover they may become more common (Green & Pickering 2002; Hughes 2003).

3.3.7 Small mammals and snow

Although there is a considerable body of work on small mammal species in Australia and to a lesser extent in the Snowy Mountains, relatively few studies have considered the biology of these species during the nival period and in particular in relation to snow cover. What is known is therefore drawn from a few studies and the extrapolation of results from overseas studies and observations.

One of the key tenets of snow ecology is the role snow plays in decoupling the subnivean environment from harsh supranivean conditions (Pruitt 1957, 1960, 1984; Halfpenny & Ozanne 1989; Auerbach & Halfpenny 1991), because,

depending on its density and thickness, the snow layer is a relatively good insulator (Marchand 1982). This also has been a key aspect of ecological thinking in the nival areas of Australia (Carron 1985; Happold 1989; Green 1998). Like their northern hemisphere counterparts, small mammals in Australian nival areas spend the winter months beneath the snow in the subnivean space (Green 1998). Although it has been demonstrated that a similar decoupling of the subnivean and supranivean environment occurs in the Australian Alps and it is likely that small mammals derive benefit from the thermally stable environment provided by the subnivean space (Carron 1985; Green 1988; Happold 1989), there is evidence to suggest that the responses of small mammals to snow in Australia are not the same as those of animals occurring at higher latitudes and altitudes in the northern hemisphere. In particular, it is possible that due to our milder climatic regime, the thermal stability of the subnivean space may not be as crucial to permit successful overwintering.

Burrhamys parvus has received considerable recent attention because it is one of the handful of true hibernating mammalian species in Australia. This species hibernates in or close to boulderfields and can remain inactive for up to seven months of the year within underground hibernacula that maintain ambient temperatures of 1.5 – 3°C (Walter 1996; Kortner & Geiser 1998; Walter & Broome 1998). Periodic arousal occurs during winter, although the energetic costs of arousal are believed to be disadvantageous to their survival (Walter 1996). Of the small mammal fauna in the mountains, this species is arguably the most dependent on the presence of adequate snow cover to provide efficient thermal buffering (Walter 1996).

Of the remaining small mammal fauna, the occurrence of *R. fuscipes* and *A. swainsonii* in the subnivean space was first reported in a general survey of fauna above 1500 m (Osborne *et al.* 1979). *Rattus fuscipes* also was captured on the snow surface, and its over snow movement subsequently described from the presence of tracks in the snow (Osborne 1980). Over snow movement by small mammals is governed by the presence of access holes to and from the subnivean space, the distances travelled over snow increasing in areas devoid of trees where access holes are sparse (Green 2000).

Carron (1985) captured *R. fuscipes*, *M. fuscus* and *A. swainsonii* in the subnivean space as part of a comprehensive study of their ecology, indicating that all three are relatively active over winter. Using life history and behavioural adaptations as an indicator of how well adapted they were to snow cover, she considered that *M. fuscus* was the best adapted and *R. fuscipes* the least well adapted, while *A. swainsonii* was intermediate between the two, describing the former as K-selected and the latter two as r-selected. These life history strategies are reflected in the demography of the three species; *M. fuscus* with its lower fecundity show less dramatic fluctuations through the year, in contrast to the other two species that show a rapid increase in population size each spring and summer, followed by a dramatic decline through autumn and winter (Carron 1985; Green 1988; Happold 1989, 1998).

Specific responses to snow by each species are not well known. In contrast to overseas workers who note that small mammals generally avoid areas of shallow snow (Pruitt 1984; Halfpenny & Ozanne 1989; Auerbach & Halfpenny 1991), small mammal detections in Australia were correlated with shallow snow depths (Carron 1985). However, these findings were based on a winter trapping grid of only 30 points located at Smiggin Holes, thus any extrapolation beyond this scale needs to be viewed conservatively.

The movement of small mammals in the subnivean space is also poorly understood and observations are conflicting in some cases. For example, trapping results indicated that *M. fuscus* was relatively active beneath the snow and that its movements were similar to those of *R. fuscipes* (Carron 1985). However, radio telemetry showed that *M. fuscus* was all but inactive throughout the nival period, apart from brief periods foraging in proximity to a communal nest (Bubela *et al.* 1991). There is an indication that snow cover provides protection from predators and enables *Antechinus swainsonii* to exploit habitats such as grasslands that are not used by them when snow is absent (Green & Crowley 1989)

3.4 Human history

Indigenous Australian peoples are thought to have been visited the alpine and subalpine areas for several thousand years (Flood 1980). Unlike indigenous peoples in other parts of the world, there is no indication that Australian aboriginals had significant interactions with the area during the nival period, instead retreating to lower lying and warmer areas. Their main activities in the Alps occurred during the warmer months when tribes gathered to feast upon Bogong moths that congregated in the mountains during the summer (Flood 1980; Good 1992).

With the arrival of Europeans in Australia, it was not long before settlement and expansion saw the Alps subject to new influences. The mountains had been recorded by several expeditionary parties commencing with Currie and Ovens in 1832 (Good 1992). Some of the most significant early investigations of the mountains were made by two Polish men, Dr John Lhotsky and Count Edmund Strezlecki. Lhotsky explored the area from the east and is thought to have possibly reached the highest peaks first, but it is Strezlecki who is credited with identifying and naming the highest peak on the mainland (Mt Kosciuszko) after the Polish patriot and hero of the American war of independence, Tadeusz Kosciuszko. This is a somewhat bemusing event given that New South Wales was a colony of the British Empire at the time; one must assume that the colonial leaders were not aware of Kosciuszko's exploits.

Scientific investigation in the mountains also become more common with workers such as William Clarke, Ferdinand von Mueller, Richard Helms and Clement Wragge making major contributions in the 19th Century. In the 20th century, the work of Alec Costin and others resulted in improved understanding of the importance and fragility of alpine biota and contributed significantly to the eventual demise of grazing in the high country of New South Wales and the conservation of the alpine and subalpine areas.

Earliest records indicate that the Snowy Mountains were being used by graziers in the early 1800's; most famed was the 'Excelsior' run of James Spencer which took in much of the alpine and subalpine areas of the Snowy Mountains in the early part of the century. Gold was discovered in the Alps in the vicinity of Kiandra resulting in an influx of tens of thousands of diggers to the region in the

1860's, but the rush had ended by 1906. Grazing continued to be the main activity in the Australian Alps, albeit under increasing levels of scrutiny and control, until 1949 when the development of the Snowy Mountains Hydro-electric Scheme commenced and ushered in its eventual demise. Grazing was eliminated from the Snowy Mountains because of concerns that the hydro scheme would be rendered useless as a result of excessive siltation from the erosion caused by livestock and the practices of graziers including yearly burning to stimulate fresh grass growth. In the southern parts of the Australian Alps located in Victoria, grazing still continues in some areas.

Skiing in the Alps was first documented in the Kiandra goldfields where the first ski club in the world was formed by miners and others who found enjoyment and sport in fixing planks of wood to their boots and sliding down the slopes (Hueneke 1994). The construction of the Snowy Mountains Scheme, involving the employment of high numbers of migrants from areas of Europe where skiing is a major winter sport, spurred the establishment of the recreational ski industry in Australia.

Today the combination of summer tourism to the high peaks of the Australian Alps and winter recreation form the basis of visitation to the area which is for the most part contained within the Kosciuszko National Park. Apart from park and ski resort operations, Snowy Hydro Ltd is perhaps the predominant non-conservation organisation functioning in the park. It undertakes a range of activities related to the operations of the Snowy Mountains Scheme and maintains a range of infrastructure and associated management access trails.

3.5 Significance and threats

The Australian Alps comprise a biologically diverse and unique part of Australia and indeed the world. Kosciuszko National Park is a UNESCO Biosphere Reserve.

The Snowy Mountains today maintain their unique character and fauna, but there are a number of threats that could have far reaching implications, not only for the integrity and conservation values of the Alps themselves but also potentially for the people and industries that have come to rely upon the mountains as a source of energy, water and income.

The geographical position of the Australian Alps combined with the low height of the mountains means that the nival climate is a rather marginal one with large variations in snow cover from year to year. It is therefore likely that this region will be one of the first to reflect any sign of climate change (Davis 1998; Green & Pickering 2002). Impacts and threats to the mountains are likely to be similar to those in other nival areas outlined in the previous chapter. More specifically, however, with decreasing snow cover, the ski industry will become more marginal over time, with some studies suggesting that in a worst case scenario there will be no possibility of supporting a ski industry by 2070 (Konig 1998; Whetton 1998). Additionally, climate change resulting in declining snow cover and changes to hydrological regimes may have a significant impact on the operation of the Snowy Mountains Hydro-electric Scheme and flow-on implications for downstream users of waters such as irrigators and urban areas that rely on water released from the system (SMHEA 1993).

The Australian Alps are climatically considerably milder when compared to other nival areas especially higher northern hemisphere latitudes. Except for *B. parvus* the small mammal fauna are not restricted to the nival areas of Australia. Almost nothing is known about their distribution and behaviour in the subnivean space, but there are some indications that their responses may not be the same as species from colder areas. Effective conservation and management requires a good understanding of the ecology of the organisms in the alps throughout the year. With snow cover being a substantial factor in the alps it is important to understand its role in the ecology of various organisms. The work that follows was undertaken in an attempt to fill in the gaps in knowledge regarding the distribution and behaviour of small mammals in the subnivean space.

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4 THE CHARACTERISTICS AND CLASSIFICATION OF AUSTRALIAN SNOW COVER: AN ECOLOGICAL PERSPECTIVE

Submitted to *Arctic, Antarctic and Alpine Research*

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4.1 Abstract

In nival areas, snow plays an important role in the ecology of flora and fauna, but is highly variable in depth, structure and other characteristics over a whole range of spatial and temporal scales. Australian research on snow ecology has relied upon, but has also sometimes been misled by, overseas research when incorrect assumptions have been made about the characteristics of Australian snow when compared to snow in other areas. One of the reasons for this is the lack of a suitable generic system that could easily be applied by researchers to classify snow cover.

We provide a description of the structural and thermal characteristics of snow cover in the Snowy Mountains of south-eastern Australia. We then use these to classify Australian snow cover using the classification system developed by Sturm *et al* (1995). Using this system, the snow cover that occurs in the main alpine and subalpine region of the Snowy Mountains is classified primarily as maritime in areas where there is sufficient accumulation, and as ephemeral at lower elevations and on ablating aspects. Maritime snow is generally deep (> 100 cm), with a density >0.30 gcm⁻³. The snow-ground interface is maintained within 1°C of freezing and relatively high air temperatures promote destructive metamorphism throughout the winter. The formation of depth hoar, which is considered to be important in facilitating the development of the subnivean space, does not occur under these conditions.

Ephemeral snow is characterised by warm shallow snow that often melts before new snow is deposited. Basal melt is a common feature of snow cover in the Snowy Mountains throughout most of the winter.

These findings have implications for the correct interpretation of research into the role of snow in ecological processes, both in Australia and elsewhere. We reappraise the processes responsible for the formation of the subnivean space under Australian snow conditions and discuss the importance of these processes for understanding the ecology of fauna in the subnivean space.

We propose that ecological researchers working in snow-covered areas need to provide a more explicit description of the snow conditions in which their work is undertaken. Where possible, the description should include the type of snow

cover conditions using a relevant classification system, or as a minimum, should include a description of basic structural and thermal properties of the snow pack that would allow other researchers to view the work in an appropriate context.

4.2 Introduction

The presence of snow in the landscape is a significant factor in the ecology of organisms (Formozov 1946; Pruitt 1960, 1984a; Halfpenny & Ozanne 1989; Green & Osborne 1994; Stenseth *et al.* 2004). Despite the considerable literature on snow itself and, to a lesser extent, on its influence in the biosphere, the study of the ecological aspects of snow remains a relatively underdeveloped discipline (Halfpenny & Ozanne 1989).

In Australia, the area subject to seasonal snow cover lasting at least 2 months comprises about 1675 km², or about 0.02 % of the mainland (Green 1998a). Nevertheless, Australian alpine and subalpine areas have developed a unique biota characterised by considerable endemism (Green & Osborne 1994; Mansergh & Broome 1994; Costin *et al.* 2000). As might be expected, snow-related research is less developed in Australia compared with regions where snow plays a much greater role in landscapes and the lives of human inhabitants. As a result, the understanding of snow ecology in Australia has been influenced by (and is to some extent reliant on) research undertaken overseas, especially in the northern hemisphere where studies are usually conducted at higher latitudes and/or elevations than in Australia. The transfer of northern-hemisphere research to Australia (or any other place for that matter) without due consideration of the possible differences in snow cover characteristics has the potential to create problems and lead to spurious assumptions and research conclusions. Any consequent misconceptions can affect the study of organisms that interact with snow at some point in their life cycles.

A further complicating factor is the tendency of research on snow as a physical phenomenon to be relatively divorced from considerations of snow as an ecological attribute. For example, although a number of workers have described meteorological and hydrological aspects of snow under Australian conditions (Costin *et al.* 1961; Brown & Millner 1989; Davis 1998), the physical characteristics of Australian snow (Ruddell 1998), the spatial distribution and duration of snowpack in the Australian Alps (Slatyer *et al.* 1984; Duus 1992; Osborne *et al.* 1998), the effects of climate change (Ruddell *et al.* 1990; Whetton *et al.* 1996; Whetton 1998) and the likely effects of climate change on the ski industry (Galloway 1988; Konig 1998; Hennessy *et al.* 2003), few of these

authors make more than a passing reference to the ecological implications of their findings. Conversely, in ecological research, snow cover is sometimes treated as if independent of local or regional influences, something that is clearly not the case (Berry 1981; McKay & Gray 1981; Davis 1998). Where ecologists have attempted to integrate snow as a factor into the study of alpine and subalpine biota (Green 1982; Carron 1985; Green 1988; Bubela *et al.* 1991; Happold 1998), some aspects of snow cover characteristics are described. However, researchers have not used their data to make meaningful comparisons between Australian snow cover conditions and those occurring elsewhere, especially those from regions from which we have derived so much of our understanding of nival ecology processes. The study of small mammals in the subnivean space provides a case in point.

The importance of snow for insulating the subnivean environment, thereby maintaining relatively stable and warm temperatures in comparison to the supranivean environment, has been acknowledged by Australian (Carron 1985; Green 1988; Happold 1989, 1998) and overseas researchers (Formozov 1946; Pruitt 1960; Marchand 1982; Pruitt 1984a; Halfpenny & Ozanne 1989; Auerbach & Halfpenny 1991). The presence of depth hoar is considered an important factor in subnivean space development (Coulianos & Johnels 1962; Pruitt 1984b). Depth hoar is low-density snow, generally occurring at lower parts of the snow pack, and is thought to enable subnivean fauna to move beneath the snow by burrowing within this layer (Pruitt 1984a; Halfpenny & Ozanne 1989; Auerbach & Halfpenny 1991). Australian researchers have assumed, based on overseas research, that depth hoar is a factor contributing to the formation of the subnivean space, particularly in the absence of suitable vegetation or other structures that are important in its development (Green & Osborne 1994; Green 1998b). If depth hoar was found not to occur under Australian snow conditions, then conclusions about the extent of the subnivean space would need to be re-examined.

Assumptions such as these regarding the characteristics of snow cover highlight the need for a suitable classification scheme that would facilitate cross-regional classification of snow cover. While the systems of Magono & Lee (1966) and Colbeck *et al.* (1992) provide a framework for classifying snow based on crystal

structure and other features, these systems are not useful for describing classes of snow cover at landscape scales (Sturm *et al.* 1995). Early attempts to devise large-scale snow classification systems did not gain wide acceptance because they were based upon different combinations of descriptors and consisted of different numbers of classes that did not necessarily correspond to classes in other systems; in general they were often of little use beyond a local area. For a review and summary of these systems see Sturm *et al.* (1995).

Sturm *et al.* (1995) noted the need for a more generic system for classifying various types of snow cover. They developed a system, which relies on observable snow cover properties and uses characteristics that are easily measured in the field or readily available from other sources.

This paper has two objectives. The first is to provide a brief description of the characteristics of Australian snow using data collected during the winters of 2002 and 2003. The second is to use these data supplemented by additional records to classify Australian snow according to the system developed by Sturm *et al.* (1995), hereafter referred to as the Sturm system, thus placing Australian snow cover in a more global context. In doing this, we hope to improve the general understanding of the characteristics of Australian snow cover and how they relate to other areas. We also discuss some of the ecological considerations arising from our findings. We highlight how it is possible to use readily available data and/or data that are easily collected during a research program to provide a classification of characteristics of snow cover within which the work was undertaken. This, in turn, will enable others to make more informed assessments of research outcomes.

4.3 Methods

4.3.1 The Sturm classification system

The details of the Sturm system are given in Sturm *et al.* (1995). What follows is an overview of the system including the elements used for this paper.

The Sturm system has six main classes that Sturm *et al.* (1995) suggest generally reflect the natural grouping of snow cover characteristics. These include: tundra, taiga, alpine, maritime, ephemeral and prairie (Figures 4.1 and 4.2). A seventh “mountain” class is defined as a highly variable snow cover greatly influenced by

varying solar radiation and wind patterns, often resulting in a number of different snow types within a relatively small area.

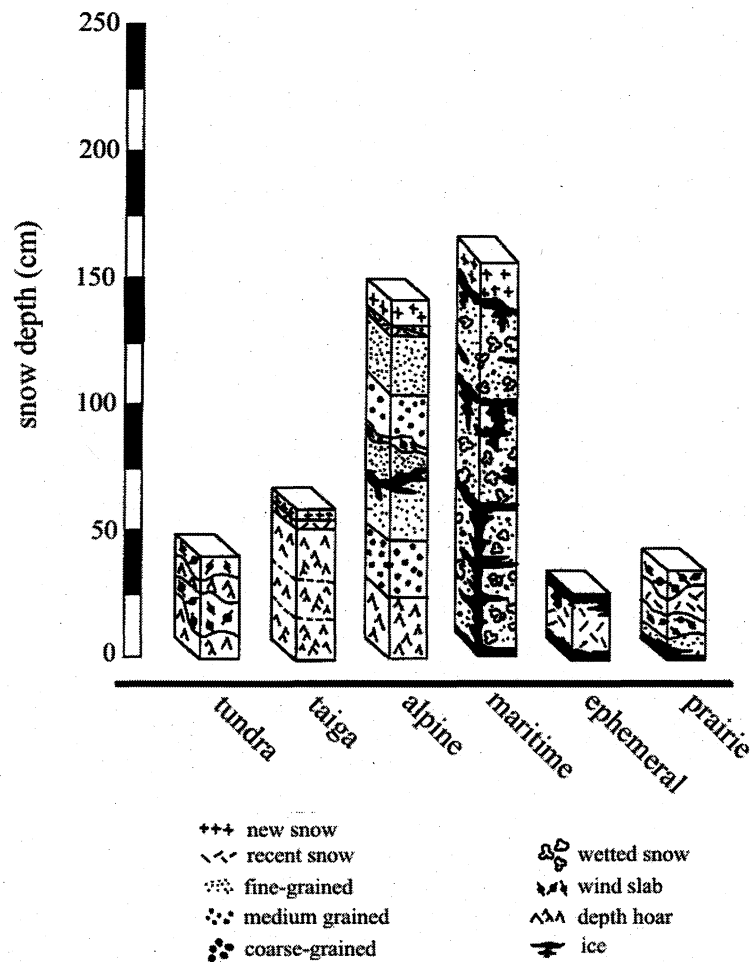


Figure 4.1 Stratigraphic and textural profiles of snow cover classes. From Sturm *et al.* (1995)

The names chosen for the classes, although referring to either a vegetation type or geographic location, do not imply that the classification is based upon the location of the snow cover or its relationship to a specific biome. The system relies solely on the physical characteristics of snow for classification; thus, “taiga” or “maritime” snow may occur in locations that are not taiga or close to the sea respectively, but have characteristics of the particular snow cover type. For example, “taiga” snow cover is of thin to moderate depth, its stratigraphic profile is dominated by depth hoar, and it exhibits few melt features. These characteristics reflect the particular conditions under which the snow was deposited and then remained. In the case of taiga snow cover, we would expect

it to occur in cold climates with consistently low average winter temperatures. Taiga snow also would not be greatly affected by wind; a reflection of its tendency to occur in forested areas.

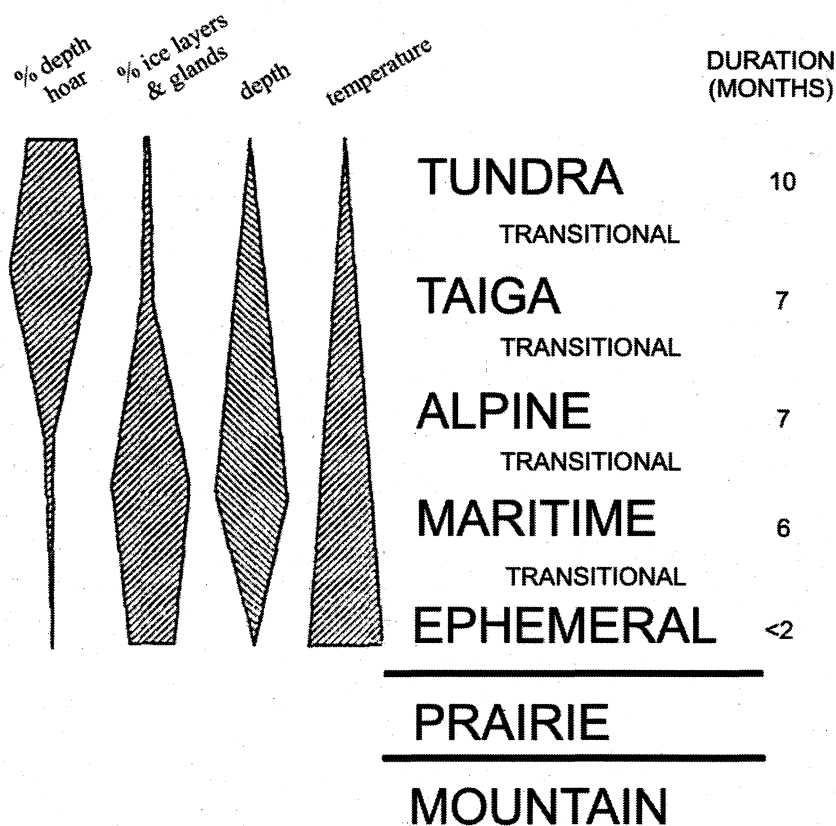


Figure 4.2 Attributes of snow cover classes. From Sturm *et al.* (1995)

The Sturm system was designed to permit classification without the need to dig snow pits and make stratigraphic observations, which can be time consuming and often require special skills and equipment. The classification can be undertaken using average winter values for four variables (snow depth, air temperature, snow-ground interface temperature and density) that are easily measured in the field, or available from routine snow course observations and weather stations. A fifth parameter, vertical temperature gradient, is based on a combination of snow depth and the difference between air and snow-ground interface temperature.

Unlike the system presented by Colbeck *et al.*(1992), the Sturm system is designed not only to consider aspects of snow properties within each snow layer, but also consider the sequence of layers in a stratigraphic manner, their interaction and lateral variation. In addition, it takes account of variations in characteristics of snow cover with time and in response to a number of factors including climate, weather and wind history both during and after deposition.

4.3.2 The study area

Our study area was located within the Snowy Mountains, Kosciuszko National Park (36.0°S 148.3°E) in south-eastern Australia. This region includes the Australian continent's highest mountain Mount Kosciuszko (36.456°S, 148.264°E, 2228 m). The Snowy Mountains include most of the northern extent of the Australian Alps and encompass the largest contiguous areas of alpine and subalpine habitats on the Australian mainland.

The Australian Alps consist of a disjunct series of peaks and plateaux extending for about 350 km in a generally north-easterly direction from their southern extent at about 37.5°S 146°E to 35°S 149°E (Figure 4.3). Snow cover that remains on the ground for any length of time occurs in two main zones. The alpine zone, defined as the area above the tree line, is characterised by continuous snow cover for at least four months per year. The subalpine zone lies between the upper limit of the tree line and the snowline at its lower limit. It is subject to continuous snow cover for at least one month (Green 1998a; Costin *et al.* 2000). The tree line occurs at 1800-1900 m in the north, descending to 1750 m in the south. In a similar manner, the subalpine zone commences at a lower elevation in the south (around 1400 m) but occurs above 1500-1600 m in the north (Green 1998b). The treeless alpine area has a diverse assemblage of vegetation communities, but is typically characterised by herbfields and heathlands (Costin *et al.* 2000). The subalpine area is a mosaic of woodlands dominated by Snow Gum, *Eucalyptus pauciflora*, wet and dry heathlands and tussock grassland (Green & Osborne 1994).

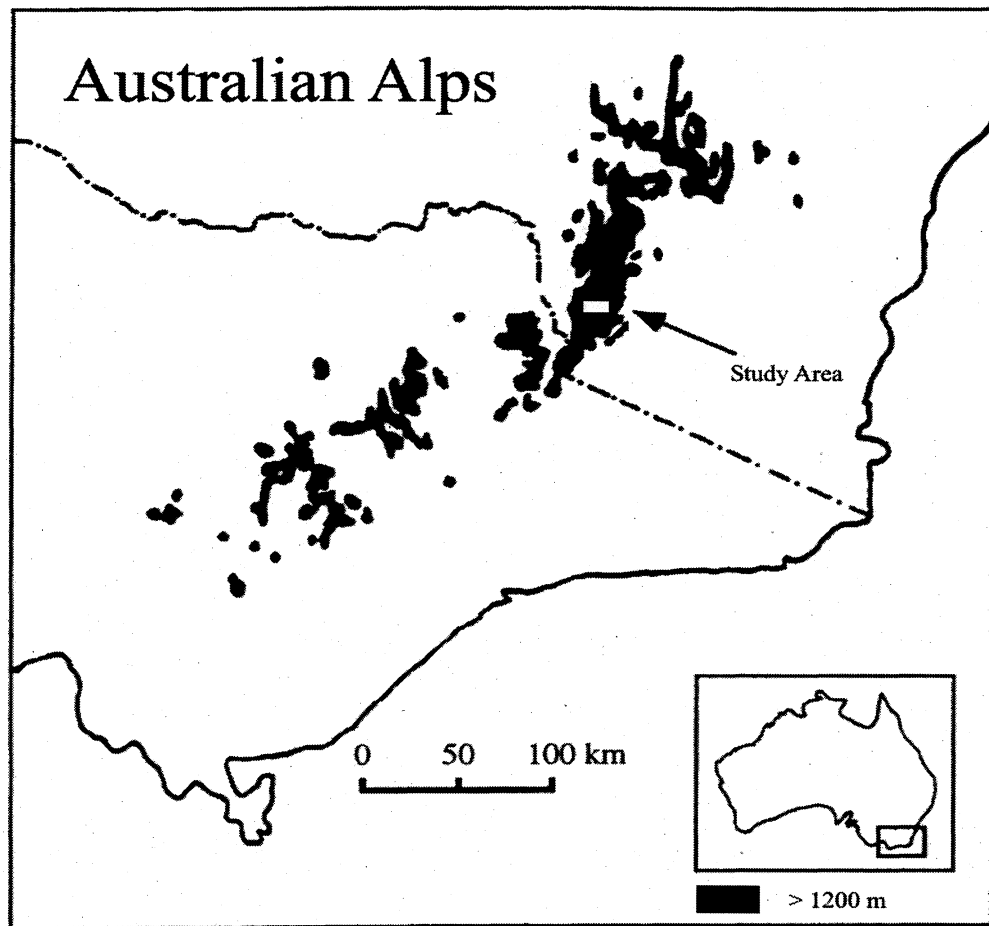


Figure 4.3 The Australian Alps showing the area above 1200 m.

4.3.3 Data collection

Data for this study were collected as part of a larger project investigating the distribution of small mammals in relation to snow cover in Kosciuszko National Park. These field measurements were supplemented with data obtained from routine snow course and meteorological records.

Snow depth measurements were made during 2002 at 72 sites, stratified across four main vegetation types (dry heath, wet heath, woodland and tussock grassland), three elevation levels (1501-1600 m, 1601-1700 m and 1701-1800 m) and two aspects (ablating and accumulating). Ablating aspects in Kosciuszko National Park are generally north-westerly and usually have lower snow depths than accumulating aspects. This is because the latter are subject to lower insolation levels and, due to the prevailing north-westerly winds, act as a snow

fence (Green & Osborne 1994). Of the 72 sites sampled in this study in 2002, 24 at the highest elevations were resampled in 2003.

Each site comprised three plots approximately 10 m apart; each plot consisted of a 200 cm timber stake marked at 10 cm intervals to enable measurement of snow depth to the nearest 5 cm. Snow depth was recorded on a weekly basis during 2002 and fortnightly or monthly during 2003. In addition, weekly snow depth data recorded at Spencers Creek snow course (36.43°S, 148.35°E, 1830 m) were obtained from Snowy Hydro Limited.

Average air temperatures for each of the study sites were derived from the ESOCIM module of ANUCLIM 5.1 (Houlder *et al.* 2000). ANUCLIM generates climate estimates for selected locations from thin plate smoothing spline surfaces fitted to continent-wide monthly mean meteorological data using ANUSPLIN 4.3 (Hutchinson 1991, 2004).

Air temperature averages for Spencers Creek were calculated from data obtained from the Thredbo Crackenback Automatic Weather Station (AWS) (36.49°S, 148.29°E, 1957 m). Although about 8.9 km from the Spencers Creek snow course, this is one of only two stations from which regular long-term records are available for the study region. The other, located at Perisher Valley (36.40°S, 148.41°E), is closer to Spencers Creek (6.4 km), and located at an elevation of 1735 m. We considered that air temperatures taken from the higher station would provide more conservative calculations than the lower one.

During 2002, snow-ground interface temperatures were measured using 24 Thermocron® iButton temperature loggers (Dallas Semiconductor Corp.), located throughout the 72 study sites. Temperature loggers were installed at all 24 high elevation sites sampled in 2003. Loggers were held in open-ended PVC tubes placed randomly within the study sites. Interface temperatures were taken for the period when continuous snow cover was present at a particular site.

Snow density data were recorded weekly and were available only for Spencers Creek. It is likely that snow density at field sites (all of which are at lower elevations than Spencers Creek) would exceed the values at Spencers Creek. This is because of higher rates of snowpack metamorphism, especially on ablating aspects where higher insolation often causes considerable melt-refreeze

metamorphism (Mckay & Gray 1981). Therefore, the Spencers Creek data provide a conservative estimate of density.

The Sturm system is based on average winter values for each parameter. Previous studies (Carron *et al.* 1990; Bubela & Happold 1993; Happold 1998) have defined winter as being the time when “snow permanently covered the ground” from June to September. In this study, we have defined the winter period as occurring from June to August (92 days) and data from this period only were used for classifying snow classes.

4.4 Results

Table 4.1 summarises the key snow cover characteristics of the three elevation classes sampled in this study. Despite the expected variations in snow depth and duration with vegetation type, aspect and elevation, and some year-to-year variations in depth and duration at the same site, there was little difference in snow/ground interface temperature among the sites. Average interface temperatures were consistently above freezing throughout winter. This was regardless of air temperature, indicating no significant thermal connectivity between the supranivean and subnivean environments. Snow-ground interface temperatures at Spencers Creek also were above freezing (Table 4.2).

Table 4.1 Average values for snow cover during 2002-03 on different aspects at 3 elevation levels in Kosciuszko National Park. Accum = accumulating aspects; Ablate = ablating aspects

	1501-1600 m		1601-1700 m		1701-1800 m	
	Accum	Ablate	Accum	Ablate	Accum	Ablate
Air Temp (°C)						
June	0.8	0.9	0.4	0.4	-0.3	-0.4
July	-0.4	-0.3	-0.9	-0.9	-1.8	-1.8
August	0.5	0.6	-0.1	-0.2	-1.2	-1.3
Average	0.3	0.4	-0.2	-0.2	-1.1	-1.2
Snow/Ground Interface Temp (°C)	0.4	0.8	0.7	0.6	0.8	0.8
Maximum Snow Depth (cm)	48	35	83	71	118	116
Snow Duration (weeks)	11.6	5.8	16.5	10.3	19.6	18.9

As expected, air temperatures at the study sites decreased with increasing elevation. This temperature decrease was less than 1°C for each 100 m increase in elevation, corresponding to the temperature lapse rate of 0.6°C per 100 m. Average winter air temperature was above -2°C for the study sites (Table 4.1) and these estimates were consistent with data recorded at Thredbo AWS (Table 4.2 Spencers Creek).

Table 4.2 compares the Spencers Creek snow characteristics with those of the four main snow classes presented by Sturm *et al.* (1995). Spencers Creek was selected because it is one of the few sites from which long-term records are available, including snow density data. Characteristics of snow at Spencers Creek most closely resemble the maritime snow class. Sturm *et al.* (1995) noted that snow-ground interface temperatures for maritime snow are generally within 1°C of freezing and often display basal melt features which would be expected at temperatures above freezing. The vertical temperature gradient also most closely corresponds to the maritime class. Snow depth falls within the values expected for the maritime class, but also the alpine class.

Table 4.2 Range of average winter values for the main snow classes defined by Sturm *et al.* (1995), and Spencers Creek, Kosciuszko National Park.

	Tundra	Taiga	Alpine	Maritime	Spencers
Snow Density (g cm⁻¹)	0.25 ~ 0.32	0.20 ~ 0.22	0.24 ~ 0.28	0.26 ~ 0.33	0.36
Air Temp (°C)	-27.52 ~ -19.84	-19.92 ~ -13.86	-12.63 ~ -10.19	-9.62 ~ -4.53	-1.61
Snow/Ground Interface Temp (°C)	-22.00 ~ -8.45	-6.60 ~ -2.37	-1.28 ~ -0.49	-0.34 ~ 0.16	0.62
Snow Depth (cm)	10.0 ~ 30.0	37.9 ~ 61.2	64.7 ~ 124.9	80.7 ~ 158.8	108.1
Vertical Temp Gradient (°C cm⁻¹)	-0.59 ~ -0.39	-0.38 ~ -0.28	-0.22 ~ -0.12	-0.18 ~ -0.07	-0.05

However, the latter exhibits a greater vertical temperature gradient resulting from lower average air temperatures. Spencers Creek air temperatures are in fact higher than the maritime air temperatures presented by Sturm *et al.* (1995). Snow density falls within the maritime range early in the winter (Figure 4.4) but increases steadily throughout the season due to the progressive development of melt features and ice layers within the snow pack (G Sanecki, unpublished data) producing a snow cover that is coarse grained and often wet. This is not only as a result of melt, but also rain, which can occur throughout the winter in the Australian Alps.

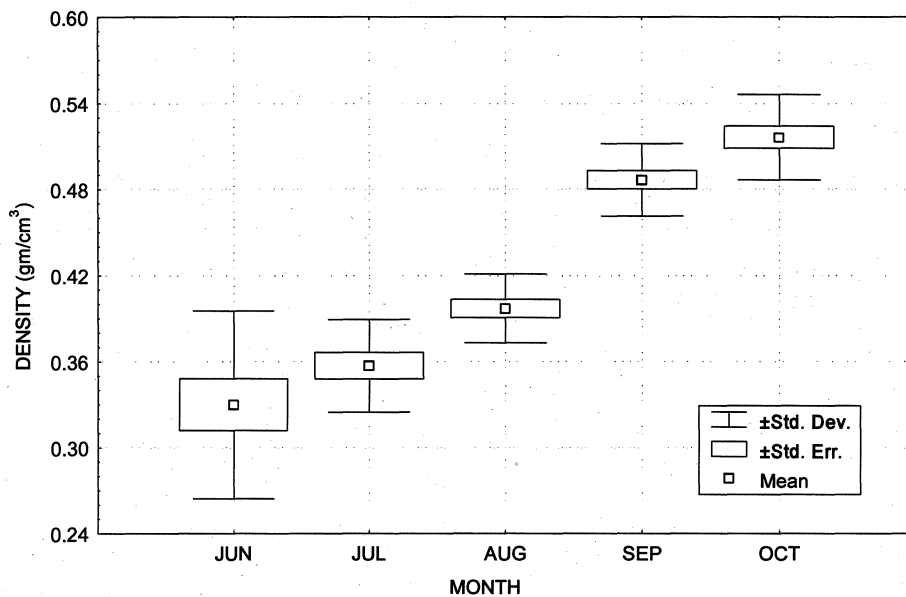


Figure 4.4 Average snow density 2002-03 by month at Spencers Creek

Sturm *et al.* (1995) described ephemeral snow as a thin, warm snow cover of short duration (<2 months) that often begins to melt shortly after deposition and is often subject to considerable basal melting. In this study, average winter air and snow-ground interface temperatures at the lowest elevation sites were above freezing throughout winter, suggesting conditions conducive to daytime snowmelt with intermittent night-time freezing. Snow duration at all abating and many accumulating low elevation sites was less than 2 months. In some cases snow remained on the ground for only 2 weeks. Snow depth for all low elevation sites did not exceed 50 cm in depth. On abating aspects at the mid-elevation level, there also were a number of sites where snow depth was less than

50 cm and duration was less than 2 months. We conclude that snow at low elevations should be classed as ephemeral. It is likely that at mid elevations, and perhaps even higher elevations during some years, snow cover also may be ephemeral in nature particularly on ablating aspects.

4.5 Discussion

Based upon the classification system of Sturm *et al.* (1995) and the data gathered in this study, snow cover at higher elevations in Australia most closely resembles maritime snow. However, since Australian snow displays some divergent characteristics, it is possible that snow of this type represents a separate "warm-temperate-tropical" category where daytime temperatures are above 0°C and night time temperatures below 0°C. These conditions favour destructive metamorphism and melt-freeze metamorphism as the dominant processes responsible for changes in the snowpack over time. In terms of areal extent in the Snowy Mountains, based on snow depth and duration data presented by Slatyer *et al.* (1984), it is likely that the snow occurring over at least half of the area subject to snow cover fulfils the criteria of ephemeral snow.

There appears to be little merit to the argument that a mountain classification is more appropriate for Australian snow to account for variations due to topography and other factors. Mountain snow is highly variable over relatively small geographic scales. For example, different classes could be described on the opposite sides of a ridge, whereas our data show that snow cover characteristics are quite similar over a range of elevations and aspects.

Similarly, the alpine snow cover class of Sturm *et al.* (1995) is not appropriate in the Snowy Mountains because both air and snow-ground interface temperatures are considerably lower, while the temperature gradient is much greater, than values observed in this study. Our study did not consider data from elevations above 1800 m, and it might be possible that alpine snow occurs at higher elevations. We do not consider this to be likely as unpublished data from snow courses in the alpine areas of Kosciuszko National Park show similar snow density trends to Spencers Creek (G Sanecki, unpublished data). Moreover, incidental measurements taken at a range of high elevation sites over a six year

period indicate that snow-ground interface temperatures almost never fall below 0°C (G Sanecki, unpublished data).

Observations from other locations are consistent with data from Kosciuszko National Park and indicate that our conclusions about snow classes in the Snowy Mountains can safely be extrapolated generally across the Australian Alps. Fifty-four years of records from the Rocky Valley snow course in the Bogong High Plains (36.87°S, 147.28°E, 1650 m), show similar snow densities to those at Spencers Creek (Figure 4.5). In addition, the two sites have similar patterns of snow accumulation (Osborne *et al.* 1998). Snow pit investigations at the summit of Mt Buller (37.13°S, 146.42°E, 1809 m) showed snow pack temperatures were at, or only slightly lower than, 0°C (Ruddell 1998). Average winter air temperatures also are consistent with, or higher than, those in Kosciuszko National Park (G Sanecki, unpublished data).

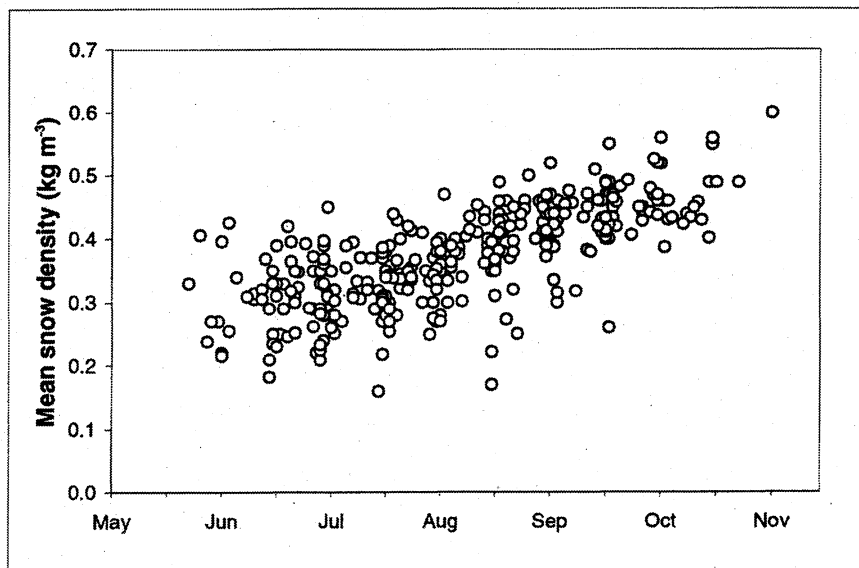


Figure 4.5 Average snow density at Rocky Valley snow course 1935-89. From Ruddell *et al.* (1990)

In the past, a lack of information about Australian snow conditions has led to misunderstandings and misinterpretations of research findings, based on assumptions that data collected elsewhere accurately reflect the situation in Australian alpine and subalpine areas. For example, Green & Osborne (1994) suggest that in areas of limited plant cover, the subnivean space forms due to

temperature gradient (TG) metamorphism whereby water vapour (formed by sublimation) is transported from the warmer lower snow levels to the cooler upper layers where it recrystallises, resulting in the development of deep layers of low-density depth hoar. However, TG metamorphism and thus the formation of depth hoar requires the snowpack to be subjected to a vertical temperature gradient in excess of $0.10\text{-}0.25^{\circ}\text{C cm}^{-1}$ for about one week (Akitaya 1974; Colbeck 1983; Ruddell 1998). This process is more characteristic of taiga snow (and alpine snow to a lesser extent). Data presented in this paper indicate that conditions conducive to the formation of taiga snow do not occur in Australia.

In the absence of a thermal gradient within a snowpack that is close to or just below 0°C , destructive metamorphism becomes the dominant process for creating structure in the vertical stratigraphy (Langham 1981; Ruddell 1998). This type of metamorphism involves the transformation of snow crystals into more compact grains that, when combined by sintering processes, causes an increase in the hardness and density of the snowpack. As air temperatures increase and the snowpack further warms, melt-freeze metamorphism becomes predominant, further increasing snowpack density (Langham 1981). These processes explain the relatively high density of Australian snow cover and the progressive increase in density throughout the nival period. The formation of the subnivean space in areas with little vegetation structure in Australia is probably related to basal melting processes as a result of snow-ground interface temperatures above 0°C .

Overseas studies have shown that the area of subnivean space can be quite extensive (Coulianos & Johnels 1962) and it is thought that depth hoar is an important factor in the ecology of winter active subnivean fauna (Pruitt 1984a; Halfpenny & Ozanne 1989; Auerbach & Halfpenny 1991). A low-density depth hoar layer does not form in Australian snow fields. Rather, the typically high snow density is likely to provide a mechanical hindrance to small mammals that move under the snow. Snow density is above 0.3g cm^{-3} throughout the snow profile for most of the season in Australia (Figure 4.5), (Ruddell 1998). However, small mammals have difficulty digging through snow with densities greater than 0.21g cm^{-3} (Spencer 1984). It follows that during winter in Australian alpine and subalpine regions, small mammals are confined to areas

where physical processes other than TG metamorphism form a subnivean space of sufficient size to enable movement. Similarly, any investigation of supranivean fauna would need to consider the implications of higher snow density and mechanical strength for the movement of fauna across the snow and their ability to dig into it.

Our study also has relevance to studies investigating the possible impact of snow compression by human activity, including the movement of over-snow vehicles or snow grooming on subnivean environments (Schmid 1971; Keddy *et al.* 1979; Adam 1981; Halfpenny & Ozanne 1989; Green 1998b, 2000). The nature of the impact is a function of the type of snow cover present at a particular site. Once it has achieved a certain depth, maritime snow has greater mechanical strength than ephemeral snow due to its depth and density. Consequently, it is probably less susceptible to compression for prolonged periods during the nival period, particularly mid to late season (Langham 1981).

Snow ecology needs more consistent snow classification. The Sturm system has been shown to provide a logical and practical paradigm for the description and interpretation of Australian snow cover conditions from an ecological point of view. However, the use of the Sturm system would also benefit from the inclusion of more global data to improve its generic applicability and strengthen its ecological significance.

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5 A TECHNIQUE FOR USING HAIR TUBES BENEATH THE SNOWPACK TO DETECT WINTER-ACTIVE SMALL MAMMALS IN THE SUBNIVEAN SPACE

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5.1 Abstract

The study of winter-active small mammals beneath the snowpack has proved challenging for researchers because of their relative inaccessibility. We present a technique that permits the detection of small mammals active in the subnivean space using hair tubes. Hair tubes are cylindrical or funnel-shaped structures containing suitable bait and an adhesive surface that harvests hairs from small mammals as they attempt to reach the bait. Hair tubes eliminate many of the difficulties often associated with live trapping and permit the expansion of systematic sampling to larger scales than allowed by conventional live-trapping methods.

The technique was used successfully to detect five small mammal species in the subnivean space in Kosciuszko National Park (KNP) in south-eastern Australia. These included the common bush-rat, *Rattus fuscipes*, the dusky and agile antechinus, *Antechinus swainsonii* and *A. agilis*, the broad-toothed rat, *Mastacomys fuscus* and the mountain pygmy possum, *Burramys parvus*.

Although hair tubes have a number of limitations, such as not providing a measure of abundance or the ability to identify individual animals, we believe that these limitations are balanced by the ability for the technique to be used at any spatial scale. Hair tubes are particularly suited to studies of animal distribution at the landscape-scale, because many hair tubes can be deployed and dispersed over large areas, and monitored on a regular basis by a small team of researchers. The technique also makes use of readily available, low-cost materials and could be easily adapted to a range of conditions and different target species.

Keywords: Ecology, distribution, landscape-scale

5.2 Introduction

Snow can play an important role in the ecology of small mammals (Formozov 1946; Pruitt 1960, 1984). While acting as a mechanical barrier that can hinder small mammal movement, it also can provide protection from predators and play a crucial role in maintaining relatively warm and stable subnivean conditions that are quite distinct from those above the snowpack. Given the ecological significance of snow cover (Pruitt 1984), it is important that studies of small mammals be undertaken throughout the year and particularly during the nival period when the interactions between small mammals and characteristics of snow cover can be quantified. However, the very presence of snow can hinder the study of small mammals. Snow provides a barrier through which research workers must gain and maintain access to the subnivean space, often for long periods of time (Carron 1985).

The study of small mammals beneath the snow has been undertaken in a number of ways, including the use of indirect methods (Spencer 1984), interpolative methods (Green 1988) and direct observation (Cranford 1984; Merritt 1984; Carron 1985; Bubela *et al.* 1991). These direct methods have generally involved live-trapping to capture small mammals in the subnivean space by placing traps through the snowpack at ground level, often with the aid of chimney-like structures that provide access to the subnivean space without causing repeated disturbance to the snowpack. Although generally successful, live-trapping methods are labour intensive, particularly as traps need to be closely monitored to ensure the welfare of trapped animals.

To date, there has not been a field method to permit systematic, landscape-scale sampling of small mammals in the subnivean space. Our aim was to develop a technique that would permit investigation of the distribution of small mammals in relation to the spatial and temporal variation of snow cover over large areas, conditions which make live-trapping impractical. In this paper, we summarise the methods that have been used for detecting small mammals active in the subnivean space, provide an overview of hair tube methods as they have been applied in non-nival areas in Australia, and describe a new technique using hair tubes for surveys beneath the snow.

5.2.1 Subnivean trapping methods for small mammals

Soper (1944) described several methods for the capture of small mammals during winter, including the use of traps in rudimentary excavated trenches in the snow to capture rodents such as voles that were active in the subnivean space. Later, Pruitt (1959) described a method for live-trapping small mammals in the taiga forests of Canada during winter. This involved using wooden chimneys that allowed repeated access to the subnivean space without causing frequent disturbance to the snowpack. The chimneys, fitted with hinged lids to prevent the ingress of snow, allowed traps to be lowered through the snowpack to the ground, where a gap at the bottom of the chimney permitted animals access to the traps. This general technique has since been further modified and applied by others (Fay 1960; Iverson & Turner 1969; Merritt & Merritt 1978; Keller *et al.* 1982).

In Australia, a number of workers have used modified drums or plastic bins for subnivean trapping. Carron (1985) used 60-l steel drums that had one end cut off to serve as a removable lid and a hole cut at the base of the drum to permit access for small mammals to traps placed in the drum. The larger 205-l steel drums used by Mansergh (1985) had their bases removed and were suspended slightly above ground level providing better access to traps. Later, 55-l plastic garbage bins were used which were lighter, cheaper and more readily available. Holes were cut at the base of the bins which were attached to timber stakes prior to the onset of snow (Green 1988; Sanecki 1999).

Live-trapping in the snow can lead to high rates of mortality of trapped animals (Beuch 1974), although the use of insulation in traps can reduce this (Green 1988; Sanecki 1999). Although drums and bins are an improvement over simply laying traps in excavated snow pits, they are still susceptible to being buried by falling or drifting snow. It is then necessary to remove snow to expose the lid before traps can be checked. This results in extra work for the researcher and potentially increases the time animals spend inside traps. Some workers have overcome this problem by using taller chimneys (Merritt & Merritt 1978; Cranford 1984). Continued excavation also can change the snowpack, and in our experience, even careful digging can still cause considerable disruption to the snow surrounding trapping bins and potentially affect trapping success. These

factors, combined with the fact that small mammal populations are often at their lowest during the winter, mean that subnivean trapping success is low when compared to trapping when snow cover is not present (Carron 1985; Green 1988; Sanecki 1999). As a result, live-trapping methods have been restricted to relatively small spatial scales. Carron (1985) undertook her winter sampling across 30 trap points with an inter-trap interval of 10 m, while Green (1988) used 40 trap points at a similar interval. More recently, groups of grids with 120 bins (Sanecki 1999) and 80 bins (G. Sanecki, unpublished data) have been established for small mammal studies in the Australian Alps. However, even these larger grids do not extend over much more than a few hectares, which limits inference for studies of distribution patterns over larger spatial scales.

Despite the drawbacks of live-trapping, it remains the only method suitable for studies requiring collection of data about individual animals, and live-trapping will continue to be widely used for fine scale behavioural and population studies.

5.2.2 Hair tubes

Hair tubes have been widely used in non-nival areas of Australia since the 1970s for detecting small- to medium-sized mammals (Mills *et al.* 2002). Suckling (1978) used hair tubes to detect arboreal mammals; later Scotts and Craig (1988) modified the design to facilitate the detection of rare terrestrial animals. Since then, a number of studies have used hair tubes either as the principal survey method or in combination with other techniques (Laidlaw & Wilson 1989; Scotts & Seebeck 1989; Lindenmayer *et al.* 1994; Lindenmayer *et al.* 1999a). One of the reasons for the rise in popularity of hair tubes is their low cost and the ability to deploy them over larger areas without the concerns that are typically associated with live-trapping. Hair tubes can be left in place for days or even weeks at a time before collection, and their use can make it much easier to conduct systematic sampling of replicate study sites in the landscape. Their use may also enable the detection of species not readily captured by trapping (Sutherland 1997).

Hair tube design has varied over time. However, their principal mode of operation remains the same. A tube or funnel-shaped structure of an appropriate size is baited with a suitable attractant for the target species. An adhesive

substance such as double-sided tape is applied to the inside surfaces of the hair tube. Samples of hair are collected from animals that come into contact with the adhesive, and the hairs can then be identified by inspection with a compound microscope (Mayer 1952; Brunner & Coman 1974; Moore 1988; Teerink 1991; Brunner & Triggs 2002). A consideration for workers in regions that do not have a guide to the identification of mammalian hair would be the need to create a reference collection of hair samples from target species. As such, it will probably be necessary to conduct live-trapping prior to the use of hair tubes. Even if a suitable guide is available, we still recommend the creation of a reference collection to allow workers to become familiar with their target species, while also ensuring that there are no local morphological differences.

Early hair tube designs consisted of a 100-mm-long PVC tube with a diameter of 30 mm. Double-sided tape was attached on the upper inside surface of each end and bait was held in place in the middle of the tube (Suckling 1978). The modifications of Scotts and Craig (1988) included the enlargement of the entrance diameter and the provision of a mesh chamber to prevent the bait being removed too quickly. Broome (personal communication) modified the design of Suckling (1978) by moulding a dimple into the upper surface of each end of the tube. This created a constriction that the entering animal would have to squeeze under, and seemed to provide a better geometry for hair collection from smaller species. More recently, a moulded plastic hair funnel using purpose designed adhesive wafers has been manufactured commercially (Lindenmayer *et al.* 1999b).

Hair tubes have a number of limitations. Perhaps the most important is that the technique cannot distinguish the number of individuals of the same species visiting a tube (Lindenmayer *et al.*, 1994). Other limitations and biases are similar to those of live-trapping (Sutherland 1997), including the fact that the technique cannot tell you anything about animals that may be present, but which do not enter the hair tubes. There has also been some dispute as to the effectiveness of hair tubes to survey a range of species. Lindenmayer *et al.* (1999b) showed that hair tube size and configuration determined the types of animals that could be detected. Although Mills *et al.* (2002) found that hair tubes of different designs frequently detected common small mammal species, they

were not particularly successful at detecting rare medium-sized species. Despite these concerns, hair tubes remain a cost-effective way of systematically surveying small mammals at landscape-scales (Mills *et al.* 2002).

5.3 Materials and methods

5.3.1 Subnivean hair tube survey methods

5.3.1.1 Snow tubes

Snow tubes are analogous to trap chimneys in that by being erected before winter, they permit the later placement of hair tubes into the subnivean space without disturbing the snowpack. Green (1997) successfully used PVC snow tubes to allow the winter placement of small pitfall traps, which were used to sample subnivean invertebrates. That technique formed the basis for the design described here.

Snow tubes were cut from 6-m lengths of 90-mm diameter PVC drainage pipe. The pipe was cut into 1-m lengths which then had holes drilled at both ends so that they could be attached to timber garden stakes. Tubes were installed before the onset of snow and wired to a 2-m-long hardwood garden stake so that there was a 50-mm gap between the base of the tube and the ground. The rough surface of the garden stake and the weight of the snow tube meant that any downward slippage of the pipe was counteracted by the camming action of the tie wires. The top of each tube was covered with a 30 x 30-cm square of strong plastic sheet and fastened with nylon cable ties (Figure 5.1). Tubes that were cut from the flanged ends of the 6 m pipe were reserved for use as extensions at sites where snow depth was greater than 1 m, so that the tubes continued to protrude through the snow (Figure 5.2).

This arrangement proved robust under the conditions prevailing during our sampling, but modifications such as additional guy wires may be required in high wind areas or under different snow conditions. Our snow tubes became more secure as snow depth increased and melt-freeze metamorphism increased the snowpack density at KNP. We found that exposed areas with shallow snow cover were most susceptible to being damaged by strong winds. We also found that it was counter-productive to install longer tubes at sites where snow cover were expected to exceed 1 m in height. Tall snow tubes were difficult to work

with when snow cover was relatively shallow at the beginning and end of winter. They also were more susceptible to being damaged by strong winds. It was easy to extend snow tubes as snow height increased and then shorten them again as it declined.

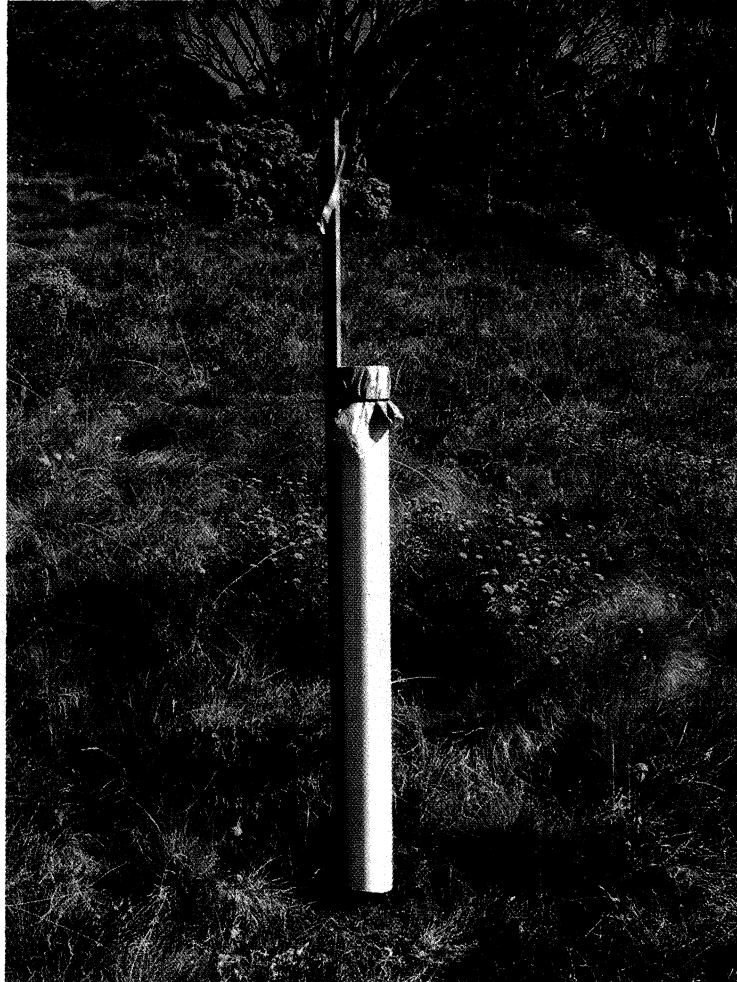


Figure 5.1 Snow tube in a grassland habitat. Note the 50 mm gap between the base of the snow tube and the ground.



Figure 5.2 Snow tube with a one metre extension fitted. Snow surface is approximately 120 cm above the ground.

5.3.1.2 Hair tubes

The effectiveness of a hair tube depends on its ability to entice an animal to come into contact with the adhesive surface and leave a hair sample. Therefore, important design considerations include tube diameter, location of the adhesive, and accessibility of the bait. The design of our hair tube was also driven by the need for it to fit within the 90-mm-diameter snow tubes. Our target species include those known to be active in the subnivean space in south-eastern Australia and include the bush rat, *Rattus fuscipes*, dusky antechinus, *Antechinus swainsonii*, agile antechinus, *A. agilis* and broad-toothed rat, *Mastacomys fuscus*. Of these, the two rodent species are the largest with an average body length of 165 mm for *R. fuscipes* and 161 mm for *M. fuscus*, and have an average mass of 125 g (Happold 1995; Lunney 1995).

Adult *A. swainsonii* are approximately 122 mm in length and, the males weigh about 65 g and females 41 g (Dickman 1995). *Antechinus agilis* is the smallest of the four species with the larger males weighing on average only 35 g (Green

& Osborne 1994). After testing a range of tube sizes and configurations we found the following to be best suited to the target species whilst fitting into the snow tube. Workers in other areas would need to experiment with tube size and configuration to suit their target species.

Hair tubes were constructed from 40-mm 88° PVC plumbing elbows manufactured by iPlex Pipelines. These elbows have flanged ends into which a plug could be inserted and held securely in place. The elbows were drilled at one end with two holes 2.5 mm in diameter through which wire could be passed to fasten the bait plug. Bait plugs were machined from softwood timber such as pine. Lengths of timber were machined in a lathe to create a rod with a diameter of 41 mm. This was the diameter that provided the best fit into the flange of the PVC elbow. The rod was then sliced into 20-mm thick discs. Each wooden disc was then drilled with a 20-mm drill bit to a depth of about 10 mm to create a well into which bait could be placed (Figure 5.3).



Figure 5.3 Subnivean hair tube. The assembled tube on the left is in the position it would be in at the base of the snow tube.

The assembly of hair tubes was completed by inserting the plug so that the bait well was facing downwards into the elbow and attaching double-sided tape to the upper inside surface of the other opening so that it would come into contact with the nape or back of an animal entering the tube. The wooden bait plug held a mixture of rolled oats, peanut butter and honey. The plug was held in place by a piece of wire passed through the two predrilled holes and twisted together to form a loop. A 1.5-m length of straight wire left inside the snow tubes between uses was attached to the top of the loop to enable the hair tube to be lowered down the snow tube into the subnivean space.

No attempt was made to prevent the bait being removed from the bait plugs. We initially tested a number of alternatives, including the use of wire mesh of different strengths to contain the bait material within the plug. In each case, we found that the wire was gnawed through and the bait removed. When we did devise a method to prevent removal of the bait, we found that the animals turned their attention to other parts of the hair tube including the double-sided tape and wire assembly. The latter, which held the device together, was crucial to our ability to place and retrieve the hair tubes from the snow tube. Therefore, we found it preferable that the bait be removed in preference to the hair tube being damaged. We suggest, however, that the inclusion of a barrier to prevent bait removal be made on a case-by-case basis depending on the species likely to be encountered.

Setting of hair tubes in the field involved removing the plastic covering and the length of wire from the snow tubes. The hair tube was attached to the wire and the double-sided tape backing was removed. The hair tube was then lowered into the snow tube so that it rested on the ground. The retrieval wire could then be bent over the top of the snow tube thus preventing excessive movement of the hair tube, and the plastic cover replaced to prevent snow entering the snow tube (Figure 5.4).

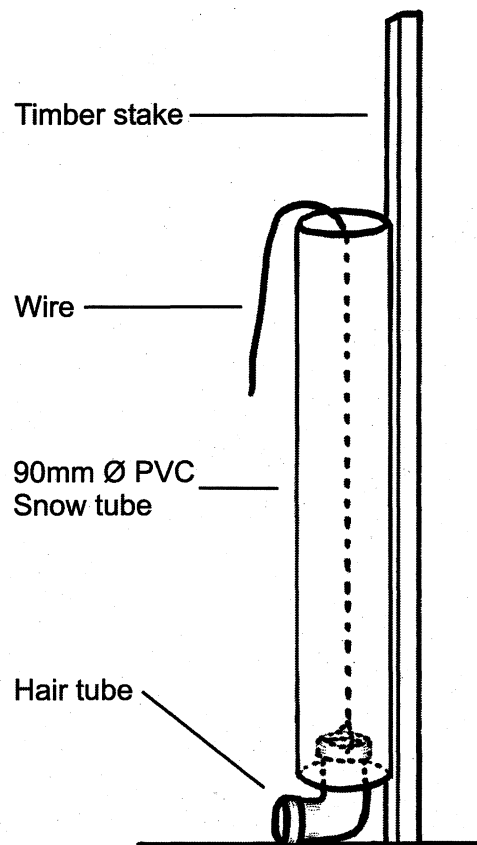


Figure 5.4 Schematic diagram showing details of hair tube placement within the snow tube. The hair tube is lowered down the snow tube using a length of 2 mm wire. Once the hair tube is resting on the ground the wire is bent over the upper edge of the snow tube and the plastic lid is replaced.

5.4 Results and discussion

The first systematic application of our hair tubing technique was during 2002 when 216 snow tubes were established as part of a study investigating the distribution of small mammals in relation to snow cover in Kosciuszko National Park, south-eastern Australia. Full results of the surveys undertaken using this technique will be presented elsewhere (Sanecki *et al.*, unpublished data). Here, we present a summary to illustrate the effectiveness of the technique followed by comments regarding the practicality and durability of the snow tubes and an assessment of the effectiveness of the hair tubes as a sampling device to detect the target species.

The 216 snow tubes were established on 72 sites, each consisting of 3 snow tubes approximately 10 m apart. Sites were stratified across 3 elevation levels, 2

aspects, and 4 habitat types. We replicated this combination 3 times. Small mammal surveys were conducted on 13 separate occasions commencing just prior to the onset of snow, then continuing throughout the nival period and ending with a final survey when all sites were clear of snow. Hair tubes were set and left for 7 days. Upon retrieval, the tape was removed and inspected for hair samples (Figure 5.5). Species were identified using previously collected hair reference samples and using the methods outlined by (Brunner & Coman 1974; Brunner & Triggs 2002).

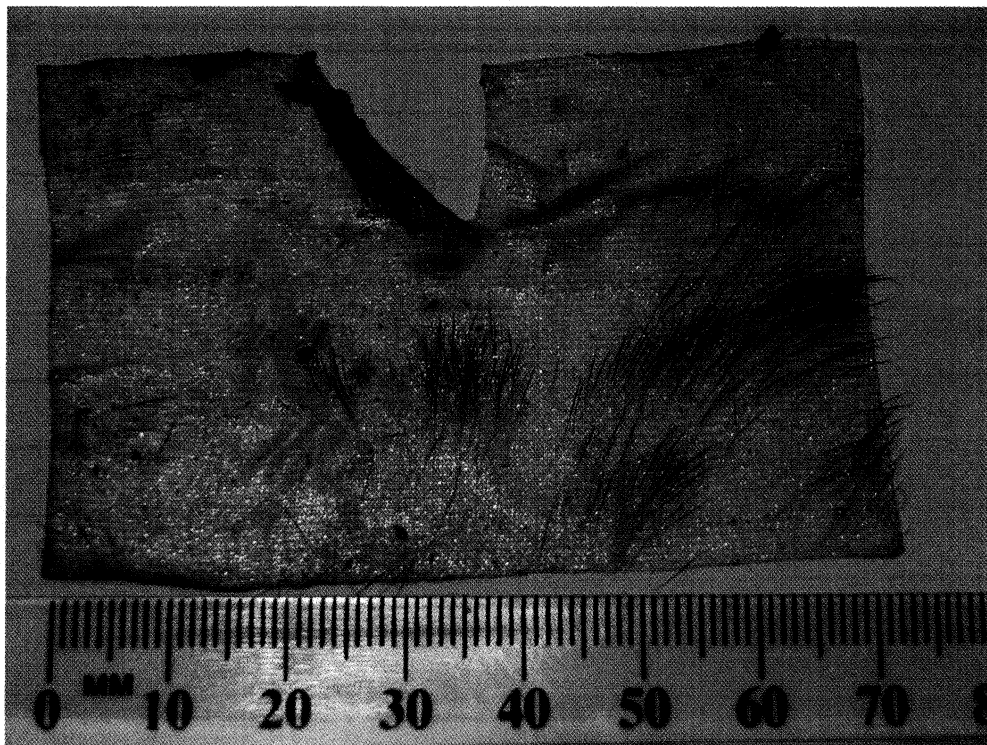


Figure 5.5 Double-sided tape after retrieval from hair tube, showing an average hair sample from *A. swainsonii*. Sample quality was highly variable, however and in some instances only a few hairs were captured.

Of 2,808 hair tubes set, 1,084 (39%) were visited by animals, indicated by the absence of bait within the hair tube upon retrieval. These provided 1,105 small mammal detections. Of these, 683 (62%) were *R. fuscipes*, 420 (38%) were *Antechinus* spp. and there was 1 detection (0.09%) each of *M. fuscus* and *B. parvus*. The similarities of hair morphology of the two *Antechinus* species meant it was only possible to identify hair to genus level in some instances. Of the 420 detections of *Antechinus* spp., 373 (89%) were identified as *A. swainsonii* and 4

(1%) were agile antechinus *A. agilis*, leaving 43 (10%) samples that could only be identified to genus level. Given that *A. agilis* is less frequently encountered than *A. swainsonii* above 1,500 m in heath and woodland (Dickman *et al.* 1983; Green 1988) it is probable that most of these were *A. swainsonii*.

The detection rate of the hair tubes was very high with only 2 (0.2%) of the hair tubes that were apparently visited not collecting hair. In almost all cases, however, hair tubes detected only one species of small mammal at a time. Of the 1,084 tubes visited, only 23 (2%) contained hair samples from more than one species. Multiple detections could be increased by inhibiting the removal of bait. However, as noted above, attempts to do this created additional problems.

During the study we found that the double-sided tape remained sticky throughout the 7-day sample period. Problems arose only toward the end of winter when a number of tubes were submerged by melt water causing tapes to lose their stickiness. Subnivean temperatures are relatively mild in Australia with average temperatures of 0.7°C under complete snow cover. Consideration would need to be given to the best material for hair capture depending on the conditions likely to be encountered in other regions. Even at high northern latitudes however, once the hiemal threshold is reached, for the most part, subnivean temperatures are still within a few degrees of freezing (Pruitt 1957), thus it is likely that double-sided tape may be still suitable in higher alpine and boreal areas. As our study progressed a number of sites became clear of snow at lower elevations exposing hair tubes to more varied temperatures including minima as low as -13 °C. There was no indication that these "exposed" tubes were any less efficient at capturing hair samples.

The use of hair tubes permitted us to undertake a systematic study of small mammal distribution at a scale previously impossible using other techniques. It was possible for two people to service all 216 snow tubes spread over 20 km easily over a 2-day period using a combination of 4WD, snowmobile and ski travel. During this time, it was possible to collect and replace hair tubes while undertaking additional weekly measurements at each site. We needed to excavate snow tubes on only one occasion after a large snowfall. Once extension tubes were fitted to these sites, no additional excavation was required.

Although it would be best to apply this technique once a suitable guide to identification or a reference collection is available, the technique could also be used to undertake preliminary investigations over a large area and thereby identify areas that might be suitable for more intensive trapping studies.

In conclusion, we believe the new technique described within this paper is a valuable addition to researchers working with small mammals in snow covered ecosystems. Although hair tubes are not a replacement for live-trapping methods, particularly in detailed small-scale studies, the limitations of the hair tube technique are balanced by the potential for its application at landscape-scales and its ability to return useful data for reasonable cost and effort.

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6 THE WINTER DISTRIBUTION OF SMALL MAMMALS IN RELATION TO THE SUBNIVEAN SPACE IN THE AUSTRALIAN ALPS

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6.1 Abstract

We present the results of a study that is the first to investigate the distribution of small mammals in direct relation to the spatial and temporal variation of snow cover at the landscape-scale. We investigated the distribution of the small mammal species, the dusky antechinus, *Antechinus swainsonii* and bush rat, *Rattus fuscipes* in relation to snow cover in the subalpine zone of Kosciuszko National Park in the Snowy Mountains of south-eastern Australia.

A new hair tube technique was used to detect the presence of small mammals active in the subnivean space. In 2002, we sampled 72 sites stratified by elevation (1501-1600 m, 1601-1700 m, 1701-1800 m), aspect (accumulating, ablating) and habitat type (woodland, wet heath, dry heath, grassland). These factors were considered important in influencing snow accumulation and generally reflected the types of habitats available to small mammals. In 2003, the presence of small mammals was investigated at 24 high elevation sites including six boulderfields.

The development of the subnivean space in the Snowy Mountains is dependent on the presence of structures such as shrubs, boulders and microtopographic features that are capable of supporting a snow layer above ground level.

When snow was present, small mammal detections were negatively correlated with snow depth and duration, and positively correlated with the complexity of structures and microtopography. At high elevations, detections were largely confined to boulderfields and at mid and low elevations small mammals were detected primarily in habitats where the subnivean space was most extensive.

Antechinus swainsonii and *R. fuscipes* responded differently to snow cover with the latter seeming better able to overwinter where snow cover was shallow and patchy, in contrast to *A. swainsonii* whose occurrence was correlated to the size of the subnivean space.

Keywords: snow, subnivean space, *Rattus fuscipes*, *Antechinus swainsonii*, Kosciuszko National Park, habitat, vegetation structure, distribution

6.2 Introduction

Snow is a significant factor in the ecology of many organisms (Formozov 1946; Pruitt 1960, 1970, 1984; Halfpenny & Ozanne 1989; Stenseth *et al.* 2004). Despite this, few studies have directly investigated the influence of snow cover on the distribution of, and habitat selection by, small mammals that remain active during the winter. This is probably due, in part, to the inherent difficulties of research work in snow covered environments and the particular problems faced by workers attempting to sample organisms in the subnivean space, that is, the space between the snowpack and the ground surface.

The decline in extent and duration of snow cover, both overseas (Houghton *et al.* 2001) and in Australia (Galloway 1988; Whetton *et al.* 1996; Osborne *et al.* 1998; Whetton 1998), as a consequence of climate change, is a matter of concern. Moreover, potential environmental impacts arising from the decline in snow cover (Green & Pickering 2002) and human activities in nival areas (Schmid 1971; Baiderin 1980; Price 1985; Ingold *et al.* 1993; Tsuyuzaki 1994) are likely to increase. Activities such as artificial snow making and precipitation enhancement (Bigg 1995; Ryan & King 1997) are already being used in Australia to reduce the negative effects of the decline in snow cover. Before consideration can be given to potential impacts of recreational and other human activities on subnivean fauna, such as small mammals, we first need a better understanding of how natural snow cover influences the distribution of snow-dwelling species.

Australian small mammals known to remain active beneath the snow through winter include the murid rodents, bush rat *Rattus fuscipes*, and broad-toothed rat *Mastacomys fuscus*, and the dasyurid marsupials, dusky antechinus *Antechinus swainsonii*, and agile antechinus *A. agilis*. None of these species is confined to nival areas and all have been the subjects of many studies in snow-free portions of their ranges (Calaby & Wimbush 1964; Wood 1971; Barnett *et al.* 1977; Barnett *et al.* 1978; Braithwaite 1978; Hall 1980; Hall & Lee 1982; Wallis *et al.* 1982; Woodside 1983; Wallis 1992; Catling & Burt 1994; Lindenmayer *et al.* 1994; Banks 1999; Lindenmayer *et al.* 1999). A few workers have investigated these species in areas subject to seasonal snow cover (Osborne *et al.* 1979; Dickman *et al.* 1983; Carron 1985; Green 1988; Green & Crowley 1989; Carron

et al. 1990; Bubela *et al.* 1991; Bubela & Happold 1993; Sanecki 1999; Green 2000, 2002). Few investigations, however, have considered how snow may influence these species during the nival period, and previous studies have been largely descriptive. For example, Osborne *et al.* (1979) completed a general survey of fauna above 1500 m including small mammals active beneath the snow and Green (2000) investigated over-snow movements by these species. The role of snow in the population dynamics and habitat selection of small mammals was studied by Carron (1985) using subnivean trapping methods (Mansergh 1985), while the winter home range and activity patterns of *M. fuscus* were described by Bubela *et al.* (1991). For these species, the development and presence of the subnivean space has been thought essential to their ability to overwinter in snow-covered environments (Happold 1989; Green & Osborne 1994; Happold 1998). However, there has been no direct investigation of the relationship between small mammals and the development of the subnivean space in Australia.

Our current understanding of subnivean ecology is, for the most part, based on overseas research, in regions where snow characteristics are very different from those occurring under Australian climatic conditions (Sanecki *et al.* In Review-a). For example, the presence of depth hoar is considered an important factor in permitting small mammal activity in the subnivean space, particularly in boreal regions (Pruitt 1984; Halfpenny & Ozanne 1989). The thermal properties of snow cover in Australia (and indeed in many parts of the world) are not conducive to the formation of depth hoar (Sanecki *et al.* In Review-a). Therefore, assumptions regarding its role in the ecology of small mammals in boreal regions are likely not to be valid in Australia.

Since depth hoar does not facilitate the development of the subnivean space in Australia, it follows that the subnivean space must form by other mechanisms. As far as we are aware, there is no research to indicate the nature of the process by which the subnivean space forms in Australia. It is also possible that the subnivean space may not be as extensive as once thought (Green & Osborne 1994). If this is the case, then a reduction in resources available to small mammals during the nival period may contribute significantly to winter mortality (Carron 1985).

In this paper we investigate the distribution of small mammals in the Australian subalpine zone in relation to factors affecting the depth and duration of snow cover. We also consider the factors that contribute to the formation of the subnivean space and its effect on small mammal distribution. The role of the thermal environment in the distribution of small mammals will be considered in a separate paper (Sanecki *et al.* In Review-c).

6.3 Methods

6.3.1 Study area

The Snowy Mountains are located in south-eastern Australia, and consist of a disjunct series of peaks and plateaux extending for about 350 km in a generally north-easterly direction from their southern extent at about 37°S 146°E to 35°S 149°E. The Snowy Mountains contain the largest contiguous alpine and subalpine areas in Australia lying above 1500 m and subject to the accumulation of snow cover during winter (Costin 1989). Sampling sites were established in a series of valleys close to the Kosciuszko Road from Charlotte Pass (36°26'S, 148°20'E) to Rennix Gap (36°21'S, 148°31'E) in the Snowy Mountains (Figure 6.1). The study was conducted over the winters of 2002 and 2003.

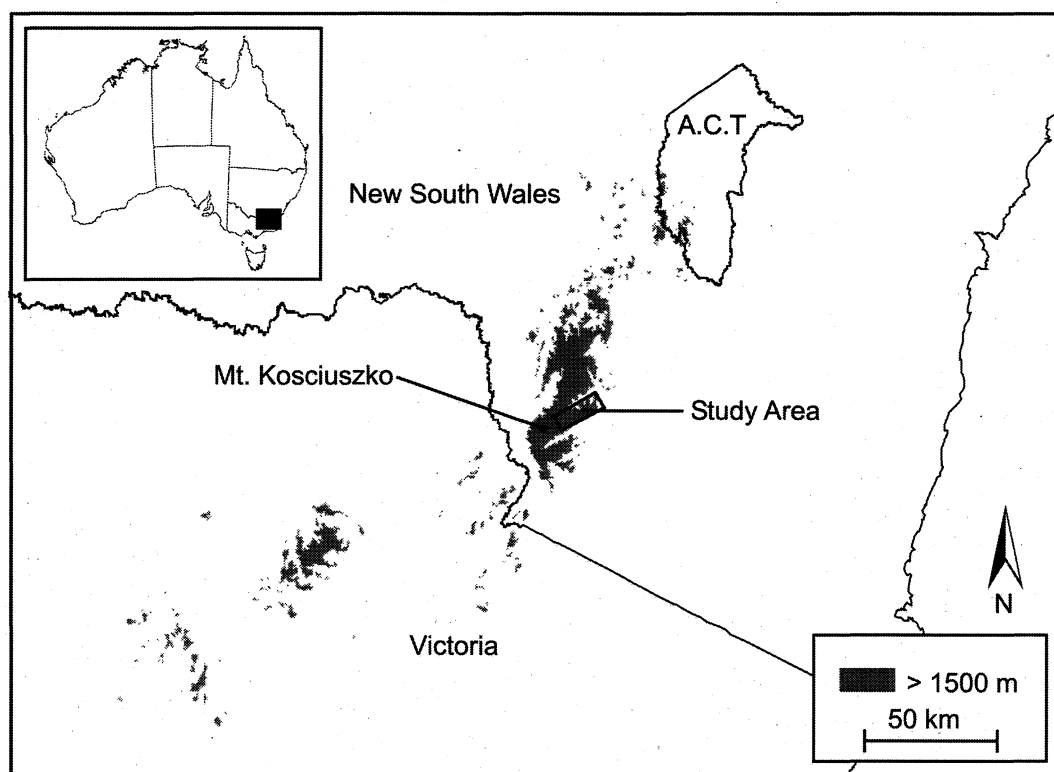


Figure 6.1 Map showing the study area.

6.3.2 Sampling in winter 2002

Sampling sites were stratified using three factors (elevation, aspect and habitat type) that were considered important in influencing the distribution of snow. In addition, we gave consideration to the factors that might be important in the development of the subnivean space, or otherwise interact with the snow cover so as to influence small mammals during the nival period.

In mountainous regions, elevation is generally considered to be the most important factor influencing snow cover (Mckay & Gray 1981). Sites were established at three elevation levels: low (1501-1600 m), mid (1601-1700 m) and high (1701-1800 m).

Aspect is an important factor in determining both accumulation and ablation rates of snow cover (Mckay & Gray 1981). Within each elevation category, study sites were located on both generally ablating and generally accumulating aspects. The former consisted of sites that faced generally north to west and experienced higher levels of insolation, while the latter faced generally south to east and were often influenced by natural 'snow fence' effects (Figure 6.2).

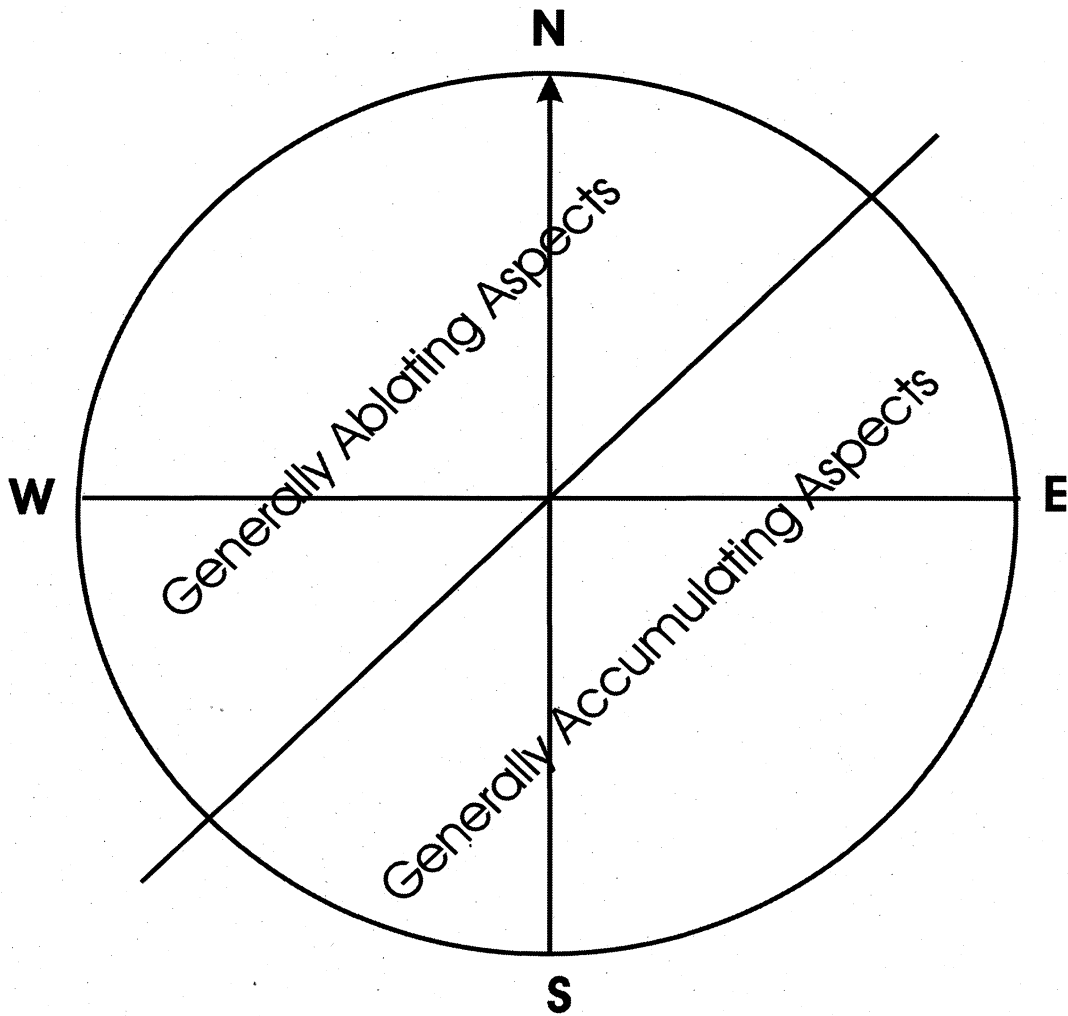


Figure 6.2 Aspect categories

The subalpine vegetation of the Snowy Mountains consists of a patchy mosaic of vegetation types (Read 1987) and there are strong relationships between vegetation types and topography in the alpine and subalpine areas (Costin 1954; Green & Osborne 1994; Costin *et al.* 2000). Four vegetation types that occurred at all elevations were sampled to represent the range of habitat types available to small mammals: wet heath, dry heath, woodland and tussock grassland.

In the Snowy Mountains, heathland is generally classified according to its floristic composition (Costin 1954; Green & Osborne 1994; Costin *et al.* 2000), but small mammals are influenced by vegetation structure and complexity rather than by floristic composition (Carron 1985; Green 1988). Accordingly we identified two heath types, with wet heath generally having denser and more

complex vegetation than dry heath. Wet heath typically occurs along drainage lines and creeks or in poorly drained low-lying areas. Floristically, it is characterised by *Baeckea* spp., *Leptospermum* spp., *Epacris* spp. and *Richea continentis* and at lower elevations by *Callistemon sieberii*. Ground cover may comprise sphagnum moss in damp areas with grasses and forbs in more open positions and bare soil under dense shrub growth. Dry heath occurs in better-drained areas typically located on mid to upper slopes, and is characterised by species such as *Bossiaea foliosa*, *Nematolepis ovatifolia*, *Prostanthera cuneata*, *Grevillea australis*, *Orites lancifolia*, *Hovea montana* and *Olearia* spp.

Trees have a significant effect on snow accumulation and ablation (Mckay & Gray 1981; Stottlemyer & Troendle 1999) and subalpine woodland is the most widespread vegetation above the winter snowline in the Snowy Mountains (Green & Osborne 1994). Subalpine woodland can be divided into climax and seral, in both cases dominated by the Snow Gum, *Eucalyptus niphophila* but also including Black Sallee, *E. stellulata* in poorly drained locations. Climax woodland is characterised by a grassy understorey almost devoid of shrubby plants. In contrast, seral woodland is one of the most structurally complex habitats in the mountains; its understorey is often of similar floristic and structural composition to nearby heathland (Costin 1954; Green & Osborne 1994). In this study, we established sites in seral woodland because it occurred right through the altitudinal range and because of its structural complexity. Tussock grassland is primarily dominated by *Poa* spp. but often includes forbs, and in more poorly drained areas it may include rushes such as *Empodisma minus*.

We replicated each combination of elevation class, aspect position and habitat type three times giving a total of 72 study sites. Small mammal surveys were undertaken using a new hair tube design; the technical details of this method are presented in Sanecki and Green (2005). The technique provides an efficient method of accessing the subnivean space, and the use of hair tubes eliminates the concerns for small mammal welfare associated with live-trapping. Each of the 72 study sites consisted of three plots, approximately 10 m apart. Each plot was centred on a timber stake, to which a one-metre long 90 mm diameter PVC tube

was affixed with a 50 mm gap at the bottom to provide access to the subnivean space.

Hair tubes were baited with a mixture of rolled oats, honey and peanut butter and left in place for seven days. The adhesive tapes were removed from hair tubes and hair samples were inspected under a compound microscope and identified using the methods outlined by Brunner and Coman (1974) and Brunner and Triggs (2002).

A preliminary survey was undertaken to establish the distribution of small mammals in the absence of any effects of snow cover. This was undertaken in April 2002, after dispersal of juveniles had occurred and several weeks before the first snowfall.

Eleven surveys were undertaken during the nival period commencing in June 2002 when snow was present at all sites and continuing at intervals of 7-21 days until October. The survey commencing on 17 August 2002, when snow cover was greatest in depth and extent, was used as a comparison with the pre-nival and post-nival surveys.

A final post-nival survey was conducted in October 2002 once all sites were clear of snow. When compared to the pre-nival survey results, this survey allowed the overall effect of the winter season on small mammal detections to be assessed.

Snow measurements were taken weekly commencing at the first snowfall and concluding when all the sites were clear of snow the following spring. Snow depths were measured to the nearest 5 cm using graduations marked on the stake supporting each subnivean sampling tube. For each plot, a visual estimate was made of the percentage of ground exposed and the percentage of protruding shrubs and boulders within a 5 m radius of the stake (Table 6.1).

Table 6.1 Snow cover variables measured during winter 2002.

Variable	Description
Snow depth	Depth of snowpack above ground measured to nearest 5 cm marked on a timber stake located at centre of the plot.
Exposed ground %	Visual estimate of ground clear of snow within the plot.
Protruding shrubs %	Visual estimate of shrubs protruding through snowpack within the plot.
Protruding boulders %	Visual estimate of boulders protruding through the snowpack within the plot.

To date, the only method that has been available to measure the size of the subnivean space has involved the excavation of a snow pit to the base of the snowpack. The subnivean space could then be inspected and measured. This method is very time consuming and a limited number of measurements can be taken during any given period. The effort required to excavate a snow pit also increases with increasing snow depth and density. More importantly, the excavation of a snow pit causes considerable interference to the physical integrity of the subnivean space, especially when the pit is filled in again. Under continuous snow cover, the excavation of large snow pits can alter the thermal coupling between the subnivean and supranivean environments which can have a significant effect on subnivean thermal regimes (Taylor & Buskirk 1996).

In Australia, snowpack density increases rapidly following deposition (Ruddell 1998; Sanecki *et al.* In Review-a). Once the snowpack reaches a point where it does not contain low density layers, it is possible to extract snow cores with a Federal Snow sampler (Carpenter Machine Works, Seattle) without causing any compression to underlying snow layers. Subnivean space measurements were recorded on 17 August 2002, a date chosen to allow sufficient time for snowpack density to attain suitable values; maximum snow depth for the winter also was recorded on this date. Using a Federal Snow sampler, we took three snow core samples randomly within 5 metres of each plot where snow cover occurred. The sampler was carefully drilled until it broke through the base of the snowpack, and then lowered until it came to rest on the ground. The depth of the subnivean space was calculated as the difference between the snow depth measured by the

sampler and the length of the snow core extracted from the hole. For analysis, we averaged the three samples per plot.

Recorded non-snow variables included those factors considered potentially important in small mammal distribution during the nival period; in particular, those that might facilitate the development of the subnivean space, or otherwise influence snow cover characteristics. These are described in Table 6.2. Five of the measured variables were obtained from five point-quadrats per plot using a 20 mm diameter extendable pole marked at 20 cm intervals. The first point-quadrat was taken at the plot centre (the snow tube stake) and then four additional point-quadrats were taken at a distance of three metres uphill, downhill and to the left and right of the plot centre. For each point-quadrat, the ranging pole was lowered vertically through any vegetation being careful not to deform any branches or stems. For each 20 cm interval, the presence or absence of vegetation contacts were recorded, along with the species and maximum height. Tree canopy was assessed visually directly above the point quadrat. Microtopography was assessed within a one-metre radius of the base of the point quadrat position. Non-snow variables were surveyed during December 2002 and January 2003.

Table 6.2 Non-snow variables. Variables indicated # were based on five point-quadrats per plot (see text). Other variables were based on a circular sampling area of 5 m radius from the plot centre.

Variable	Description
Shrub species#	Number of contacts with point-quadrat ranging pole per species, total per plot.
Shrub height#	Maximum shrub height at point quadrats, average per plot.
Shrub structure#	Aggregate number of shrub contacts with point-quadrat ranging pole, total per plot.
Tree canopy cover#	Sum of scores from the five point quadrat positions. 0 = No canopy. 1 = Discontinuous canopy cover, a few living or dead branches. 2 = Thin continuous canopy cover with simple upper stratum. 3 = Thick continuous canopy cover with complex upper stratum and/or lower storey.
Microtopography#	Sum of scores from the five point quadrat positions. 0 = Flat. 1 = Small ground undulations and irregularities up to 10cm in amplitude, small grass tussocks. 2 = Uneven ground up to 30cm in amplitude, large grass tussocks. 3 = Very rough ground, such as drainage line with steep banks, undercuts and/or overhangs.
Coarse Woody Debris (CWD)	Score, 0 = None, 1 = Scattered branches < 20cm diameter. 2 = Scattered larger branches and fallen logs > 20cm diameter up to 50% of sampling area. 3 = Branches and fallen logs >20cm diameter forming large intertwined piles or over more than 50% of the sampling area.
Boulders	Score, 0 = None. 1 = Small scattered boulders <25% of sampling area. 2 = Large scattered boulders covering up to 50% of the sampling area and/or providing no complex habitat structure. 3 = Large boulders covering over 50% of the sampling area and/or providing complex habitat structures such as overhanging edges, crevices and cavities. 4 = Boulderfield.
Number of tree stems	Number of tree stems, >10cm diameter within the sampling area.
Tree height	Average height of trees in the sampling area in metres.
Distance to nearest tree stem	Distance in metres from centre of sampling area to nearest tree stem at ground level.
Shrub cover %	Visual estimate of shrub cover as a percentage of the sampling area.
Grass cover %	Visual estimate of grass cover as a percentage of the sampling area.
Bare soil %	Visual estimate of bare soil as a percentage of the sampling area.
Leaf and bark litter %	Visual estimate of leaf and bark litter as a percentage of the sampling area.
Sphagnum %	Visual estimate of sphagnum moss as a percentage of the sampling area.
Rushes %	Visual estimate of rushes <i>Empodisma minus</i> as a percentage of the sampling area.

6.3.3 Sampling in winter 2003

During January and February 2003, a wildfire burnt 69% of the area above 1500 m in the Snowy Mountains (Green & Sanecki In Review), resulting in the destruction of 83% of the study sites used in 2002. Twelve of the original 24 high elevation sites were burned.

During winter 2003, we resampled the high elevation sites. We re-established 12 new sites to provide three replicates of the four habitat types on both accumulating and ablating aspects. In addition, we established sampling sites in six boulderfields (3 ablating, 3 accumulating). Boulderfields in the Snowy Mountains are generally of glacial or periglacial origin and are characterised by the dominance of granitic boulders. The boulders may form a layer several metres thick (Mansergh & Broome 1994), providing deep crevices and overhangs. *Podocarpus lawrencii* is often the predominant species when shrubs occur, but species from other adjacent vegetation types are also often present.

Six small mammal surveys were undertaken at all high elevation sites, comprising one survey in May before the onset of snow, four surveys during the nival period, and a final survey once all the sites were clear of snow. Snow and non-snow variables were recorded as described above for winter 2002.

6.3.4 Statistical analysis

6.3.4.1 Changes in small mammal distribution between seasons

To examine whether there were differences in the distribution of *R. fuscipes* and *A. swainsonii* between the pre-nival, nival and post-nival periods in 2002, we used binomial generalised linear models (GLMs), with the presence or absence of each species as the response variable and the three stratification variables (habitat type, elevation class and aspect class) as fixed effects.

6.3.4.2 Factors affecting nival period detections

To determine factors affecting the probability of detecting each species during the nival period in 2002, we used binomial generalised linear mixed models (GLMMs). The response variable was the presence or absence of each species on each plot at each site on each survey date. The variables used as fixed effects are listed in Tables 6.1 and 6.2, and the random effect terms were site, plot and

survey date. We fitted two models for each species, the first including sites where snow cover was present and the second for sites where snow cover was absent. Continuous explanatory variables were fitted using regression splines where appropriate. Models were reduced using Wald tests.

6.3.4.3 Subnivean space

To determine whether there was an association between the size of the subnivean space and the stratification variables, GLMMs were fitted with the stratification variables as fixed effects and site as a random effect. To determine whether there was an association between the size of the subnivean space and the presence of each species, binomial GLMMs were fitted, with the size of the subnivean space as fixed effect and site as a random effect. The response variable was the presence or absence of *R. fuscipes* and *A. swainsonii* based on the survey conducted during the seven days following the measurement of the subnivean space size.

6.3.4.4 Boulderfields

To determine whether boulderfields at the high elevation level were used by *R. fuscipes* and *A. swainsonii* in preference to other habitats, we used binomial GLMs with the presence or absence of each species as the response variable and habitat type (wet heath, dry heath, seral woodland and boulderfield) and aspect as fixed effects. We performed this analysis using 2003 data collected during the pre-nival, nival and post-nival periods. The four nival period surveys were combined into one dataset.

6.4 Results

Thirteen hair tube surveys were conducted between April and October 2002. A total of 2,808 hair tubes was set, of which 1,084 were visited by animals. This provided 1,105 small mammal detections, or a 39% detection rate.

Only two species were detected in sufficient numbers to permit analysis: *R. fuscipes* (683 detections) and *Antechinus* spp. (420 detections). The similarities of hair morphology meant that it was not possible to differentiate between the two species of *Antechinus* in all instances. Of the 420 *Antechinus* detections, 373 (89%) were *A. swainsonii* and 4 (1%) were *A. agilis*, leaving 43 (10%) samples

that could be identified to genus only. *Antechinus swainsonii* is more common than *A. agilis* above 1500 m (Dickman *et al.* 1983; Green 1988); it is probable that the unidentified animals were *A. swainsonii* and they were included in analyses as *A. swainsonii*. There was only one detection (0.09%) each of the endangered *M. fuscus* and mountain pygmy-possum *Burramys parvus*.

During 2002, we measured snow for 22 weeks, giving a total of 4,752 measures; the results are summarised in Table 6.3. The duration of snow cover varied from one week at a low elevation ablating site to 21 weeks at a high elevation accumulating site. Snow duration was significantly different between elevations ($P < 0.0001$). Within elevation classes, duration was significantly different between aspects ($P < 0.0001$). A similar pattern also was apparent for maximum snow depths, which ranged from 20 cm at a low ablating site to 250 cm at a high accumulating site. Again, there were significant differences in maximum snow depths at different elevations ($P < 0.0001$) and between different aspects within elevations ($P < 0.0001$). Maximum snow depths on ablating aspects were 15-25% lower than on accumulating aspects. At low and mid-elevations, duration of snow cover was about 50% shorter on ablating aspects, but at high elevations only about 20% shorter.

Snow cover at low elevation sites and mid-elevation ablating sites has shallow snow of short duration, characteristic of ephemeral snow in the classification system of Sturm *et al.* (1995). The deeper snow cover at the mid-elevation accumulating sites and the high elevation sites lasted for at least three months and is classified as maritime snow in the Sturm system.

Table 6.3 Average snow duration and maximum snow depths for 2002.

	Ablating Aspects		Accumulating Aspects	
	Duration (Weeks) (+/-SD)	Max Depth (cm) (+/-SD)	Duration (Weeks) (+/-SD)	Max Depth (cm) (+/-SD)
1701-1800 m	14.6 (+/-2.8)	101.7 (+/-42.4)	18.3 (+/-1.8)	141.0 (+/- 42.4)
1601-1700 m	7.0 (+/-2.5)	65.3 (+/- 24.4)	12.8 (+/-2.4)	83.5 (+/-18.0)
1501-1600 m	4.4 (+/-1.7)	39.0 (+/-11.3)	9.0 (+/-1.6)	46.9 (+/-12.8)

6.4.1 Pre-nival, nival and post-nival surveys 2002

During the pre-nival survey, there were 43 detections of *R. fuscipes* and 25 *A. swainsonii*. Neither elevation nor aspect was a significant factor in predicting the occurrence of either species. Habitat type was a significant factor for both species (*R. fuscipes* $p=0.0026$, *A. swainsonii* $p<0.0001$) with both species less likely to be detected in grassland and no significant difference between the other three habitat types.

During the survey commencing on 17 August 2002, there were 20 detections of *R. fuscipes* and 49 of *A. swainsonii*. Aspect was again not a significant factor for either species, but elevation was highly significant for both *R. fuscipes* ($p<0.0001$) and *A. swainsonii* ($p<0.0001$), with both species less likely to be detected at high elevations. Habitat type was significant for *R. fuscipes* ($p=0.0072$) but was no longer significant for *A. swainsonii* ($p=0.0699$) indicating that this species was using grassland habitats during the nival period.

There was an increase in the number of *R. fuscipes* detections during the post-nival survey with 104 detections. *Antechinus swainsonii* was detected 20 times. During the post-nival survey, habitat type was again a significant factor for both species (*R. fuscipes* $p<0.0001$, *A. swainsonii* $p=0.0021$). Elevation was not significant for *R. fuscipes*, but remained significant for *A. swainsonii* ($p=0.0004$) with this species less likely to be detected at high elevation sites. For *R. fuscipes*,

there was a significant interaction ($p=0.0046$) between elevation and aspect reflecting the fact that at the high elevation it was more likely to be detected on the ablating than the accumulating aspects.

6.4.2 2002 nival period – effect of snow cover

Detections for all nival period surveys are summarised for each species by elevation and habitat type in Table 6.4 and Table 6.5. In the presence of snow cover, both species were significantly less likely ($p<0.0001$) to be detected at higher elevations. This also was observed for *A. swainsonii* in the absence of snow ($p<0.0001$), but not *R. fuscipes* which had a similar detection rate in the absence of snow at all elevations.

The highest detection rates for both species were in wet heaths, although the difference was not as pronounced for *R. fuscipes* (either with or without snow cover). For *A. swainsonii*, woodland and dry heath had similar detection rates. Grassland habitats were all but unused by both species in the absence of snow, with no *R. fuscipes* and only one *A. swainsonii* detection. In the presence of snow cover, there were 30 *A. swainsonii* detections in grasslands, but only two *R. fuscipes* detections.

Final nival period GLMMs are presented in Table 6.6 and Table 6.7. For the snow model, *A. swainsonii* was more likely to be detected at the mid and low elevation levels and at sites with high shrub structural complexity and microtopography. *Antechinus swainsonii* was more likely to be detected in mid-winter and at snow depths of less than 50 cm and above 100 cm (Figure 6.3 and Figure 6.4).

In the non-snow model, *A. swainsonii* was more likely to be detected through the middle of the nival period and less likely towards the end (Figure 6.5). Aspect was important, with more animals detected on ablating aspects.

R. fuscipes was more likely to be detected as shrub structural complexity increased, in both the presence and absence of snow. *R. fuscipes* was more likely to be detected in areas with shallow snow (Figure 6.6), and was less likely to be detected during the nival period whether snow was present or not, with detections increasing towards the latter part of the period, especially in areas that were free of snow cover (Figure 6.7 and Figure 6.8).

Table 6.4 Small mammal detection success rates (%) by elevation during the nival period.

	Snow		Non-snow	
	<i>A. swainsonii</i>	<i>R. fuscipes</i>	<i>A. swainsonii</i>	<i>R. fuscipes</i>
1701-1800 m	3.4	9.2	1.5	45.0
1601-1700 m	16.8	11.8	10.1	41.0
1501-1600 m	36.7	17.8	24.8	42.7

Table 6.5 Small mammal detection success rates (%) by habitat type during the nival period.

	Snow		Non-snow	
	<i>A. swainsonii</i>	<i>R. fuscipes</i>	<i>A. swainsonii</i>	<i>R. fuscipes</i>
Grassland	8.2	0.5	0.4	0
Woodland	13.5	14.6	18.0	57.1
Dry Heath	13.1	14.1	21.6	51.0
Wet Heath	24.4	17.7	31.7	67.7

Table 6.6 . Final nival period models for *A. swainsonii*. (s) indicates that a regression spline was fitted to the term. p values are indicated for terms fitted to the model in the order shown.

Factor	F-Value	DF	p-Value
Snow Model			
Elevation	15.60	2, 69	<0.0001
Shrub Structure	7.04	1, 139	0.0089
Microtopography (s)	5.37	4, 139	0.0005
Snow Depth (s)	14.27	1, 1316	<0.0001
Day (s)	8.66	4, 1316	<0.0001
Non-Snow Model			
Habitat	4.22	3, 61	0.0089
Aspect	5.45	1, 61	0.0229
Day (s)	21.15	4, 639	<0.0001

Table 6.7 . Final nival period models for *R. fuscipes*. (s) indicates that a regression spline was fitted to the term. p values are indicated for terms fitted to the model in the order shown.

Factor	F-Value	DF	p-Value
Snow Model			
Shrub Structure	27.43	1, 143	<0.0001
Snow Depth (s)	17.26	4, 1316	<0.0001
Day (s)	47.67	4, 1316	<0.0001
Non-Snow Model			
Shrub Structure	37.85	1, 126	<0.0001
Day (s)	22.19	4, 639	<0.0001

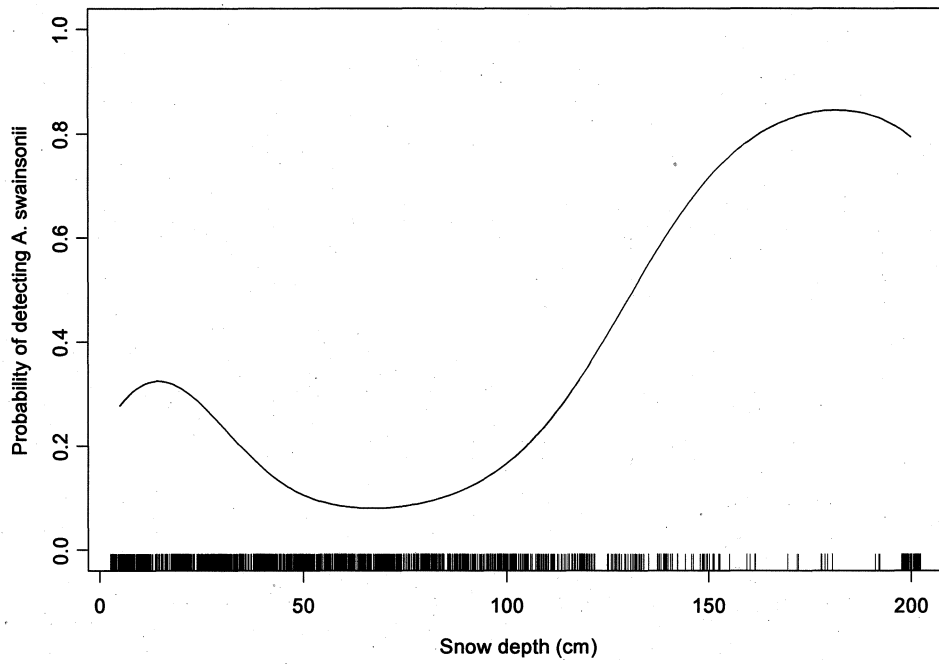


Figure 6.3 Probability of detecting *A. swainsonii* in relation to snow depth. Bars on x axis indicate small mammal detections.

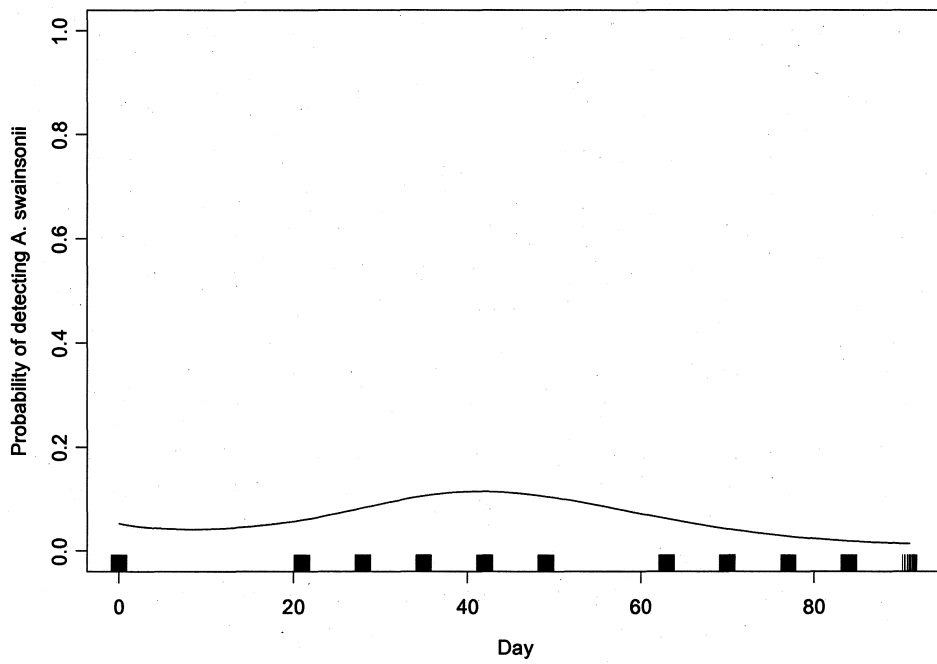


Figure 6.4 Probability of detecting *A. swainsonii* in relation to day where snow cover was present. Bars on x axis indicate the time at which surveys were undertaken.

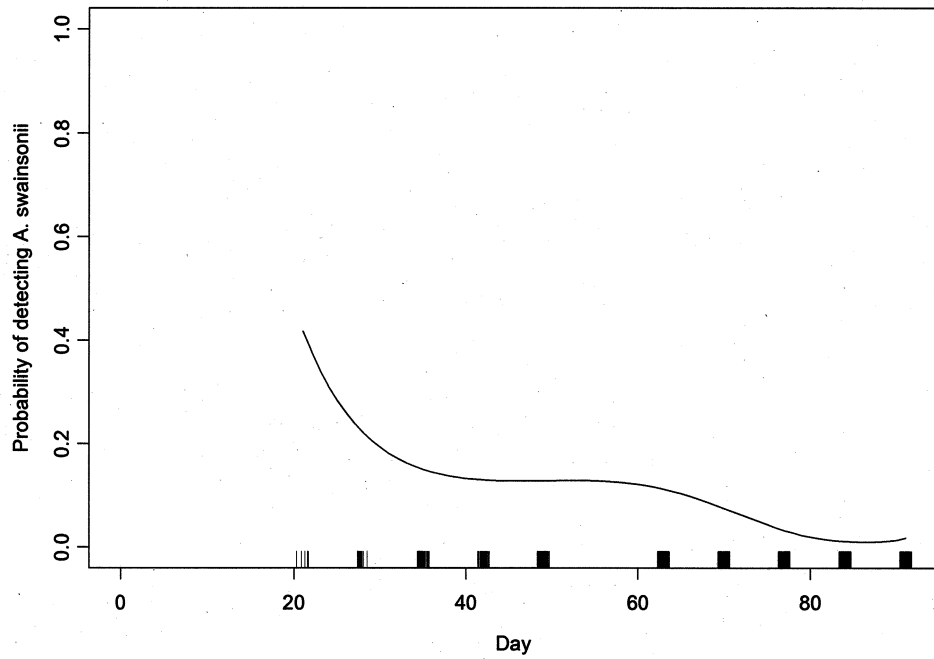


Figure 6.5 Probability of detecting *A. swainsonii* in relation to day in the absence of snow. Bars on x axis indicate the time at which surveys were undertaken.

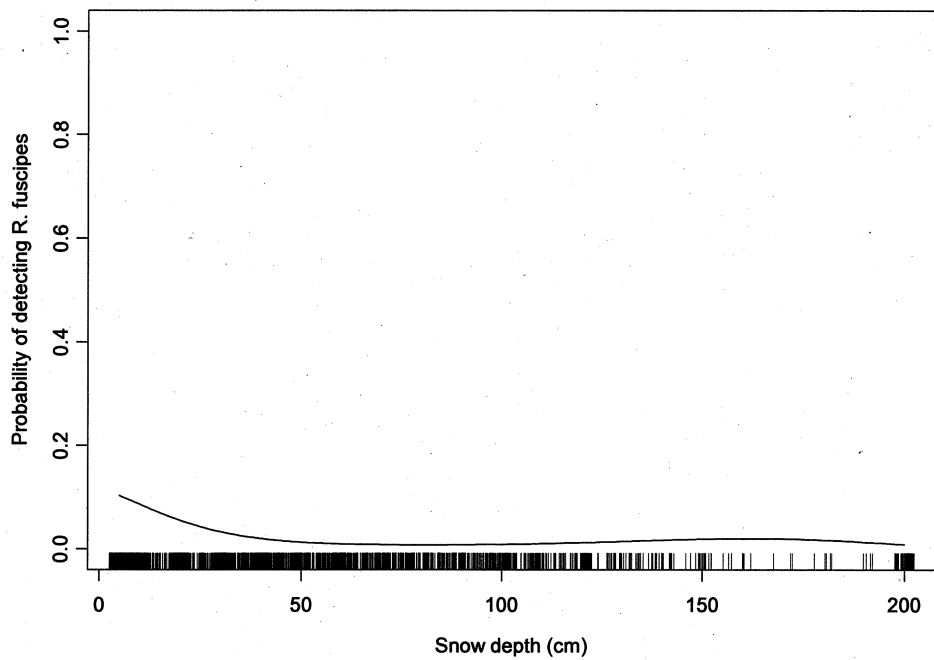


Figure 6.6 Probability of detecting *R. fuscipes* in relation to snow depth. Bars on x axis indicate small mammal detections.

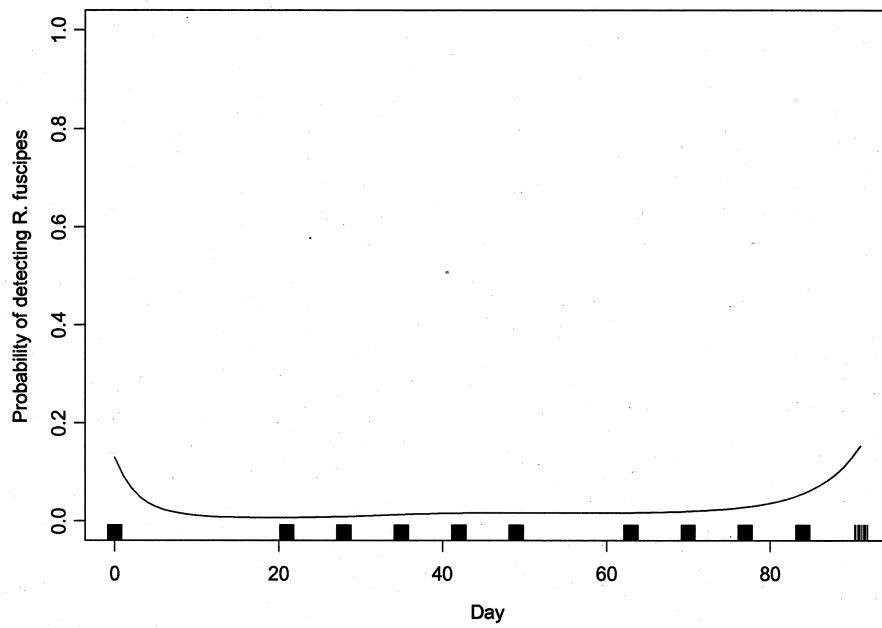


Figure 6.7 Probability of detecting *R. fuscipes* in relation to day where snow cover was present. Bars on x axis indicate the time at which surveys were undertaken.

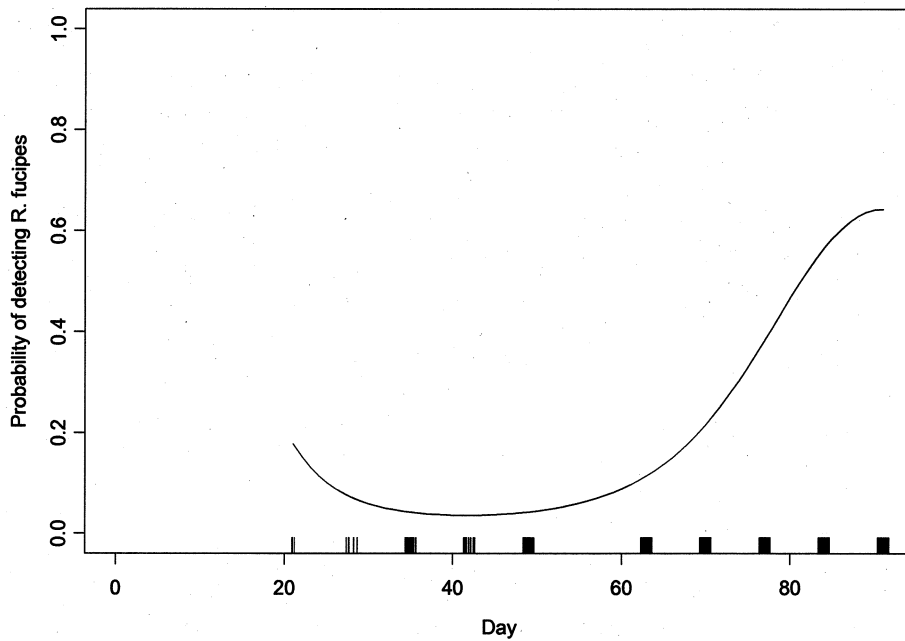


Figure 6.8 Probability of detecting *R. fuscipes* in relation to day in the absence of snow. Bars on x axis indicate the time at which surveys were undertaken.

6.4.3 Small mammals and the size of the subnivean space

The presence of *A. swainsonii* was strongly related to the size of the subnivean space ($F_{1,93} 18.81357, p < 0.0001$). In contrast, *R. fuscipes* showed no significant relationship ($F_{1,93} 2.73287, p = 0.1017$) (Figure 6.9).

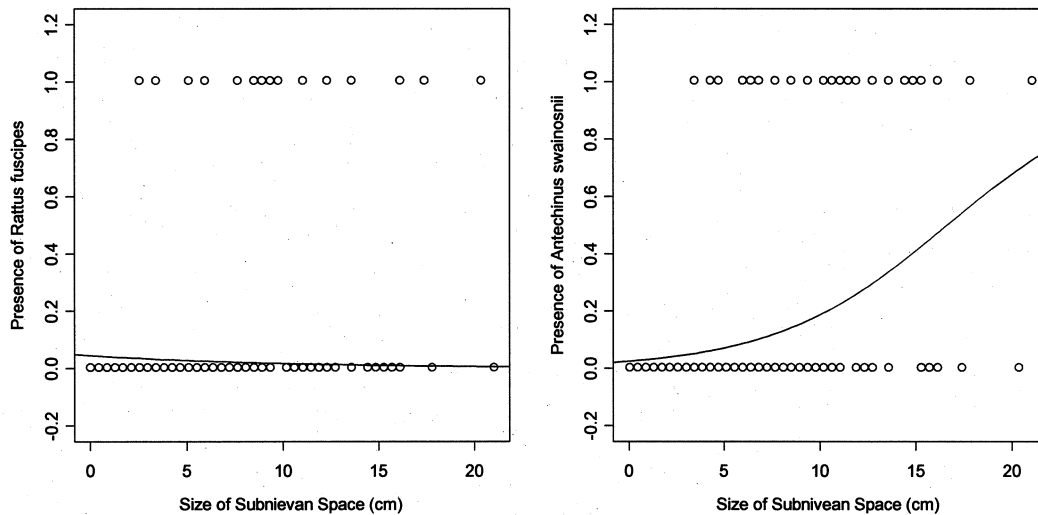


Figure 6.9 Fitted model showing the probability of detecting *R. fuscipes* and *A. swainsonii* in response to the size of the subnivean space.

6.4.4 Factors influencing the size of the subnivean space

An initial model showed that the size of the subnivean space was significantly different between habitat types ($F_{3,44}=7.37, p=0.0004$) and elevations ($F_{2,44}=9.06, p=0.0005$). The size of the subnivean space was not related to snow depth or aspect and there were no interactions between habitat and elevation. Final model predictions for an average site (Table 6.8) showed that the subnivean space at the low and mid-elevation sites was significantly larger than at the high elevation sites. There was no significant difference between the low and mid-elevations. At each elevation, grassland sites had the smallest subnivean space when compared to the other habitat types at the same elevation. At each elevation, wet

heath subnivean spaces were significantly larger than those of the other three habitat types ($p=0.0103$).

Table 6.8 Model predictions for the size (cm) of the subnivean space by elevation and habitat type for an "average" site.

	Wet Heath	Dry Heath	Woodland	Grassland
1701-1800m	7.36	4.24	4.55	1.97
1601-1700m	10.57	7.46	7.77	5.18
1501-1600m	11.40	8.28	8.59	6.0

When shrub structure and microtopography were added to the model before habitat type and elevation, structure and microtopography were each highly significant ($F_{1,92}=54.10$, $p<0.0001$ and $F_{1,92}=30.59$, $p<0.0001$ respectively), but habitat type was no longer significant. This showed that variation attributed to habitat type was probably the result of differences in shrub structure and microtopography. Elevation was still significant ($F_{2,44}=4.64$, $p<0.0148$).

6.4.5 Winter 2003

During the pre-nival survey, there were 44 detections of *R. fuscipes* and 23 of *A. swainsonii*. Neither aspect nor habitat type was significant with both species occurring in all habitat types other than grassland.

There were 30 detections of *R. fuscipes* and 44 of *A. swainsonii* during the nival surveys. Small mammals were detected in all boulderfields throughout the nival period. Aspect was not a significant factor for either species, but habitat type was ($p<0.0001$), with both species more likely to be detected in boulderfields. No small mammals were detected in dry heath or woodland habitats, with wet heath the only other habitat in which they were detected (*A. swainsonii*, 10, *R. fuscipes*, 5).

During the post-nival survey, we detected 33 *R. fuscipes* and seven *A. swainsonii*. Detections of *A. swainsonii* were not significantly different between habitats or aspect, although the relatively few detections of this species do not provide a clear result. Both habitat ($p=0.05$) and aspect ($p=0.004$) remained significant factors in the final model for *R. fuscipes* except in the boulderfields where almost all detections were on abating aspects.

6.5 Discussion

In nival areas, winter mortality of small mammals is attributed to the harsh climatic conditions typical of these areas (Pruitt 1957, 1984; Carron 1985; Halfpenny & Ozanne 1989; Happold 1989). Snow is believed to ameliorate some of the negative climatic effects by providing a stable thermal environment (Pruitt 1957; Merritt & Merritt 1978; Pruitt 1984; Halfpenny & Ozanne 1989). Our study shows that this may not be the case in Australia. Both *R. fuscipes* and *A. swainsonii* were more likely to be detected at lower elevations where snow cover duration was shortest and where there was either no snow or where snow cover was patchy and often discontinuous. This suggests that, in Australia, snow cover has a negative effect on the abundance and survival of small mammals.

Some of the observed changes in detectability in this study were probably the result of variation in the likelihood of animals visiting hair tubes. During the early part of the nival period the subnivean space was poorly developed, particularly where the first snowfall penetrated through the vegetation cover to ground level. Sampling of small mammals at this time may not provide a true indication of their occurrence, because some tubes may be inaccessible until the subnivean space begins to form. The sudden decline in *R. fuscipes* detections at all elevations after the first snowfall (with a particularly marked decline at the highest elevation) was probably the result of animals failing to find hair tubes.

In the post-nival survey, *A. swainsonii* detections were only slightly lower than those observed during the pre-nival survey, despite the fact that at this time almost all of the male population had died after breeding (Green 1988; Dickman 1995). This suggested that the activity level of the surviving *A. swainsonii* increased after snow had melted. Similarly, the increase in *R. fuscipes* detections during the post-nival survey probably reflects increased activity resulting from

the onset of breeding which commences around the middle of October (Carron 1985; Green & Osborne 1994).

6.5.1 The subnivean space

In boreal and colder alpine regions around the world, the development of the subnivean space is linked to the presence of depth hoar or pukak (Pruitt 1984; Halfpenny & Ozanne 1989), whereby a low-density snow layer forms at ground level and more dense layers higher in the snowpack provide structural support. The low-density depth hoar has been thought to permit small mammal movement and activity under the snow. The predominant snow types in Australia are maritime and ephemeral snow (Sanecki *et al.* In Review-a), neither of which is conducive to the formation of depth hoar (Sturm *et al.* 1995); rather, these snow types promote the development of higher density snow at ground level.

Our results indicate that, under Australian snow conditions, the development of the subnivean space depends on the presence of structures able to support the snowpack above ground level (Green & Osborne 1994; Green 1998a). The important factors are the structural complexity of the shrub layer and microtopographic features. As a consequence, the development of the subnivean space is strongly associated with specific habitat types; in particular those with a well developed shrub layer and sites with sufficient microtopographic relief, such as drainage lines. Wet heaths often combine both of these characteristics and therefore could be considered prime nival habitats for small mammals.

The structural factors significantly associated with small mammal detections were shrub structure (for *A. swainsonii* and *R. fuscipes*) and microtopography (for *A. swainsonii*). These factors most probably indirectly affect small mammals through their association with subnivean space formation. This interpretation is supported by the positive relationship between *A. swainsonii* and subnivean space size (Figure 6.9). The absence of a relationship between *R. fuscipes* and the size of the subnivean space is probably a reflection of the fact that *R. fuscipes* was rarely detected under the snow (Figure 6.6) and was recorded primarily at mid and low elevations where snow cover was shallow, discontinuous or absent during the nival period. It is possible that the larger *R.*

fuscipes was physically unable to access hair tubes at some high elevation sites where subnivean spaces were small (Table 6.8).

Neither boulders nor coarse woody debris (CWD) was a significant factor in the subnivean space model, but in our 2002 surveys, few sites supported many such structures and many of these sites did not have any snow cover remaining when subnivean space measurements were taken in August. The 2003 surveys showed that large, complex agglomerations of boulders (boulderfields) were associated with high numbers of detections of small mammals, most likely as a result of the contribution that boulders make to providing structural support to the overlying snowpack. Where they occur, shrubs such as *Podocarpus lawrencii* provide additional structure because of their horizontal growth habit (Costin *et al.* 2000). Boulderfields are probably important refugia for small mammals during winter, at least at higher elevations, and are considered to be valuable habitats for small mammals (Green & Osborne 1994). It is likely that CWD also plays a role in subnivean space formation in Australia, as researchers elsewhere have found that CWD is important in structuring the subnivean space, and also providing connectivity between the subnivean and supranivean environments (Sherburne & Bissonette 1994).

The increase in detections of *R. fuscipes* at high elevations subsequent to the disappearance of snow indicates that this species was resident throughout the winter, most probably in boulderfields (or other structurally complex habitats) that were not sampled during 2002. This is supported by the fact that small mammals took several weeks to be detected in otherwise suitable habitats immediately after the disappearance of snow. In the post-nival survey, *R. fuscipes* were more likely to be detected on ablating aspects, which had been clear of snow for about four weeks, than on accumulating aspects where snow had disappeared about one week before the survey.

The smaller subnivean space size at higher elevation corresponds to the findings of Green (1988) and Green and Osborne (1994), who noted that the weight of a deep snow cover compresses the subnivean space. The fact that snow depth was not a significant factor in our model for the development of the subnivean space suggests that, even under deep snow, the subnivean space will still form, provided there is sufficient structural support. We do not discard the notion that

deep snow may reduce the size of the subnivean space, but consider that other factors also play a part. In particular, with increasing elevation the height and density of the shrub layer decreases and at high elevations may not be sufficiently robust to support the deeper snowpack. This point will be considered in more detail in a separate paper.

The presence of trees provides connectivity between the supranivean and subnivean environments (Green 2000). This can benefit small mammals because, with increased access to the subnivean space, risks of predation are smaller when they move across the snow surface (Green 1998b, 2000). Trees also facilitate the removal of carbon dioxide from the subnivean space (Penny & Pruitt 1984). Conversely, increased connectivity between the supranivean and subnivean environments can have detrimental effects because it allows the ingress of cold air into the subnivean space, thereby reducing temperatures and increasing temperature fluctuations in an otherwise stable environment (Taylor & Buskirk 1996). There was no indication in our study, however, that the presence of trees was an important factor in the subnivean distribution of small mammals.

6.5.2 Winter ecology of *R. fuscipes* and *A. swainsonii*

The results of this study indicate that *A. swainsonii* and *R. fuscipes* have different strategies for optimising survival during the winter. Compared to the pre-nival survey, the detection rate of *A. swainsonii* doubled in the nival period while detections of *R. fuscipes* halved whether snow was present or not (Figure 6.7 and Figure 6.8), suggesting that activity of the former increased while the latter became less active. When snow is absent *A. swainsonii* is nocturnal and/or crepuscular (Carron 1985; Green & Crowley 1989; Green & Osborne 1994) while *R. fuscipes* is almost exclusively nocturnal (Hall 1980; Lunney 1995). Changes in small mammal activity patterns have been observed during the nival period (Kucera & Fuller 1978; Stebbins 1984; Carron 1985) and may account for the changes in detections observed in this study.

The almost complete lack of *R. fuscipes* detections in areas with continuous snow cover indicates that this species does not utilise the subnivean space to the same extent as *A. swainsonii*. This may reflect the fact that *A. swainsonii* is an insectivore (Dickman *et al.* 1983; Green & Crowley 1989; Dickman 1995) and

forages actively throughout the nival period (Green 1988), while *R. fuscipes* is an omnivore and responds to the lack of foraging space in winter by including a higher proportion of plant material in its diet (Carron *et al.* 1990). Diet switching to a more abundant food source may mean that *R. fuscipes* can meet its increased energy demands without increasing foraging activity or foraging area.

The inclusion of shrub structure in the non-snow model for *R. fuscipes* indicated that structurally complex habitats were important whether or not snow was present, and that snow did not appear to modify its habitat utilisation patterns. By contrast, shrub structure was not important to *A. swainsonii* when snow was absent, suggesting that during winter this species foraged in shrub habitats irrespective of their structural complexity in order to maximise the opportunities for locating scarce food items.

Our findings confirm the findings of Green and Crowley (1989) who observed that *A. swainsonii* used grassland habitats when snow cover was present and speculated that this was in response to a need to maximise foraging area and that they could do so because the snow provided cover. In contrast, the fact that *R. fuscipes* was not detected in any numbers in grassland seems to support our hypothesis that they do not need to forage broadly to fulfil their energetic needs. However, of all the habitats we examined, grasslands had the smallest subnivean space size at any given elevation. *Rattus fuscipes* has a body size almost double that of *A. swainsonii* and thus may not be able to exploit this habitat to the same extent.

Overseas workers have reported that small mammals generally avoid areas of shallow snow cover (Pruitt 1960; Auerbach & Halfpenny 1991). This does not appear to be the case in Australia. Carron (1985) found that, during the nival period, *R. fuscipes* showed a preference for shallow snow, and our study confirms this observation. Carron (1985) also reported that *A. swainsonii* was unaffected by snow depth, while Green (1988) suggested that *Antechinus* spp. was negatively affected by both shallow and deep snow, the former being unable to provide adequate thermal insulation, while the latter acts to compress the subnivean space and reduce available foraging area. In our study, *A. swainsonii* detections were lowest at moderate snow depths of 50-100 cm (Figure 6.3). It appears that, under Australian snow conditions, shallow (and probably patchy)

snow benefits both species by increasing habitat availability. The positive relationship between deep snow and *A. swainsonii* detectability may reflect the outcome of interspecific competition with *R. fuscipes*. However, it may be a statistical artefact of the sampling regime where *A. swainsonii* was repeatedly detected at a handful of high elevation sites with deep snow cover.

Because the subnivean space is confined to areas of suitable structure, it is likely that the total extent of accessible habitat for small mammals is reduced during winter. Combined with harsh climatic conditions occurring in winter, a reduction of available habitat resources imposes stresses on resident animals leading to increased winter mortality (Spencer 1984; Carron 1985). In our study, it is not possible to draw conclusions about the adequacy of available resources, because the hair tube technique records the number of visitations without identifying the number of individuals.

6.6 Conclusion

To our knowledge this is the first study anywhere in the world to investigate the distribution of small mammals in nival environments in relation to the spatial and temporal variation of snow cover at the landscape-scale. Previous studies that used live-trapping or indirect methods have been restricted by logistical constraints to small scales. As a result, the conclusions that can be drawn about broad-scale animal distributions have been limited.

In Australia, which has predominantly maritime and ephemeral snow, small mammals are generally associated with shallow or patchy snow cover, most probably due to the limited extent of the subnivean space, which is dependent upon the presence of structural components such as shrubs, microtopographic relief and boulders.

Patterns observed in our study do not correspond to the findings of workers in boreal or high elevation areas overseas, where climatic conditions are more conducive to the formation of depth hoar. However, they are probably relevant to areas with climatic regimes and snow conditions similar to those occurring in the Australian alpine and subalpine areas. With changes in snow cover regimes in response to global warming and climate change, it is possible that the dynamics of Australian nival systems may become more relevant to other areas.

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7 THE THERMAL ENVIRONMENT OF SMALL MAMMALS IN RELATION TO SNOW COVER IN THE AUSTRALIAN ALPS

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7.1 Abstract

During winter 2002, we examined the effects of snow cover on the thermal characteristics of small mammal habitats in the Snowy Mountains, south-eastern Australia. The temperature in the subnivean space was virtually constant beneath the snowpack, ranging between 0 and +1°C. When snow was patchy or absent, temperatures at ground level were highly variable with a minimum as low as -13°C and maximum as high as +47.5°C. Two species of small mammals, *Antechinus swainsonii* and *Rattus fuscipes*, were detected more regularly at sites that were thermally variable; the snow cover at these sites was discontinuous, patchy and transient and was classified as ephemeral. At sites with deep and persistent snow cover (maritime snow), subnivean temperatures were stable, but small mammals were detected at low frequencies. At high elevations, boulderfields are favoured by small mammals during the nival period but were no different thermally from other habitats. These findings contradict the commonly held beliefs that small mammals prefer thermally stable winter environments, and that boulderfields experience low temperatures due to cold air drainage. In snow-free areas, diurnal temperature ranges varied with vegetation type, with the highest temperatures occurring in grasslands at most elevations. In mountainous regions, some areas are subject to a deep snow cover that persists for most of the winter, but in many areas poor and short-lived snow cover means that thermal instability may continue throughout the winter. One of the likely consequences of global warming is an increase in the extent of areas with thermally unstable winter conditions in mountainous regions throughout the world; it is possible that this change could actually benefit some small mammals at the expense of other species.

Keywords: Subnivean space, Snowy Mountains, Kosciuszko National Park.

7.2 Introduction

It is generally believed that the survival of small mammals over winter in nival areas is dependent on the relative thermal stability of the subnivean space (Formozov 1946; Pruitt 1984; Halfpenny & Ozanne 1989; Happold 1998). This stability is achieved when snow cover is of sufficient thickness to decouple the supranivean and subnivean thermal environments. This creates conditions in the subnivean space that are quite distinct from the supranivean environment. The threshold snow depth for achieving thermal stability (hiemal threshold) is a function of snow thickness and density (Marchand 1982) but is of the order of 15-50 cm of unbroken snow (Coulianos & Johnels 1962; Pruitt 1970; Halfpenny & Ozanne 1989; Courtin *et al.* 1991). Once the requisite snow depth has been deposited, the snowpack provides a thermal buffer, allowing subnivean temperatures to remain within one or two degrees of freezing throughout the nival period regardless of fluctuations in air temperature above the snow.

Small mammals are only able to exploit the thermal stability provided by snow cover if a subnivean space forms between the snow and the ground surface (Pruitt 1984; Halfpenny & Ozanne 1989). In boreal zones such as the taiga or in high alpine regions, the formation of the subnivean space and the activity of small mammals is thought to be facilitated by the presence of depth hoar (Pruitt 1984). In the Australian Alps, however, snow conditions are not conducive to the formation of depth hoar (Sanecki *et al.* In Review-a). Rather, the formation of the subnivean space depends almost exclusively on the presence of structures that are physically capable of supporting the weight of the snowpack, in particular dense shrubs, boulders and microtopographic features. Habitats combining these features, such as wet heaths, are occupied throughout the nival period by active small mammals such as the dusky antechinus *Antechinus swainsonii* and the bush rat *Rattus fuscipes* (Sanecki *et al.* In Review-b).

Boulderfields are considered prime habitats for small mammals in Australian high country areas (Green & Osborne 1994; Mansergh & Broome 1994), especially at higher elevations where other habitats become incapable of supporting a subnivean space. Indeed, this is the only habitat within which *A. swainsonii* and *R. fuscipes* are regularly detected throughout the nival period at high elevation sites (Sanecki *et al.* In Review-b). Boulderfields, however, are

believed to be susceptible to cold air drainage, especially in shallow snow conditions, which could reduce their thermal stability (Walter 1996; Green 1998). This suggests that factors other than the thermal environment are important in determining small mammal distribution during the nival period.

Small mammals are thought to experience particularly challenging climatic conditions during late autumn (pre-nival) and early spring (post-nival) (Formozov 1946; Fuller *et al.* 1969; Pruitt 1970; Merritt 1984; Courtin *et al.* 1991). During these times, and in the absence of a well-developed snow cover, small mammals are subject to temperatures often well below freezing. In autumn, snowfall may not persist whilst sleet and/or rain may "freeze out" animals (Formozov 1946; Halfpenny & Ozanne 1989). Similar conditions may occur during spring, and snowmelt can also result in localised flooding (Halfpenny & Ozanne 1989; Happold 1998).

In areas where snow cover is of short duration and/or in years of shallow snow, the thermal conditions experienced by small mammals during much of the winter are likely to be similar to those occurring during pre-nival and post-nival periods where or when snow cover is more extensive. It would be expected, therefore, that more congenial thermal conditions should be present in snow covered areas than in areas free from snow, provided that a subnivean space is present to permit small mammals to remain active during the nival period.

Human activities in nival areas, such as snow grooming and the use of over-snow vehicles, often result in compression of the snowpack, reducing the insulating qualities of snow (Schmid 1971; Keddy *et al.* 1979). The loss of insulation is thought to be detrimental to subnivean fauna (Halfpenny & Ozanne 1989; Auerbach & Halfpenny 1991). Therefore, increasing human exploitation of nival areas for winter sports could have significant consequences for resident small mammals. Global warming is also an issue of growing concern, with snow cover decline already apparent and expected to continue both overseas (Houghton *et al.* 2001) and in Australia (Whetton *et al.* 1996; Whetton 1998). If this occurs, the small mammal fauna occupying large areas of the world's alpine regions could experience extended periods of thermal stress, with unknown effects on the long-term survival of these species.

In this paper we describe the thermal characteristics of small mammal habitats in the subalpine zone in relation to snow cover. We also investigate the role of snow as a thermal buffer and the importance of thermal stability to small mammals during the nival period in Australia.

7.3 Methods

7.3.1 The study area

The study area was located in the Snowy Mountains, south-eastern Australia ($36^{\circ}30'S$, $148^{\circ}15'E$) and is described in detail elsewhere (Sanecki *et al.* In Review-b). The study area extended from Charlotte Pass ($36^{\circ}26'S$, $148^{\circ}20'E$) to Rennix Gap ($36^{\circ}21'S$, $148^{\circ}31'E$) (Figure 7.1). This configuration was chosen because it included an appropriate range and combination of elevation, aspect and habitat types whilst also being reasonably accessible.

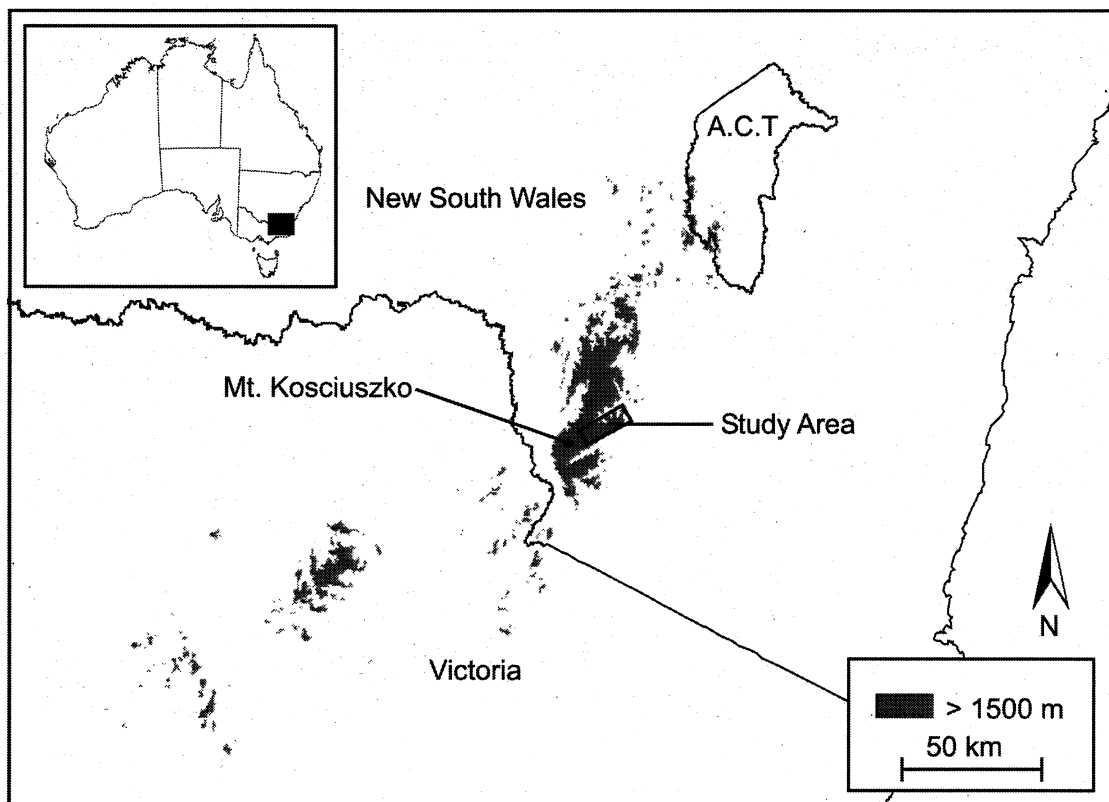


Figure 7.1 Map of the study area.

7.3.2 Winter 2002

7.3.2.1 Study design

The study design is described in detail elsewhere (Sanecki *et al.* In Review-b) and a brief summary is presented below.

Sampling sites were stratified by elevation (1501-1600 m, 1601-1700 m and 1701-1800 m), aspect (accumulating, ablating) and vegetation formation (wet heath, dry heath, seral woodland, grassland). Three replicate sites were established at each combination of elevation, aspect and vegetation, giving a total of 72 sites. Each site consisted of three plots each centred on a wooden stake that had a PVC pipe 1 m long and 90 mm in diameter attached and held 50 mm off the ground. The pipe allowed access to the subnivean space without disturbance to the snowpack.

7.3.2.2 Snow measurements

Snow depth was measured weekly from the first snowfall (mid-May) to when the sites were clear of snow the following spring (mid-October). Snow depths were measured to the nearest 5 cm using graduations on each stake. At the same time, a visual estimate was made of the percent ground exposed and the percentage of protruding shrubs and boulders within a 5 m radius of each stake.

7.3.2.3 Small mammal surveys

Small mammals were detected using a novel hair tube design (Sanecki & Green 2005). Baited hair tubes containing adhesive tape were lowered to the bottom of the pipe and left in place for seven days before retrieval; any hairs adhering to the tape were identified under a compound microscope.

A total of 11 hair tube surveys was undertaken at intervals of 7-21 days during the nival period commencing in July 2002.

7.3.2.4 Temperature recording

Subnivean thermal regimes were recorded using 24 Thermochron® iButton temperature loggers (Dallas Semiconductor Corp.). The iButton reads temperatures from -30°C to +70 with a resolution of 0.5°C and is accurate to $\pm 1^\circ\text{C}$. Eight loggers were set out at each elevation level so that one randomly selected replicate of each habitat type was sampled on both accumulating and

ablating aspects. Within each selected site, one plot was randomly chosen and a logger was placed inside a small open-ended PVC tube and attached to the base of the stake with a 1 m length of wire. The loggers were set to record at 2 hourly intervals. They were set out one week before the first winter snowfall, and retrieved once all sites were clear of snow.

7.3.3 Winter 2003

During January and February 2003, a wildfire burnt 12 of the original 24 high elevation sites. We re-established 12 new sites to provide three replicates of the four vegetation types on each aspect. In addition, we established sampling sites in six boulderfields (three ablating, three accumulating).

Six hairtube surveys of the high elevation sites were undertaken, comprising one pre-nival survey in early May, four surveys during the nival period and a post-nival survey in late October. Snow depths were recorded as described above for winter 2002.

Temperature loggers were located as described above at a randomly chosen plot at each of the boulderfield sites and two of the three replicates of the other four habitat types on each aspect.

7.3.4 Statistical analysis

7.3.4.1 Small mammals and thermal stability

Generalised linear models (GLMs) were used to investigate the relationship between small mammals and thermal stability. The response variable was the number of detections of *A. swainsonii* and *R. fuscipes* by site whilst the predictor variable was the number of thermally stable days. A thermally stable day was defined as one in which the 24 hour temperature range was less than or equal to 1°C. Thermally stable days were summed between 12 May and 18 October 2002.

7.3.4.2 Degree days (DDs)

The concept of degree days (DDs), or thermal units, has been used to describe the timing of developmental processes in agricultural crops (Cross & Zuber 1972; Davidson & Campell 1983); investigate patterns of embryonic development in animals (Gillooly & Dodson 2000) and assess the likelihood of

invertebrate pest outbreaks (Ives 1973; Pruess 1983; Zipp & Blommers 1997). Degree days are calculated as a sum of the difference between the daily average temperature and an appropriate base temperature, usually ranging from 7 to 12°C in temperate climates (McMaster & Wilhelm 1997).

We used degree days as an index of the cumulative thermal environment to which small mammals were exposed. Since low as well as high temperatures have effects on the physiology of endothermic animals (Young 1957), we calculated degree days as the sum of daily average temperatures, in other words no base temperature was used. Degree days were compared by elevation and aspect using Analysis of Variance. Data were log-transformed to satisfy assumptions of normality and homogeneity of variance.

7.3.4.3 Thermal conditions in boulderfields

We used Analysis of Variance to test whether there were any significant differences between boulderfields and the other habitats in the number of thermally stable days and winter mean, maximum and minimum temperatures. Again, where appropriate, data were log-transformed to satisfy assumptions of normality and homogeneity of variance.

7.4 Results

7.4.1 Winter 2002

7.4.1.1 Snow duration and thermal stability

The first snowfall was recorded on 18 May 2002, however, snow depth was no more than 5 cm at any site. One week later, snow at the high elevations and some mid-elevation sites was sufficiently deep to achieve the hiemal threshold. All sites were clear of snow by mid-October.

General snow cover and thermal conditions are summarised in Table 7.1. Snow depth and duration were significantly different between elevations and between aspects within elevations (Sanecki *et al.* In Review-b).

Table 7.1 Average snow depth, duration and ground level temperature values (\pm SD) for 2002. Values in brackets are monthly maximum and minimum temperatures.

	Low (1501-1600 m)		Mid (1601-1700 m)		High (1701-1800 m)	
	Ablating	Accumulating	Ablating	Accumulating	Ablating	Accumulating
Snow Duration (Weeks)	4.4 \pm 1.7	7.0 \pm 1.6	7.0 \pm 2.5	12.7 \pm 2.4	14.6 \pm 2.8	18.3 \pm 1.8
Max Snow Depth (cm)	39.0 \pm 11.3	46.9 \pm 12.8	65.3 \pm 24.4	83.5 \pm 18.0	101.7 \pm 42.4	141.0 \pm 42.4
Days Thermally Stable Subnivean Temperature	30.8 \pm 7.8	61.3 \pm 12.0	47.3 \pm 10.0	104.8 \pm 7.6	128.3 \pm 10.0	136.3 \pm 6.3
	0.2 \pm 0.0	0.1 \pm 0.0	0.0 \pm 0.0	0.1 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
May						
Average	1.2 \pm 1.5	0.7 \pm 0.8	1.5 \pm 0.6	1.0 \pm 0.2	1.2 \pm 0.2	1.2 \pm 0.3
Maximum	12.3 \pm 4.7 (18.5)	8.8 \pm 1.3 (10.5)	14.3 \pm 9.3 (28.0)	8.3 \pm 1.2 (9.5)	8.6 \pm 1.3 (10.5)	7.0 \pm 1.1 (8.5)
Minimum	-7.5 \pm 3.9 (-12.5)	-8.4 \pm 3.4 (-11.0)	-6.3 \pm 3.5 (-11.0)	-3.6 \pm 1.4 (-5.5)	-1.8 \pm 0.9 (-2.5)	-1.4 \pm 0.6 (-2.0)
June						
Average	1.7 \pm 0.9	0.6 \pm 0.6	1.3 \pm 0.7	0.7 \pm 0.4	0.8 \pm 0.1	0.9 \pm 0.1
Maximum	14.8 \pm 3.8 (18.5)	10.0 \pm 1.1 (11.0)	19.3 \pm 9.9 (32.0)	6.9 \pm 1.8 (9.5)	6.4 \pm 0.6 (7.0)	4.0 \pm 2.3 (6.5)
Minimum	-5.8 \pm 3.0 (-8.5)	-6.5 \pm 3.8 (-10.0)	-5.1 \pm 2.7 (-8.5)	-2.9 \pm 2.1 (-5.5)	-1.5 \pm 1.4 (-3.5)	-0.5 \pm 0.4 (-1.0)
July						
Average	0.9 \pm 0.7	0.4 \pm 0.3	0.6 \pm 0.4	0.7 \pm 0.2	0.8 \pm 0.2	0.8 \pm 0.2
Maximum	8.5 \pm 7.8 (17.5)	0.8 \pm 0.3 (1.0)	5.0 \pm 4.9 (9.5)	1.0 \pm 0.0 (1.0)	0.9 \pm 0.3 (1.0)	0.9 \pm 0.3 (1.0)
Minimum	-3.8 \pm 2.6 (-6.0)	-1.4 \pm 1.0 (-2.5)	-2.1 \pm 1.2 (-3.0)	0.3 \pm 0.6 (-0.5)	0.6 \pm 0.3 (0.5)	0.5 \pm 0.4 (0.0)
August						
Average	1.6 \pm 1.3	-0.1 \pm 0.6	1.1 \pm 0.8	0.8 \pm 0.2	0.7 \pm 0.2	0.7 \pm 0.3
Maximum	16.6 \pm 8.8 (29.0)	5.4 \pm 7.2 (16.0)	15.8 \pm 10.5 (27.0)	1.0 \pm 0.0 (1.0)	0.9 \pm 0.3 (1.0)	0.9 \pm 0.3 (1.0)
Minimum	-8.9 \pm 4.3 (-13.0)	-5.0 \pm 4.7 (-11.5)	-6.9 \pm 2.4 (-10.0)	0.3 \pm 0.3 (0.0)	0.5 \pm 0.0 (0.5)	0.5 \pm 0.4 (0.0)
September						
Average	4.5 \pm 0.8	2.9 \pm 1.0	4.2 \pm 1.2	1.9 \pm 0.5	1.2 \pm 0.3	0.6 \pm 0.5
Maximum	21.9 \pm 7.3 (32.5)	17.3 \pm 8.7 (29.5)	25.4 \pm 10.0 (39.0)	14.6 \pm 3.1 (18.5)	12.9 \pm 7.8 (20.5)	3.0 \pm 4.7 (10.0)
Minimum	-5.5 \pm 3.5 (-8.5)	-5.6 \pm 3.1 (-9.5)	-5.5 \pm 1.7 (-7.5)	-2.4 \pm 1.3 (-4.0)	-0.8 \pm 1.0 (-2.0)	0.4 \pm 0.8 (-0.5)
October						
Average	6.9 \pm 0.6	5.9 \pm 1.4	6.5 \pm 1.3	5.6 \pm 0.9	4.6 \pm 1.8	3.7 \pm 1.1
Maximum	25.3 \pm 3.8 (29.0)	21.6 \pm 11.2 (36.0)	28.5 \pm 13.4 (47.5)	21.9 \pm 8.0 (31.5)	23.5 \pm 4.8 (30.0)	19.0 \pm 2.5 (22.5)
Minimum	-4.5 \pm 2.4 (-8.0)	-4.9 \pm 3.2 (-8.0)	-5.1 \pm 2.0 (-8.0)	-3.0 \pm 2.1 (-6.0)	-4.0 \pm 4.5 (-10.5)	-2.6 \pm 1.9 (-4.5)

As might be expected, the number of thermally stable days was strongly correlated to the snow cover duration ($R^2=0.89$, $F_{1,22}$ 169.21, $p<0.0001$). Where the two differed, the number of thermally stable days exceeded the snow cover duration; this discrepancy was the result of a combination of factors. First, snow cover was recorded weekly, while thermal stability was recorded daily. Second, the locations of temperature loggers did not coincide exactly with the points of snow measurement (but were generally within one metre). Third, on some days the daily temperature range did not exceed 1°C despite the absence of snow, possibly because temperature loggers were in contact with melt water during spring.

Stable subnivean temperatures in the presence of sufficient snow cover were independent of elevation or aspect, and temperatures remained within 1.0°C of freezing.

There were two distinct thermal patterns. At the low elevation sites and mid-elevation ablating sites, thermal stability was relatively short-lived and appeared to be confined to the early part of the winter (June to early August). By contrast, the mid-elevation accumulating sites and high elevation sites displayed thermal stability lasting more than three months (June to early October).

7.4.1.2 Small mammals and thermal stability

The numbers of detections of both *A. swainsonii* ($F_{1,16}$ 8.5844, $P<0.01$) and *R. fuscipes* ($F_{1,16}$ 21.665, $P<0.0001$) were negatively correlated with the number of days that were thermally stable (Figure 7.2 and Figure 7.3).

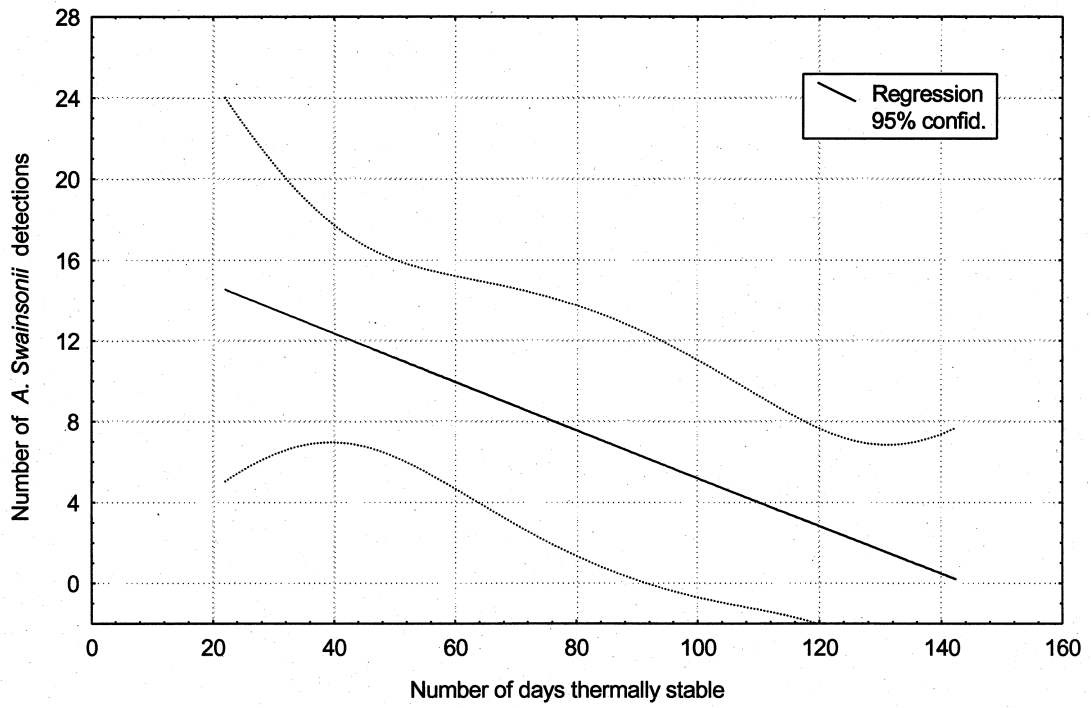


Figure 7.2 The relationship between the number of *A. swainsonii* detections and the number of thermally stable days.

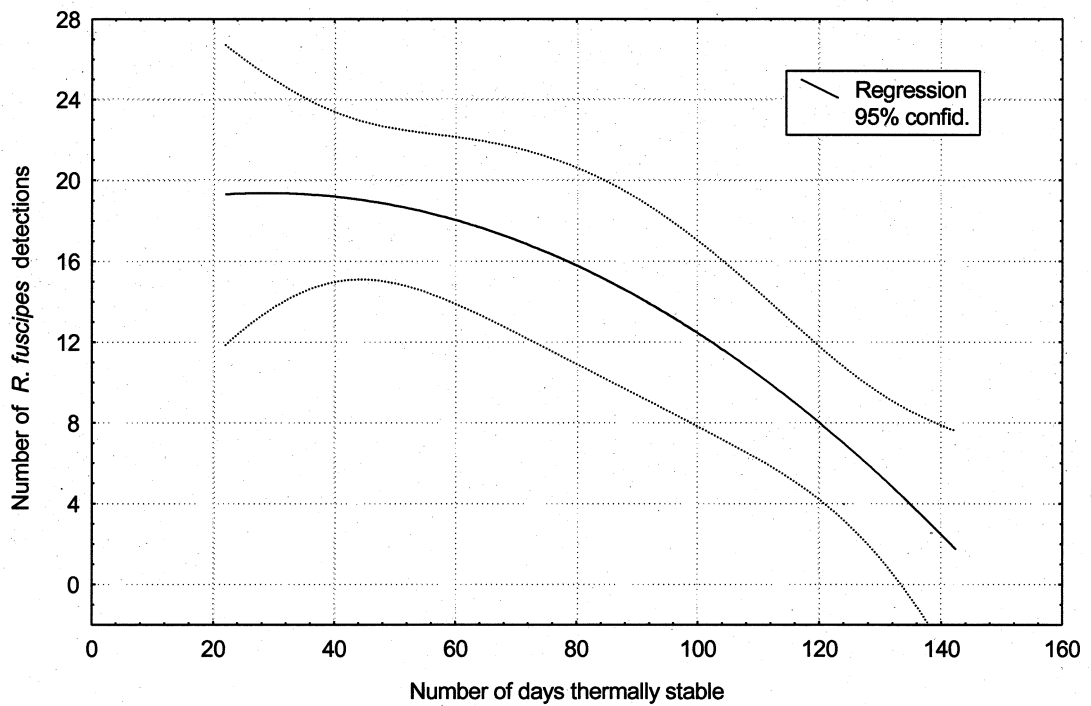


Figure 7.3 The relationship between the number of *R. fuscipes* detections and the number of thermally stable days.

7.4.1.3 Diel temperatures

Mean diel temperatures for each elevation and aspect are shown in Figures 7.4, 7.5, 7.6, 7.7, 7.8 and 7.9. At low elevations and mid-elevation ablating sites, the spikes in daytime average temperature were considerably higher and persisted longer than at mid-elevation accumulating and high elevation sites. Where a daytime spike occurred, temperatures in grassland habitats were higher than those in other habitats, except for the low elevation ablating sites; here the grassland comprised large, dense tussocks and the data logger was in deep shade throughout the day, while it is likely that the data logger in woodland received direct sun in the late morning as a result of a gap in the tree canopy.

1701-1800m Accumulating

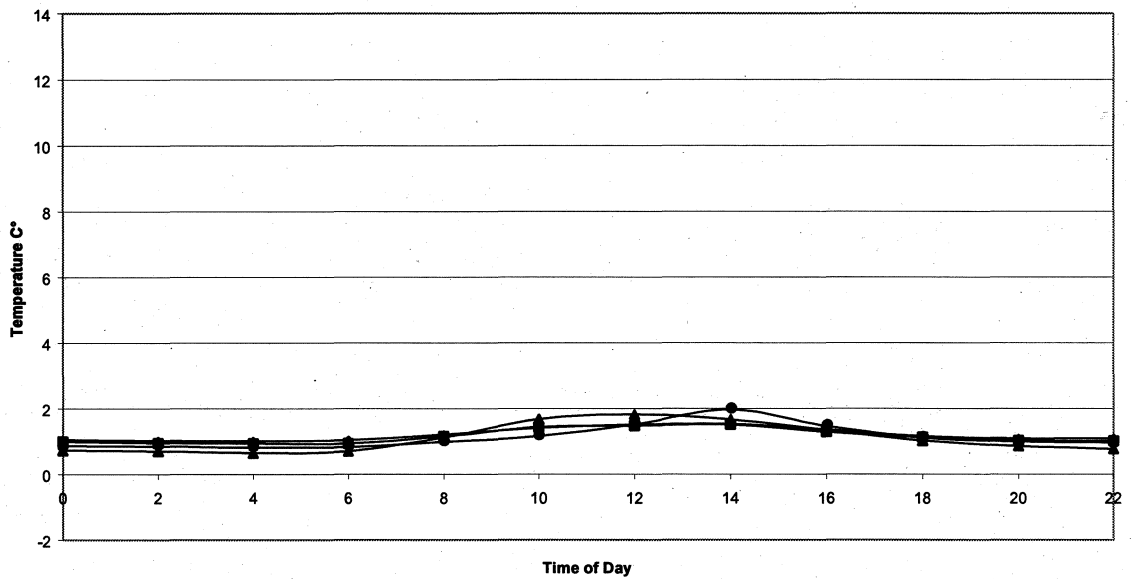


Figure 7.4 Average hourly temperatures for accumulating high elevation sites (▲=Grassland, ■=Dry Heath, ◆ = Wet Heath, ●=Woodland)

1701-1800m Ablating

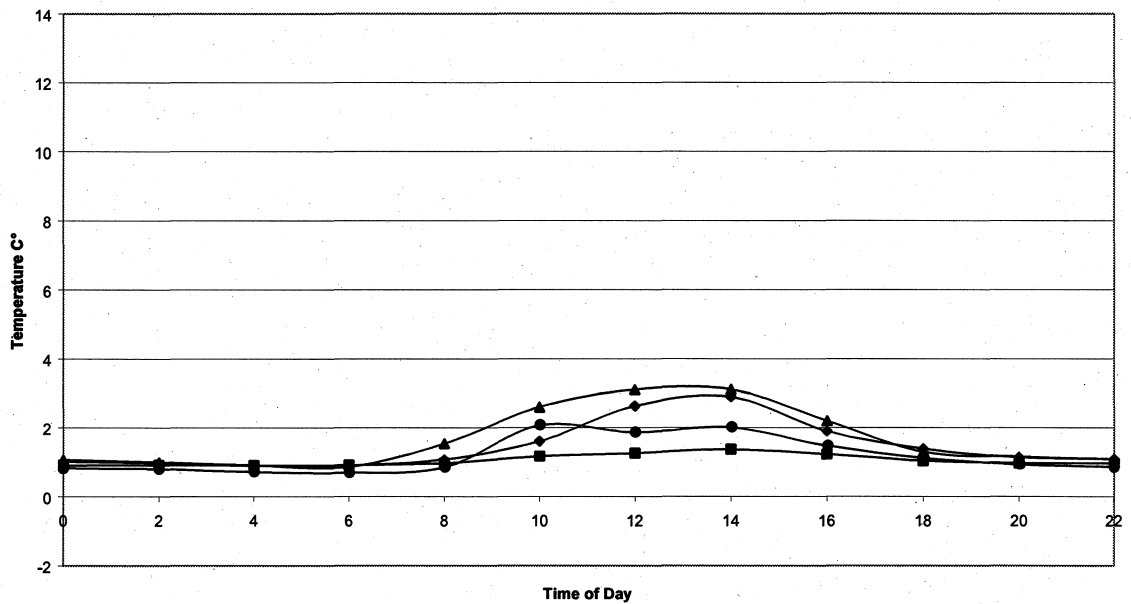


Figure 7.5 Average hourly temperatures for ablating high elevation sites (▲=Grassland, ■=Dry Heath, ◆ = Wet Heath, ●=Woodland)

1601-1700 Accumulating

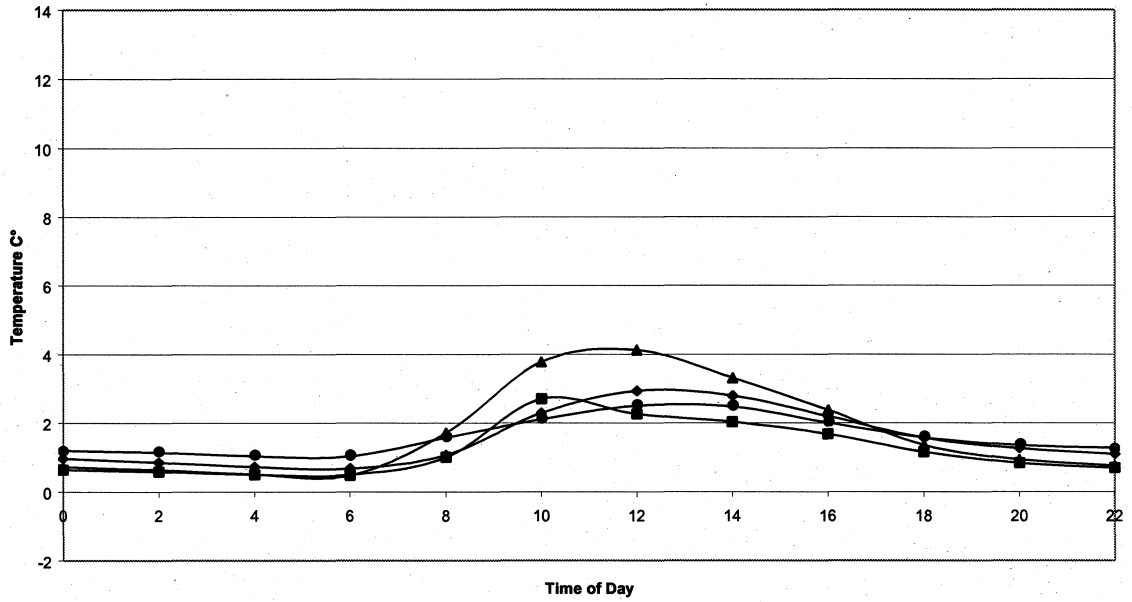


Figure 7.6 Average hourly temperatures for accumulating mid-elevation sites (▲=Grassland, ■=Dry Heath, ◆= Wet Heath, ●=Woodland)

1601-1700 Ablating

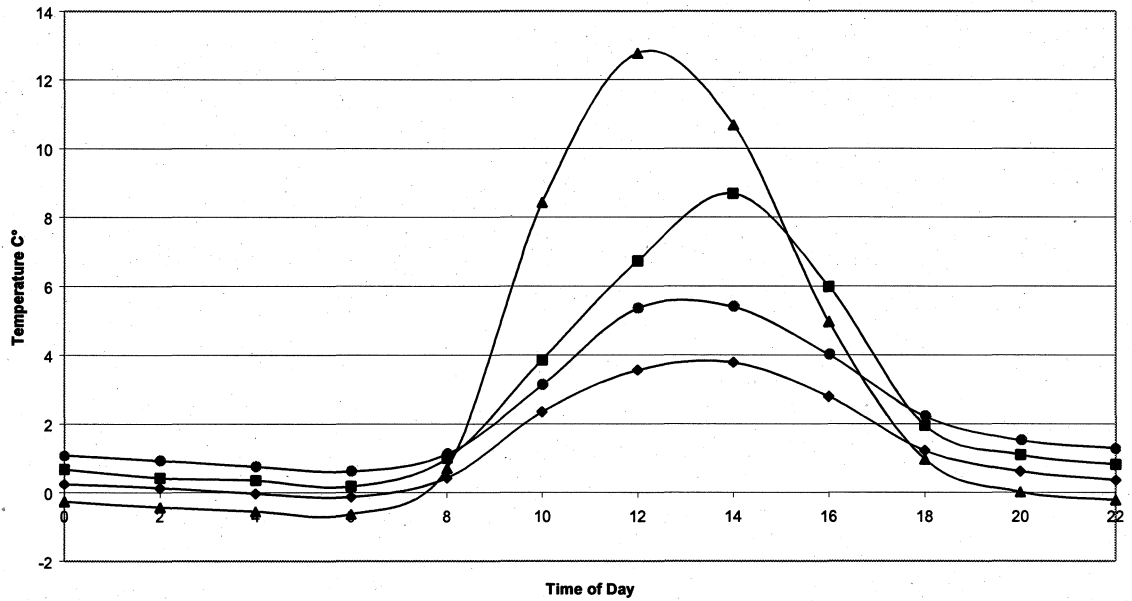


Figure 7.7 Average hourly temperatures for ablating mid-elevation sites (▲=Grassland, ■=Dry Heath, ◆= Wet Heath, ●=Woodland)

1501-1600m Accumulating

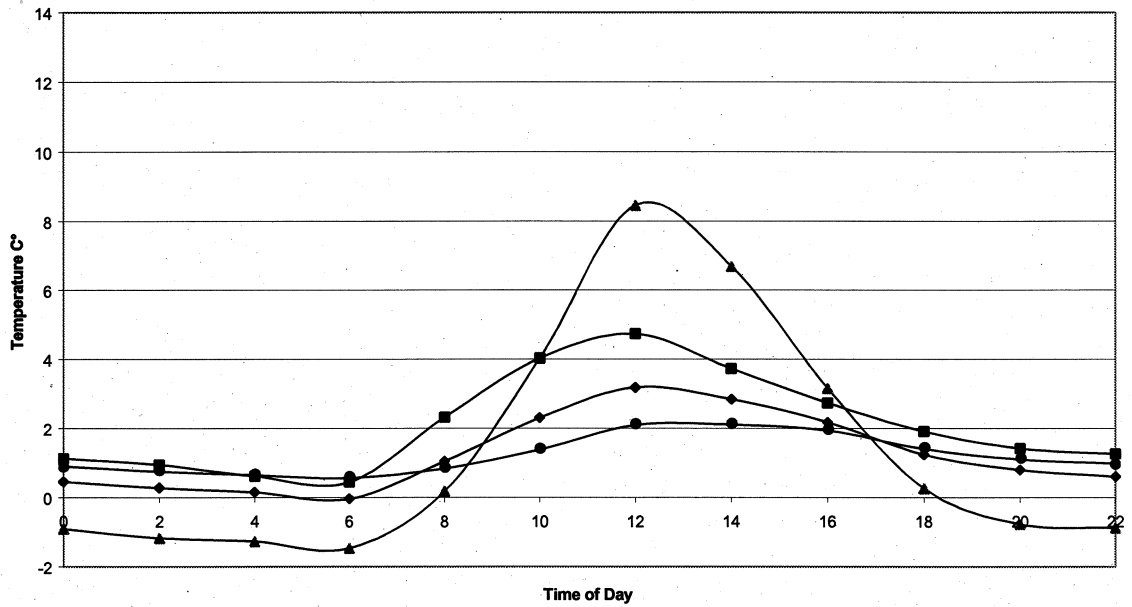


Figure 7.8 Average hourly temperatures for accumulating low elevation sites (▲=Grassland, ■=Dry Heath, ◆= Wet Heath, ●=Woodland)

1501-1600m Ablating

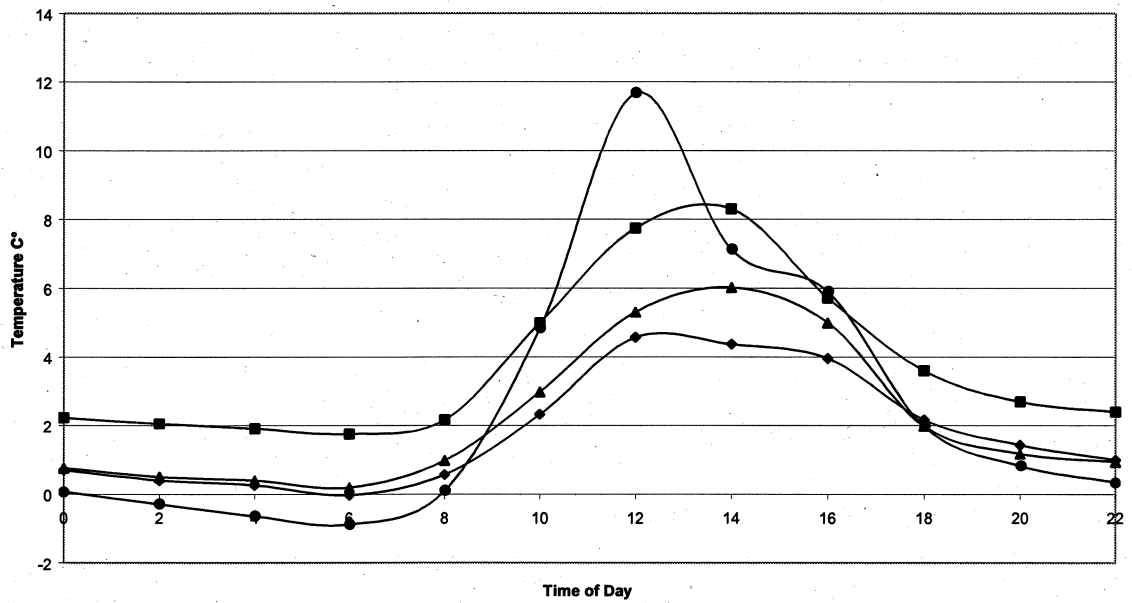


Figure 7.9 Average hourly temperatures for ablating low elevation sites (▲=Grassland, ■=Dry Heath, ◆= Wet Heath, ●=Woodland)

7.4.1.4 Degree Days

Figure 7.10 shows cumulative degree days for each elevation and aspect. DDs were significantly different among elevations ($F_{2,18} 7.36, p<0.0046$) and aspects ($F_{1,18} 12.01, p<0.0028$), with no significant interaction.

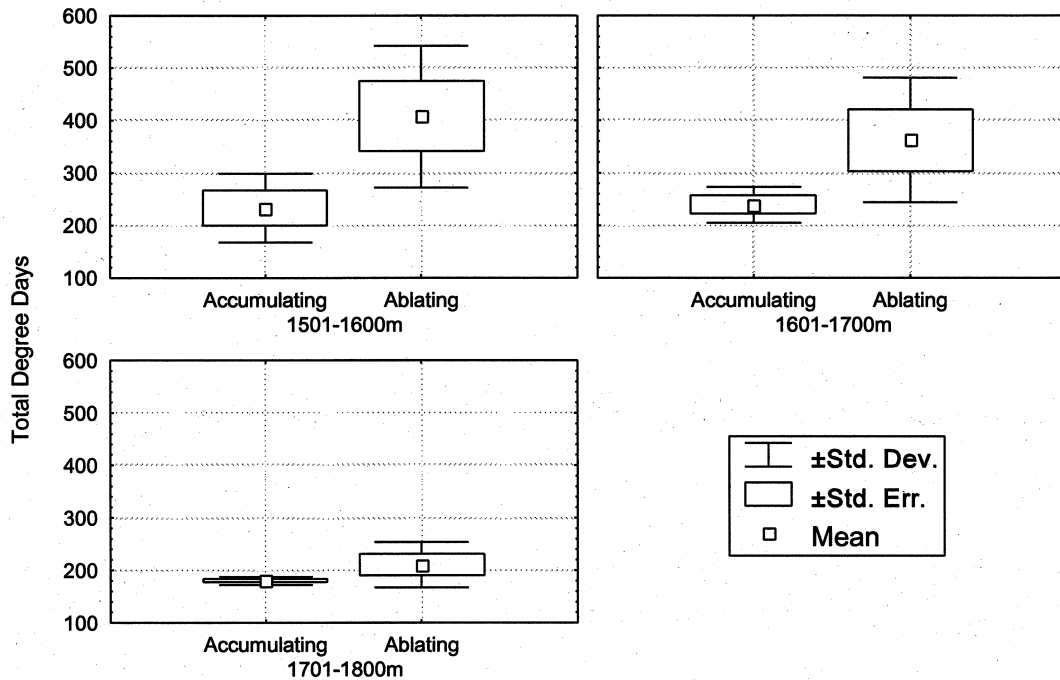


Figure 7.10 Degree days by elevation and aspect.

The low and mid-elevation sites displayed identical patterns; in each case the abating aspect had significantly higher cumulative DDs than the accumulating aspect. At the high elevation sites, accumulating and abating aspects had similar DD values. There was no significant difference among accumulating sites regardless of elevation (Table 7.2).

Table 7.2 Results of pairwise comparisons of DD values among sites (p values).

	Low Ablating	Low Accumulating	Mid Ablating	Mid Accumulating	High Ablating
Low Accumulating	0.0065				
Mid Ablating	NS	0.0299			
Mid Accumulating	0.0109	NS	0.0484		
High Ablating	0.0021	NS	0.0100	NS	
High Accumulating	0.0003	NS	0.0017	NS	NS

7.4.2 Winter 2003

Table 7.3 summarises the thermal conditions at high elevation sites in 2003. Thermal stability lasted significantly longer on accumulating slopes ($F_{1,16} 5.37$, $p=0.0340$), confirming the 2002 results. There was no significant difference in winter mean, minimum and maximum temperature between aspects or habitats with the exception of grassland which had a significantly higher maximum temperature ($F_{4,10} 3.99$, $p=0.0345$).

No significant difference was observed in the numbers of thermally stable days between boulderfields and other habitats.

Table 7.3 Number of thermally stable days and ground level temperature values (\pm SD) for 2003, by habitat type and aspect.

	Ablating	Accumulating
Grassland		
Days Thermally Stable (Days)	84.0 \pm 0.0	127.0 \pm 32.5
Average ($^{\circ}$ C)	-0.5 \pm 0.1	1.2 \pm 0.7
Maximum ($^{\circ}$ C)	34.5 \pm 5.7	28.3 \pm 11.7
Minimum ($^{\circ}$ C)	-15.5 \pm 6.4	-17.0 \pm 14.1
Dry Heath		
Days Thermally Stable (Days)	109.5 \pm 2.12	148.0 \pm 7.1
Average ($^{\circ}$ C)	0.9 \pm 0.56	0.7 \pm 0.1
Maximum ($^{\circ}$ C)	21.8 \pm 6.72	14.3 \pm 5.3
Minimum ($^{\circ}$ C)	-10.0 \pm 4.24	-17.0 \pm 14.1
Wet Heath		
Days Thermally Stable (Days)	107.5 \pm 1.0	147.0 \pm 0.0
Average ($^{\circ}$ C)	1.54 \pm 0.3	1.3 \pm 0.0
Maximum ($^{\circ}$ C)	16.8 \pm 6.0	11.5 \pm 0.0
Minimum ($^{\circ}$ C)	-7.3 \pm 6.7	-6.5 \pm 0.0
Woodland		
Days Thermally Stable (Days)	127.5 \pm 13.4	137.0 \pm 0.0
Average ($^{\circ}$ C)	0.1 \pm 1.74	1.0 \pm 0.0
Maximum ($^{\circ}$ C)	20.8 \pm 14.5	21.0 \pm 0.0
Minimum ($^{\circ}$ C)	-10.8 \pm 9.6	-2.0 \pm 0.0
Boulderfield		
Days Thermally Stable (Days)	114.7 \pm 16.4	123.7 \pm 18.2
Average ($^{\circ}$ C)	0.6 \pm 1.7	1.5 \pm 0.4
Maximum ($^{\circ}$ C)	13.5 \pm 9.1	9.0 \pm 0.5
Minimum ($^{\circ}$ C)	-8.3 \pm 9.3	-2.7 \pm 0.8

7.5 Discussion

If thermal stability was an important factor in the winter ecology of small mammals in the Snowy Mountains of south-eastern Australia, then detections should have been more frequent at sites with longer snow cover durations and hence, longer periods of thermal stability. At many sites that experienced a short nival period, the small mammal residents were subject to conditions throughout the winter that were similar to those occurring in the pre-nival and post-nival periods in areas with persistent snow cover (in other words, variable thermal regimes and temperature extremes). Contrary to expectations, small mammals were more likely to be detected in these less thermally stable areas (Figure 7.2 and Figure 7.3). Furthermore, despite significant differences in DDs between ablating and accumulating aspects at low and mid-elevations (Figure 7.10), differences in small mammal detections were not related to aspect (Sanecki *et al.* In Review-b). These findings suggest that neither temperature variability nor overall thermal environment during winter affects small mammal detectability.

While snow-free sites had more variable temperatures, conditions at these sites were substantially warmer than snow covered sites for a portion of the diel cycle, especially at low and mid-elevations (Figure 7.6 to 7.9). It is possible that small mammals are active during more favourable temperatures, a behaviour that has been exhibited by the sympatric broad-toothed rat *Mastacomys fuscus* (Bubela *et al.* 1991), *A. swainsonii* (Green & Crowley 1989) and perhaps also by *R. fuscipes* (Happold 1998). By contrast, small mammals at snow covered sites experienced a thermally stable environment, but the continuous temperature of 0-1°C would be well below their lower critical temperature and would have required a substantial metabolic energy expenditure for thermoregulation (McDevitt & Speakman 1994).

Exposure to temperatures well below freezing is believed to be responsible for the inability of small mammals to survive supranivean conditions in boreal regions (Pruitt 1984). However, in our study, temperatures as low as -13°C were recorded at snow-free sites (lower than those noted by Green (1988) at higher elevations), but did not appear to adversely affect small mammal detections. The ability of *A. swainsonii* to absorb solar radiation by basking (Green & Crowley 1989), even when air temperatures are low, may enable them to maintain an

appropriate core body temperature (Walsberg *et al.* 1997). Both species also utilise burrows or nests during the winter (Green & Osborne 1994) and may thereby have avoided subzero temperatures.

Contrary to conventional wisdom, the occurrence of active small mammals in the Snowy Mountains does not appear to be dependent on a thermally stable environment. It is also apparent that thermal stability does not explain the relationship between small mammal detections and the subnivean space (Sanecki *et al.* In Review-b). Karlsson (1986) suggested that several factors, including social interactions, patchy and restricted food resources, and subnivean microclimate, interact to regulate small mammal populations during the nival period. However, our results show that subnivean temperatures have no significant effect on small mammal detections, and there is evidence that food resources during winter are not limiting in the Australian Alps (Green 1982, 1989; Carron *et al.* 1990; Happold 1998; Green 2001). Our contention is that the physical presence of a subnivean space is the overriding factor, particularly for species that forage widely during winter.

At high elevation sites, small mammals were more likely to be detected in boulderfields than in any other habitat (Sanecki *et al.* In Review-b). Boulderfields are the preferred habitat for small mammals in nival areas (Bolshakov 1984; Green & Osborne 1994; Mansergh & Broome 1994) despite the fact that they did not provide any thermal benefit over habitats such as wet heaths that are heavily utilised at lower elevations. The low DD values recorded at the high elevation sites are consistent with the general observation that the duration of the growing season in alpine areas, and hence primary productivity, decreases with elevation (Körner 1999). It follows that at high elevations, the shrub layer is shorter and less dense than comparable habitats at lower elevations, and may be unable physically to support the snowpack (Green & Osborne 1994; Sanecki *et al.* In Review-b). At high elevations, boulderfields are the major habitat capable of sustaining a subnivean space large enough to allow small mammal movement.

The difference in thermal pattern between low elevation and mid-elevation ablating sites on one hand, and mid-elevation accumulating and high elevation sites on the other (Table 7.1), is consistent with our research (Sanecki *et al.* In

Review-a) indicating that snow cover in the Australian Alps falls into two of the categories described by Sturm *et al.* (1995). Snow cover at sites with transient snow cover and variable temperatures is classed as ephemeral, while snow characteristics at sites with persistent snow and stable temperatures most closely conform to the maritime snow cover class. The detectability of *A. swainsonii* and *R. fuscipes* is greater in areas with ephemeral snow.

7.5.1 Implications for management

As global temperatures increase in future years, the extent and duration of snow cover in the Australian Alps is forecast to decline (Whetton *et al.* 1996; Whetton 1998), resulting in increasing areas either completely free of snow throughout winter or subject to ephemeral snow cover conditions. Based on our findings, *A. swainsonii* and *R. fuscipes* are likely to benefit from this change at the possible expense of other species, such as the mountain pygmy-possum, *Burramys parvus* (Broome 2001), that are thought to be dependent on more stable thermal conditions under continuous snow cover. Another negatively affected species may be *M. fuscus* which is the preferred winter food of the introduced red fox *Vulpes vulpes* and gains protection from continuous and deep snow (Green 2002).

In light of the fact that the integrity of the subnivean space is more important than thermal stability for the overwinter survival of small mammals, the potentially detrimental effects of snow compression on subnivean thermal regimes (Schmid 1971; Keddy *et al.* 1979) may not be as significant as previously thought, particularly for species such as *R. fuscipes* and *A. swainsonii*, and particularly in areas with maritime or ephemeral snow. However, changes to thermal environments may have secondary implications for small mammals. For example, lower temperatures under compacted snow have the potential to affect plant growth which in turn has implications for the development of the subnivean space (Pickering & Hill 2003).

7.6 Conclusions

Interpretations of the nival population dynamics of small mammals in Australia have been based on research in boreal regions where winter temperatures are more extreme and thermal conditions in autumn and spring are critical to animal survival (Halfpenny & Ozanne 1989). In the Australian Alps, winter-active small mammals are associated with thermally unstable ephemeral snow conditions. Under these conditions, pre-nival and post-nival thermal regimes (which can last all winter in areas of ephemeral snow cover) may not be as stressful for small mammals as has been previously assumed.

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8 HOME RANGE AND ACTIVITY OF THE BUSH-RAT, *RATTUS FUSCIPES* AND DUSKY ANTECHINUS, *ANTECHINUS SWAINSONII* BENEATH THE SNOW

Submitted to *Wildlife Research*

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8.1 Abstract

Radio telemetry was used to investigate changes in home range sizes and activity patterns of *Rattus fuscipes* and *Antechinus swainsonii* in a subalpine heathland at Perisher Creek, in the Snowy Mountains, south-eastern New South Wales, in response to the accumulation of snow during the winter.

We estimated home range area for each animal during the autumn and winter using two methods, minimum convex polygon and 95% and 50% utilisation contours using the kernel method. With both methods, the home ranges of *R. fuscipes* and *A. swainsonii* were significantly smaller ($P < 0.001$) during the winter when compared to autumn home range size. Both species were restricted to areas of dense wet heath close to the main drainage line.

Rattus fuscipes showed signs of social interaction during both seasons in contrast to *A. swainsonii*, which appeared to remain solitary. In winter, *R. fuscipes* nested communally at a single location, while during autumn it appeared to use a number of nest sites.

There was no significant change in daily activity patterns between autumn and winter in either species. *R. fuscipes* remained primarily nocturnal during both pre-nival and nival periods while *A. swainsonii* continued to be active throughout the diel cycle, although there was a slight shift in its peak activity time.

Keywords: Radio tracking, subnivean space, communal nesting, winter diet, Australian Alps.

8.2 Introduction

Although it is widely acknowledged that snow is an important ecological factor for organisms that live in nival areas (Formozov 1946; Pruitt 1960; Halfpenny & Ozanne 1989; Green & Osborne 1994), there is a paucity of research on the effect of natural snow on the ecology of small mammals in the subnivean space. One aspect that has received relatively little attention, particularly in Australia, is the effect of snow cover on the home range and activity patterns of small mammals.

Home range was originally defined as 'the area traversed by the individual in its normal activities of food gathering, mating and caring for young' (Burt 1943). The home ranges of small mammals have been studied extensively in Australia and elsewhere, for example, Banks *et al.* (1975); Wolton (1985); Bubela *et al.* (1991) and Morzillo *et al.* (2003).

Radio tracking of individual animals is currently the method of choice for collecting data about animal locations and movements (Wilson *et al.* 1996). This is because trapping techniques are unlikely to provide a reliable estimate of home range area due to the disruption of normal behaviour following repeated trapping (Banks *et al.* 1975; Lance & Watson 1980; Bubela *et al.* 1991). The most widely used method for estimating home range area from radio tracking location data is the minimum convex polygon (MCP) (Mohr 1947). In addition, a range of parametric (Jennrich & Turner 1969) and nonparametric methods (Dixon & Chapman 1980) has been developed, including kernel methods (Worton 1989). All of the currently available estimators of home range area have some limitations (Wolton 1985). Despite this, home range estimation can provide useful information about behaviour and habitat utilisation patterns of individual animals and about interactions among conspecifics that is not revealed by other techniques (White & Garrott 1990).

In Australia, three species of small mammal are active in the subnivean space of mainland mountains during winter: the dusky antechinus *Antechinus swainsonii*, a dasyurid marsupial, and two murid rodents, the bush-rat *Rattus fuscipes* and the broad-toothed rat *Mastacomys fuscus* (Green & Osborne 1994). Radio tracking of *A. swainsonii* (Green 1988) and *M. fuscus* (Bubela *et al.* 1991) has been

undertaken, but home range estimates are available only for *M. fuscus* and only during the non-nival period (Bubela *et al.* 1991).

Rattus fuscipes is predominantly nocturnal in non-nival areas and during the non-nival period in the Snowy Mountains, but tends towards more diurnal activity during winter (Carron 1985). The situation with *A. swainsonii* is less clear, with Green and Osborne (1994) contending that the species is largely crepuscular or nocturnal during the non-nival periods but becomes more active during the day in winter. Conversely, Carron (1985) and Green and Crowley (1989) suggest that it is active throughout the diel cycle regardless of season.

In a landscape-scale study of small mammal distribution in relation to variations in snow cover conditions, it was observed that once snow cover was established, small mammals were virtually excluded from habitats without shrub layers that permit the development and maintenance of a sufficiently large subnivean space (Sanecki *et al.* In Review-b). These findings suggest that the subnivean space may not be as extensive as previously thought by Green and Osborne (1994). If this is the case, then we would expect that the home ranges of small mammals would contract during the nival period. In this context, the objective of this study was to investigate how snow cover affects the home range areas and activity patterns of *R. fuscipes* and *A. swainsonii*.

8.3 Materials and methods

8.3.1 Study area

The study area was located along Perisher Creek, 2.5 km north of Perisher Valley (36°24'S, 148°26'E.) in Kosciuszko National Park within the Snowy Mountains. The study site was located at an elevation of 1650 m.

In January and February 2003, the Snowy Mountains experienced a major bushfire that burned 69% of the area above 1500 m (Green & Sanecki In Review). The study area is a remnant patch of subalpine vegetation that was not burnt, approximately 400 m by 150 m in size, and consists of a mosaic of vegetation communities typically found at this elevation (Sanecki *et al.* In Review-b). Wet heath occurs along the creek and in other poorly drained locations, interspersed with areas of dry heath and tussock grassland where soils

are better drained. Seral woodland, dry heath and tussock grassland occupy the adjacent slopes.

8.3.2 Field methods

Four trapping lines were established running parallel to the creek, each with either 18 or 20 trap points. Two lines were located on each side of the creek. Trap lines were used in preference to a uniformly spaced grid because these allowed traps to be placed in optimal locations for capture, increasing trapping success (Read *et al.* 1988). This was particularly important as trapping success is greatly reduced once snow cover is established (Carron 1985; Sanecki 1999). Trapping points were marked with 1.8 m long numbered timber stakes. A 55 litre plastic garbage bin was attached to each timber stake to permit trapping beneath the snow during winter (Carron 1985; Mansergh 1985; Green 1988; Sanecki 1999). Each bin had a hole cut at ground level to permit access to the traps by small mammals, and positioned so that the base opening would provide the best access to the subnivean space once snow cover was established.

Small mammals were trapped using Type A Elliot traps (Upwey, Vic), baited with a mixture of peanut butter, honey and oats. A handful of Dacron® wadding was added to each trap which was then placed in a plastic bag to provide additional insulation and protection from water. Traps were placed in the bins during both pre-nival and nival trapping periods. Traps were set for three nights and checked twice daily prior to winter and three times daily during the winter. Individual *R. fuscipes* were marked with numbered ear tags, while *A. swainsonii* were marked by clipping toenails.

8.3.3 Radio tracking

For the purpose of this study, we defined two distinct periods during which tracking was undertaken. The pre-nival period was prior to the first winter snowfall, while the nival period commenced once a continuous snow cover was established across the study site. We refer to these periods as autumn and winter respectively from here on.

Preliminary small mammal surveys were conducted during November 2002, February 2003 and April 2003 to monitor population numbers and identify the most suitable animals to be fitted with radio collars.

Small mammals were trapped for radio tracking in autumn immediately following the April 2003 survey. At this time, small mammals have completed breeding and juvenile dispersal has taken place (Carron 1985).

Eleven adult animals (Table 8.1) were fitted with radio transmitters (Titley Electronics Ltd, Ballina, NSW). Radio collars were fitted around the neck, and each animal was then briefly held in an observation cage before release to ensure that the collars were not causing discomfort and also were unlikely to be slipped off. Tracking commenced after all animals were collared and released, and all traps were removed from the trapping grid so that animal movements were not biased by their presence.

Location fixes were obtained over a seven day period, after which tracking was no longer considered useful, due to the rate of radio collar failure. Fixes were recorded at hourly intervals spread evenly over the diel cycle. Only those individuals for which a minimum of 40 fixes was recorded were included in subsequent analyses (Table 8.1). Intervals of one hour are thought to be sufficient to ensure independence of successive fixes (Swihart & Slade 1985). Location fixes were determined by triangulation from telemetry points using a Telonics TR-4 tracking receiver and a collapsible 3-element yagi antenna (Sirtrack Ltd, NZ). Telemetry points were established adjacent to the trapping grid to minimise interference with the animals, and were selected to provide the best geometry for each pair of location fixes. For each fix, a compass bearing was taken from one of the telemetry points, followed immediately by another taken from a point that was as close as possible to a 90° angle from the first bearing.

At the end of the seven day period, animals were recaptured and remaining radio collars were removed. Only two collars were retrieved from *A. swainsonii* of which one was still functioning. Two had been shed by animals and were unable to be retrieved and one animal was not recaptured. None of the collars attached to *R. fuscipes* were functioning: one had been shed and all others were found to have been gnawed so that either the aerial had been removed or the transmitter housing had been damaged. In several cases, all electronics had been removed so that all that remained on the animal was the nylon collar and a small part of the resin transmitter housing.

Table 8.1 Numbers of radio-collared *Rattus fuscipes* and *Antechinus swainsonii* for which a minimum of 40 location fixes were obtained. Numbers in brackets indicate the number of animals with failed or slipped collars.

Species	Autumn		Winter	
	Male	Female	Male	Female
<i>R. fuscipes</i>	2	3 (1)	3	1
<i>A. swainsonii</i>	2 (1)	1 (1)	1	3

Winter radio tracking did not commence until the second week in September when there was a continuous snow cover 50-100 cm deep at the study site. Prior to this, snow cover at the site was patchy. Small mammals were trapped as described above and radio collars (Sirtrack Ltd, NZ) were attached to eight animals (Table 8.1). Despite gnawing damage on collars fitted to *R. fuscipes*, six of the eight collars were still functioning when retrieved. Animal location fixes were obtained as described above over a 5 day period. The only difference was that fixes were not only taken from telemetry points but, because the snow was capable of supporting a person on skis, fixes were also taken from trap point marker stakes.

8.3.4 Data analysis

The trapping points and radio telemetry points were surveyed using a Nikon™ D50 Total Station (a combination theodolite and laser distance survey station). These data were mapped and location fixes for each animal were plotted using AutoCAD® 2002 (Autodesk Inc.). The base map and location maps for each animal were then transferred to ArcView™ 3.2 (ESRI). Home range analysis was performed using the Animal Movement extension to ArcView™ (Hooge & Eichenlaub 1997).

Home ranges were calculated using the minimum convex polygon (MCP) method (Mohr 1947) and the kernel method (Worton 1989). For the kernel method, we calculated the area contained within the 95% and 50% utilisation contours (UC). Home range areas were log transformed to satisfy assumptions of normality and homogeneity of variances and analysed using analysis of variance (ANOVA). Home range overlap was assessed visually.

Small mammal activity was determined from radio telemetry and follows Bubela *et al.* (1991) who considered that an animal was active if it had moved more than 10 m between hourly fixes and its transmitter signal was fluctuating. Animals were considered to be inactive when the signal was steady. The percentages of observations representing active animals were plotted by hour and observations were divided into daytime (0600-1700h) and night-time (1800-0500h) based on the times of sunrise (autumn 0613, winter 0603) and sunset (autumn 1734, winter 1740) during which radio tracking was undertaken. We compared activity patterns between seasons and time of day using ANOVA.

8.4 Results

Due to small sample sizes, it was not possible to compare home ranges of different sexes for each season. Therefore, we pooled autumn and winter data. No significant differences were found in home ranges or activity patterns between males and females of either species. Subsequent analyses were performed on pooled male and female data for each species.

8.4.1 Home Ranges

Home range estimates for individual animals are presented in Table 8.2. Home ranges were significantly smaller ($P < 0.001$) in winter than autumn for both species (Table 8.3 and Figures 8.1, 8.2 and 8.3). Except for the 95% UC, there was no significant difference in home range area between the two species in either season. With 95% UC, the winter home range for *R. fuscipes* was significantly larger ($P < 0.01$) than for *A. swainsonii* (Figure 8.1). Winter home range areas for both species were less variable than autumn home ranges.

Home ranges based on kernel 95% UC were larger than those based on MCP (Table 8.2). This was more marked in winter when 95% UC estimates were more than double MCP estimates for two of the four *A. swainsonii* and all *R. fuscipes*.

Table 8.2 Home range area estimates (m²) for individual *Antechinus swainsonii* and *Rattus fuscipes* in autumn and winter 2003, based on kernel 95% and 50% utilisation contours (UC) and minimum convex polygon (MCP).

Season	Species	Sex	Number of Fixes	95% UC	50% UC	MCP
Autumn	<i>A. swainsonii</i>	F	40	14967.5	2526.7	8208.1
		M	48	9205.6	866.6	5901.2
		M	44	12490.7	1601.9	8523.8
	<i>R. fuscipes</i>	F	41	9294.8	1511.1	7394.1
		F	40	12124.7	3350.8	7382.4
		F	44	9697.9	1265.5	6506.8
		M	46	16513.1	1504.5	10825.5
M	43	13771.6	2275.3	8446.2		
Winter	<i>A. swainsonii</i>	F	40	2293.9	425.7	1970.0
		F	40	2951.1	691.9	1216.7
		F	41	3814.3	858.5	1820.9
	M	42	2578.3	357.7	2454.0	
	<i>R. fuscipes</i>	F	40	6515.9	723.5	3069.3
		M	41	4559.4	665.6	2109.9
		M	40	6309.0	782.5	2896.9
M		40	7069.0	803.7	3004.8	

Table 8.3 Results of ANOVAs for autumn and winter home range areas of *R. fuscipes* and *A. swainsonii* based on kernel 95% and 50% utilisation curves (UC) and minimum convex polygon (MCP).

	95% UC		50% UC		MCP	
	F	P	F	p	F	p
Season	86.09	<0.001	25.24	<0.001	123.18	<0.001
Species	10.73	<0.01	1.69	N.S.	4.7	N.S.
Season x Species	10.66	<0.01	0.07	N.S.	2.38	N.S.

Since it is likely there were uncollared conspecifics in the same area, conclusions about home range overlap must be viewed conservatively. The home ranges of *R. fuscipes* in winter showed a greater level of overlap than in autumn, with all four individuals restricted in winter to a narrow strip of dense wet heath along the creek line. Autumn home ranges did not overlap to the same extent with animals moving over larger areas. However, there were several foci of activity for all animals in dense wet heath near the creek.

In winter, *R. fuscipes* appeared to nest communally with all animals spending daytime periods of minimal activity within 10-20 m of a small patch of boulders. The possibility of communal nesting also was supported by the fact that recovered radio collars were found to have been gnawed by conspecifics. Considerable interaction among individuals also appeared to occur during autumn as evidenced by damage to radio collars, but periods of inactivity were not restricted to one location. Rather, each animal appeared to use a number of nest sites within its home range. However, the extent of the home range overlap meant it was possible that communal nesting was occurring and on several occasions collared females were located in close proximity to each other.

There appeared to be less home range overlap among *A. swainsonii* than *R. fuscipes* in both seasons, especially in autumn when one *A. swainsonii* home range did not overlap at all with the home range of a conspecific. Home ranges of *A. swainsonii* did not show the same level of overlap as those of *R. fuscipes* during winter, however, their home ranges were again mainly associated with vegetation along the creek line. Periods of inactivity were not as obviously associated with specific locations during either season and the absence of gnawing damage to radio collars suggests that individuals spent little if any time in close proximity to conspecifics.

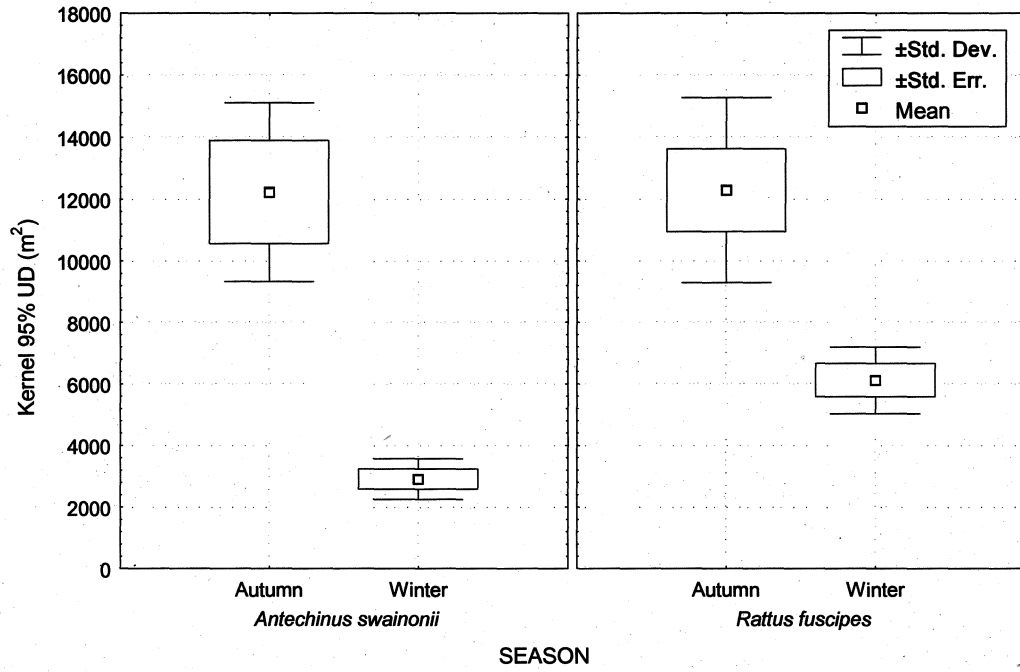


Figure 8.1 Autumn and winter home range of *Antechinus swainsonii* and *Rattus fuscipes*, kernel 95% utilisation contour.

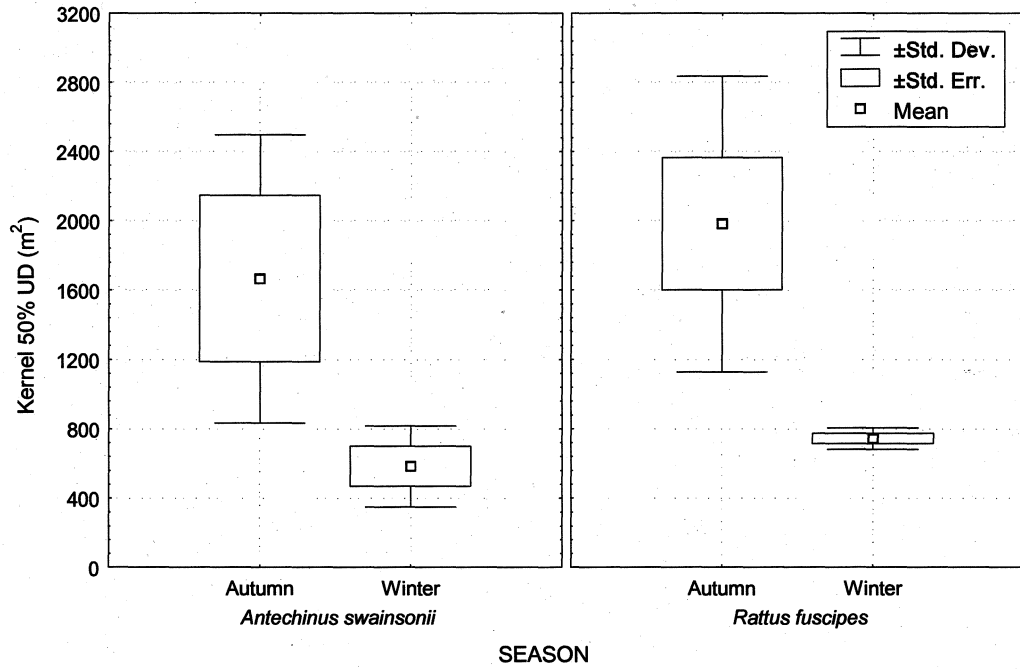


Figure 8.2 Autumn and winter home range of *Antechinus swainsonii* and *Rattus fuscipes*, kernel 50% utilisation contour.

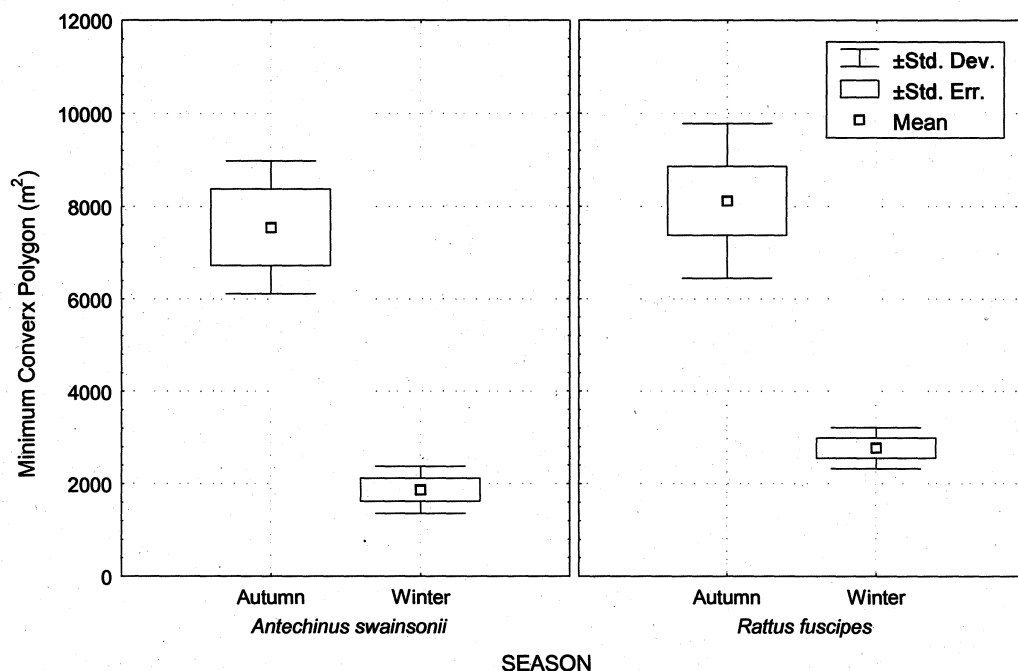


Figure 8.3 Autumn and winter home range of *Antechinus swainsonii* and *Rattus fuscipes*, minimum convex polygon.

8.4.2 Activity Patterns

Activity patterns for both *A. swainsonii* and *R. fuscipes* are shown in Figure 8.4. *Rattus fuscipes* was significantly more active ($P < 0.001$) during the night than the day in both seasons (Table 8.4). In contrast, *A. swainsonii* did not display significantly greater activity levels between day and night, although there was an interaction ($P < 0.01$) between activity pattern and season (Table 8.4). In autumn, the peak activity of *A. swainsonii* was before and just after dusk, while in winter, animals were most active in the early morning (Figure 8.4).

Table 8.4 Results of ANOVAs for the autumn and winter activity patterns of *A. swainsonii* and *R. fuscipes*.

	<i>A. swainsonii</i>		<i>R. fuscipes</i>	
	F	P	F	P
Season	0.1	N.S.	0.05	N.S.
Time of Day	0.06	N.S.	62.65	<0.001
Season x Time of Day	9.24	<0.01	2.22	N.S.

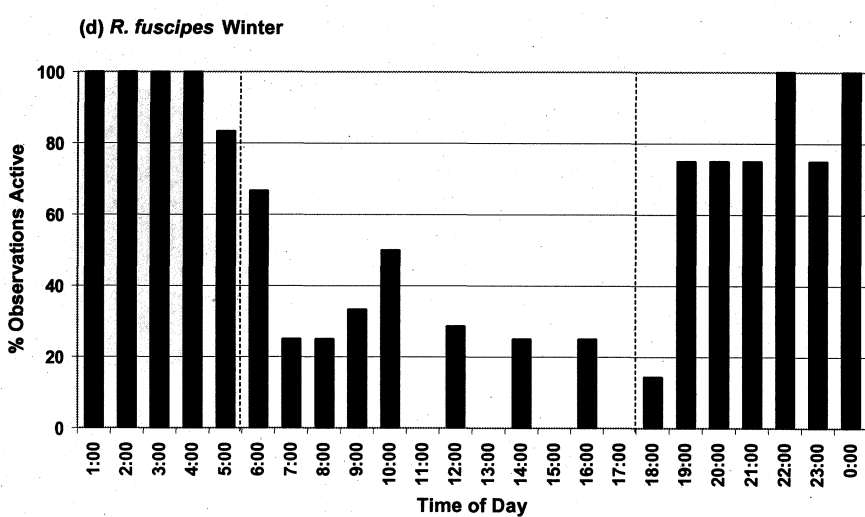
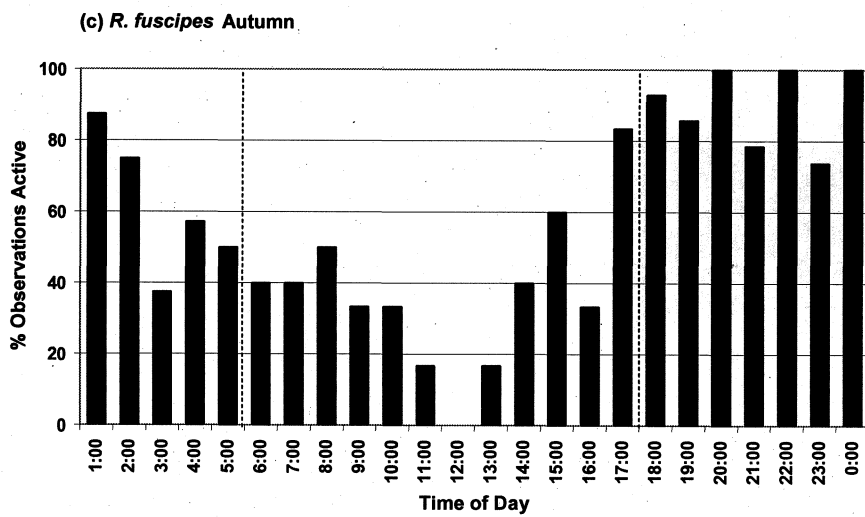
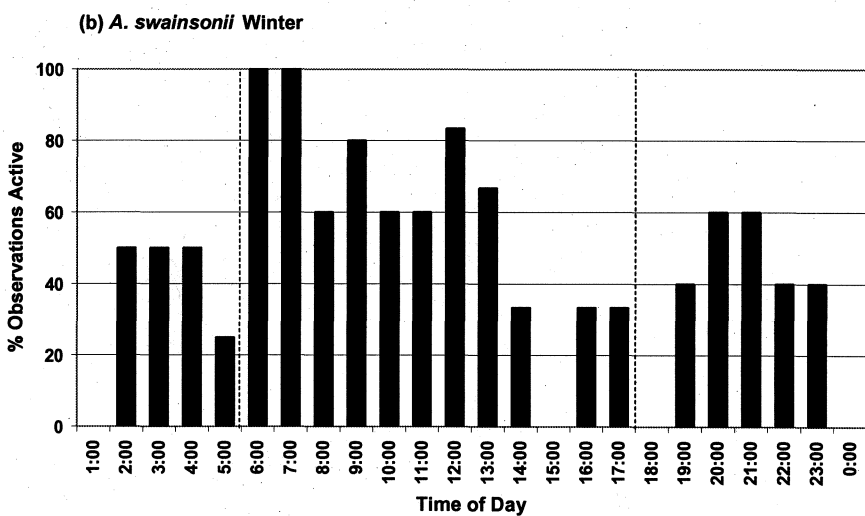
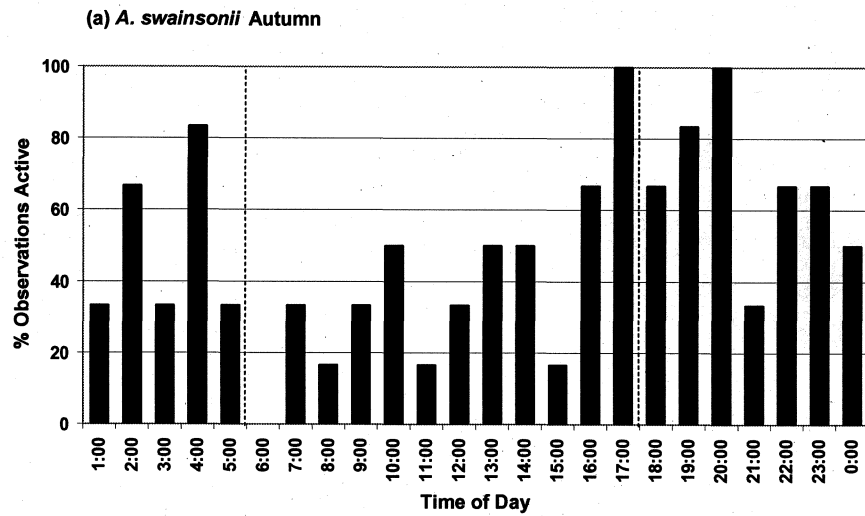


Figure 8.4 Activity patterns for *A. swainsonii* and *R. fuscipes* during autumn and winter. Dotted vertical lines indicate the boundary between night and daytime observations. Proportion of location fixes between day and night were 53% and 47% respectively.

8.5 Discussion

8.5.1 Home range

Small mammals in nival environments depend on the development of a subnivean space between the ground surface and the overlying snowpack to enable access to resources necessary for survival (Formozov 1946; Pruitt 1984; Green & Osborne 1994). The climatic conditions in the Snowy Mountains are such that a thermal gradient through the snow, sufficient to facilitate the development of the subnivean space as a result of depth hoar formation, does not occur (Ruddell 1998; Sanecki *et al.* In Review-a). The formation of the subnivean space, and hence small mammal activity, depends on the occurrence of structures of sufficient physical strength to support the weight of the overlying snow cover, such as dense shrubs, boulders and/or other micro-topographic features (Green & Osborne 1994; Sanecki *et al.* In Review-b). In the Snowy Mountains, small mammals are all but undetectable in nival habitats where such structures are absent (Sanecki *et al.* In Review-b).

In this study, the home ranges of *A. swainsonii* and *R. fuscipes* were significantly smaller in winter than in autumn. These findings support our contention that the relatively dense snow cover of the Snowy Mountains does not permit the widespread development of the subnivean space. Rather its development, and thus the amount of winter habitat available to small mammals, is dependent on the presence of suitable habitat structure (Sanecki *et al.* In Review-b). In our study area, habitat used by both species during the nival period comprised wet heath where the shrubs were dense enough to enable subnivean space formation. The creek line also was used, where the combination of flowing water and high micro-topography facilitated the development of the subnivean space (Sanecki *et al.* In Review-b). This is in contrast to the non-nival period when, although still heavily utilising structurally complex habitats, small mammals were also able to exploit habitats that would not be available to them during the winter (Sanecki *et al.* In Review-b).

Changes in home range size and movement between seasons have been reported for both *A. swainsonii* and *R. fuscipes* in nival areas (Carron 1985) and for *R. fuscipes* in non-nival areas (Woodside 1983). In general, however, the greatest

reduction occurs between breeding (spring/summer) and non-breeding (autumn/winter) seasons (Woodside 1983; Carron 1985). Our radio tracking surveys occurred within the non-breeding period and thus should not have been affected by breeding or dispersal activities. In the Snowy Mountains, Carron (1985) reported reduced winter movement in *A. swainsonii* but not in *R. fuscipes*, based on average adjusted distances moved (AADM) derived from trapping grid data. In this study, *A. swainsonii* and *R. fuscipes* winter home ranges were similar in size. Only for the 95% UC was the home range of *R. fuscipes* larger than *A. swainsonii*, but it is possible that this may be an artefact of the small sample size and/or the limitations of the kernel home range estimation method (Worton 1989).

The significant reduction in home range size has implications for the overwinter survival of these species in nival areas. At 1650 m (the elevation at which this study was undertaken) vegetation and microtopography are key factors in the development of the subnivean space. As such, its development is more extensive than that occurring at higher elevations where small mammals are all but limited to boulderfields and areas of high microtopographic relief (Sanecki *et al.* In Review-b).

Antechinus swainsonii is insectivorous (Wakefield & Warneke 1967; Dickman *et al.* 1983; Green 1989) and a reduction of foraging capacity during winter could jeopardise its ability to find sufficient food for survival, since insectivores tend to have higher metabolic rates than omnivores (Aitchison 1987). This species appears to compensate for the reduced home range size in winter by increasing activity (Sanecki *et al.* In Review-c). Food availability also may not be limiting since, at a study site of similar elevation, Green (1989) reported that the numbers of invertebrates detected in pitfall traps reached a peak in September and included a substantial proportion of the preferred dietary items of *A. swainsonii* (Araneae, Coleoptera and Hemiptera).

Diet switching has been reported in the omnivorous *R. fuscipes* (Watts 1977; Carron *et al.* 1990). When snow is absent, the diet of *R. fuscipes* largely comprises mycorrhizal fungi and insects, while during winter their diet includes a greater proportion of plant material, in particular monocotyledons (Carron *et al.* 1990). Reduced consumption of insects during winter also may reduce potential

competition with the insectivorous *A. swainsonii*. The different activity patterns of these two species may further reduce competition with *A. swainsonii* (see below).

The minimum amount of habitat required by either species of small mammal to successfully overwinter is not known. We speculate, however, that as home range decreases, diet switching enables *R. fuscipes* to survive without needing to forage as widely for resources, but rather to adopt an energetically more conservative strategy similar to the sympatric *Mastacomys fuscus*. The latter species, an almost obligate herbivore, displays very little winter activity, relying almost exclusively on monocotyledons in the vicinity of its winter nest site (Carron *et al.* 1990; Bubela *et al.* 1991). This interpretation is supported by the observation that *R. fuscipes* is less active during winter compared to autumn (Sanecki *et al.* In Review-c).

Communal nesting is believed to enhance overwinter survival by imparting energy conservation benefits in cold climates (Madison 1984; Happold 1989), and has been found to occur with *M. fuscus* during winter (Bubela & Happold 1993). Our findings confirm the observations of (Green 1988) that *A. swainsonii* is solitary and does not nest communally; its diet of invertebrates must provide sufficient energy for thermoregulation in all seasons, although Green (1988) suggests that basking may occur during winter. *Rattus fuscipes* displays considerable social interaction in non-nival areas (Woodside 1983) but whereas Woodside (1983) contends that adult females maintain discrete and non-overlapping home ranges, we found that adult females during autumn showed considerable home range overlap. On a number of occasions during autumn collared females were located within a few metres of each other. Based on the destruction of radio collars during autumn, it is also clear that there is considerable social contact with conspecifics.

Due to the small number of females tracked during winter, we are unable to draw conclusions about possible gender differences in spatial organisation. All four of the animals tracked during winter nested in proximity to each other, and again damage to radio collars indicated close social contact with conspecifics. It is possible that this contact was with uncollared individuals, but the proximity of

nesting during the daytime and synchrony of activity patterns of the collared animals suggests that there was contact between these individuals.

8.5.2 Activity patterns

Increased diurnal activity during winter has been reported among rodents and other small mammals in nival areas around the world (Kucera & Fuller 1978; Stebbins 1984). In this study, *R. fuscipes* remained primarily nocturnal during autumn and winter. *Rattus fuscipes* is mainly nocturnal in other areas (Hall 1980; Woodside 1983), and it would appear that despite snow cover, this pattern is maintained during the winter, at least in areas with ephemeral snow cover (Sanecki *et al.* In Review-a; Sanecki *et al.* In Review-b).

Our observations contrast with the findings of (Carron 1985) who noted an increase in diurnal activity of *R. fuscipes* during winter. Before the winter tracking period in 2003, snow cover was patchy, and animals were exposed to non-nival or supranivean photoperiods. Continuous snow cover of sufficient depth to eliminate a diurnal light cycle from the subnivean space was established at the study site for no more than two weeks before tracking commenced. It is possible that *R. fuscipes* may not have had sufficient time to alter its activity pattern before winter radio tracking commenced. However, as substantial areas of the Snowy Mountains experience patchy snow cover of short duration (Osborne *et al.* 1998; Sanecki *et al.* In Review-a), it is likely that the maintenance of a nocturnal activity pattern by *R. fuscipes* during winter is common.

It also has been suggested that increased diurnal activity of small mammals in winter may be encouraged by daytime temperatures that are higher than at nighttime (Carron 1985). This seems unlikely under continuous snow cover as subnivean space temperatures are stable, remaining between 0°C and 1°C regardless of air temperature (Dimpel & Calaby 1972; Sanecki *et al.* In Review-a). If increased day temperatures are beneficial for small mammals in winter, this benefit is only realised when snow cover is patchy and the subnivean space is more thermally coupled to the supranivean environment, or when animals could find snow-free habitat patches in which to forage or bask during the day (Sanecki *et al.* In Review-c). This would have occurred earlier in the winter

when snow cover was not completely established. However, there is an increased risk of predation at this time, with small mammals becoming a more important component of the diet of foxes during winter (Green & Osborne 1981). As such, more diurnal activity might increase predation risk early in the winter.

The non-nival activity pattern of *A. swainsonii* has been variously described as largely crepuscular or nocturnal (Carron 1985; Green & Osborne 1994), diurnal (Green & Crowley 1989) or throughout the diel cycle (Hall 1980). Carron (1985) and Green & Osborne (1994) noted that during winter *A. swainsonii* is active throughout the day. The results of this study also showed no significant difference in activity levels between night and day.

Based on our findings there was no apparent change in activity patterns for either *A. swainsonii* and *R. fuscipes* as a result of short exposure to complete snow cover. This suggests that in nival areas under short-term or ephemeral snow, both species maintained activity patterns observed among conspecifics in non-nival areas (Warden & Wallis 1979; Hall 1980). Therefore, snow *per se* did not influence temporal activity immediately and it may require longer exposure times to an environment lacking diurnal light cycles to force changes to activity patterns. To determine whether this pattern is maintained throughout the winter, further investigations are required comparing activity patterns at sites with deep and persistent snow (for example, boulderfields, (Sanecki *et al.* In Review-b) and sites where snow is shallow enough to allow light to penetrate to the subnivean space.

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9 THE IMPLICATIONS OF SNOW-BASED RECREATION FOR SMALL MAMMALS IN THE SUBNIVEAN SPACE IN SOUTH-EAST AUSTRALIA

Submitted to *Biological Conservation*

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9.1 Abstract

The increasing popularity of winter recreation activities and the development of ski resorts and associated infrastructure have the potential to affect adversely small mammal fauna that over-winter in the subnivean space in many parts of the world that experience snow conditions. We investigated the effects of human activities on the maintenance of the subnivean space, which is critical to the over-winter survival of small mammals in Kosciuszko National Park, south-eastern Australia.

Human activities associated with snow-based recreation, such as the creation of ski pistes, surface ski lifts and over-snow routes, involve compression of the snowpack and resulted in small or absent subnivean spaces (average 1.2 cm) and high snow cover densities (generally over 0.5 g cm^{-3}). By contrast, the subnivean spaces associated with unmodified snow cover averaged 8 – 20 cm depending on vegetation type. The density of unmodified snowpack was less than 0.35 g cm^{-3} in June but increased throughout the season to levels comparable to those of compressed snow.

When the snowpack was experimentally compressed at 22 sites, destroying the subnivean space, detections of two small mammal species (*Rattus fuscipes* and *Antechinus swainsonii*) significantly ($p < 0.0001$) declined by 75-80%. These species remain active below the snow throughout the winter and depend on the presence of an adequate subnivean space. The removal of vegetation by fire significantly ($p < 0.0001$) reduced the size of the subnivean space regardless of habitat type. Vegetation clearing occurs as part of ground preparation prior to establishing ski runs. Supergrooming, in which surface soil is also disturbed, is likely to have similar (if not more extreme) effects.

Nival areas used for snow-based recreation should be managed to minimise negative effects on subnivean fauna, by confining developments to areas of low habitat value and maintaining natural features associated with subnivean space formation (dense shrubs, boulders and/or microtopography).

Keywords: Management, ski resorts, snow grooming, ski pistes, Australian Alps.

9.2 Introduction

Demand for snow-based recreation continues to increase globally, fuelling the development of new ski resorts and the expansion of existing resorts (Young & Boyce 1971; Tsuyuzaki 1994; Pickering & Hill 2003). In Australia, however, the limited extent of alpine and subalpine areas, comprising only 0.02% of the continental land mass (Green 1998a), means that scope for expansion of snow-based recreation is limited (NPWS 1988; Konig 1998). Most of the areas subject to the accumulation of suitable snow occur in national parks with high conservation values, placing additional constraints on development. Added to this is the prospect of global warming which may reduce the areas of snow cover in Australia (Whetton *et al.* 1996) and elsewhere (Houghton *et al.* 2001). It seems probable that these increased recreation demands will need to be met by an ever decreasing snow resource, and consequently there is an imperative to understand the potential impacts on a range of biota that may result from human activities in snow-covered environments.

For small mammals, the subnivean space between the base of the snowpack and the ground surface is essential for survival under snow (Formozov 1946; Pruitt 1984; Green & Osborne 1994; Green 1998b; Sanecki *et al.* In Review-b). In Australian snow conditions, the formation and maintenance of the subnivean space (and hence the movement of small mammals) does not occur as a result of the development of depth hoar (Sanecki *et al.* In Review-a) as it does elsewhere (Sturm *et al.* 1995). Rather, it depends almost exclusively on the presence of structures (shrubs, boulders and microtopographic features) able to support the weight of the snowpack above the ground (Sanecki *et al.* In Review-b). Human activities that affect the development and persistence of the subnivean space may have impacts upon the winter survival of small mammals (Schmid 1971; Halfpenny & Ozanne 1989; Green 1998b; Sanecki 1999), but there has been little empirical work undertaken to investigate the extent and severity of these impacts.

The compression of the snowpack associated with the movement of over-snow vehicles (Schmid 1971; Maysk 1973; Foreman *et al.* 1976; Keddy *et al.* 1979) has been of concern for some time (Young & Boyce 1971). Similar impacts would be expected as a result of snow grooming for the creation of ski pistes (downhill ski slopes and cross-country trails) and surface ski lifts (Rixen *et al.*

2003). Snow compression can cause the subnivean space to collapse, preventing movement of subnivean fauna (Schmid 1971). Supergrooming, the clearing of vegetation and levelling of the ground surface to enable skiing on shallower snow, is also likely to reduce the extent of the subnivean space by removing structures vital to its formation and maintenance (Sanecki *et al.* In Review-b).

Activities such as the grooming of ski slopes and trails and the preparation of ski lift lines are generally not undertaken by resort operators until a minimum depth of snow cover is obtained (Perisher 2000). Often, however, this depth is determined by safety considerations for the operation of machinery rather than on ecological grounds. If suitable depths of snow are achieved in one or two early season snow falls which have low initial physical strength (Seligman 1962; McKay & Gray 1981), the snowpack is easily compacted to ground level.

In this paper, we consider the potential effects of snow cover modification associated with ski resort operation in Kosciuszko National Park, south-eastern Australia. In particular we examine: 1) how snow cover is affected by recreational use and associated activities; 2) how the distribution of small mammals in the subnivean space is affected by the compression associated with these activities; and 3) how the extent of the subnivean space is modified by removal of surface vegetation by opportunistically using the landscape denuded of vegetation by a fire.

9.3 Methods

9.3.1 Study Area

The Australian Alps are located in south-eastern Australia. They comprise a disjunct series of peaks and plateaux extending for about 350 km in a generally north-easterly direction from their southern extent at about 37°S 146°E to 35°S 149°E. The Alps contain 13 ski resorts with a total downhill skiable area of 2734.5 ha and 379 km of cross country ski trails (Australian Snow Ski Resorts 2004). A number of small resorts are also located on the island of Tasmania but ski slope and trail development are not extensive there.

The study area for this investigation was located in the Snowy Mountains, (36°S, 148°E) (Figure 9.1). The Snowy Mountains contain the largest contiguous alpine and subalpine areas in Australia lying above 1500 m and subject to the

accumulation of snow cover during winter (Costin 1989). The Snowy Mountains are, for the most part, contained within the Kosciuszko National Park. Four ski resorts are located within the boundaries of the park including Australia's largest ski resort at Perisher Valley (36.42°S 148.41°E) with a downhill skiable area of 1245 ha and about 104 km of cross country ski trails. In total, the four ski resorts in the Snowy Mountains contain 1820 ha or about 67% of Australia's downhill skiable areas and 155 km (41%) of cross country ski trails.

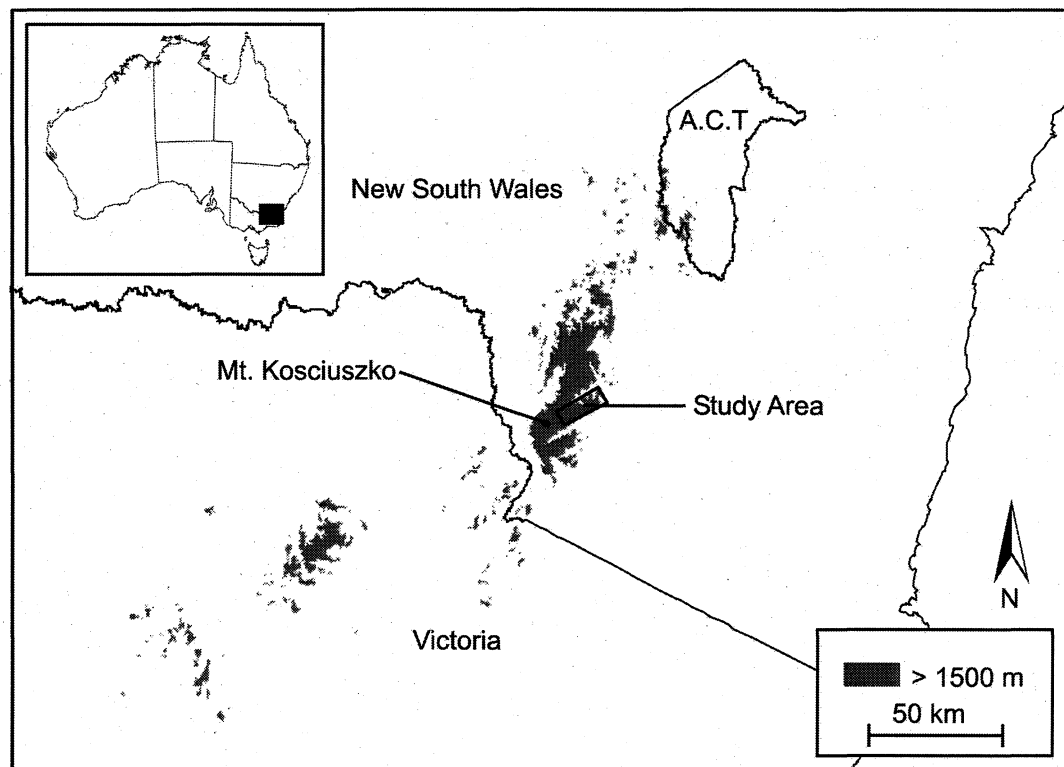


Figure 9.1 Map of the study area

9.3.2 Characteristics of modified snow

The characteristics of four types of modified snow were investigated: groomed downhill ski slopes, groomed cross-country ski trails, surface ski lift tracks and over-snow routes. Groomed downhill ski slopes and groomed cross-country ski trails may occur across a range of habitat types. Surface ski lift tracks generally require relatively smooth ground surfaces and thus are located in grasslands or where woody vegetation has been cleared. Over-snow routes which are used by snowmobiles and larger tracked vehicles usually occur on formed roads, but they also may be developed across other ground surfaces.

We measured snowpack density for 15 replicates of each of the four modified snow types at sites within and adjacent to the ski resorts at Charlotte Pass and Perisher Valley in Kosciuszko National Park. Cores were drilled using a PICO hand auger (ESRSF, University of Nebraska - Lincoln) and weighed in the field using a spring balance. Subnivean space size was measured after removal of the core, although this was not practicable in some cases due to snow depth.

Analysis of Variance was used to determine differences in snowpack density and subnivean space size between the various types of modified snow. Modified snow density was then compared to natural snow cover density throughout the winter using data obtained from Snowy Hydro Limited for the Spencers Creek snow course (36.43°S, 148.35°E, 1830 m asl).

9.3.3 Snow compression experiment

Twenty-two sites were established at locations on snow accumulating aspects between approximately 1550 m and 1700 m asl. Sites were established where there was sufficient habitat structure to permit the development of the subnivean space during the nival period (Sanecki *et al.* In Review-b), and where we detected the presence of small mammals during a hair tube survey prior to the onset of snow (see Sanecki and Green 2005 for hairtubing methods). Each site consisted of two snow-tubes (1 m long and 90 mm diameter) attached to timber stakes located approximately 5 m apart with sufficient habitat structure to permit small mammal movement between them during all seasons.

A hair tube survey was conducted once adequate snow cover was established. Snow cover was considered adequate if it was at least 50 cm deep and there was

no exposed ground and no visible connectivity between the subnivean space and the snow surface within at least a 5 m radius of each snow-tube.

After the initial survey, we randomly selected one snow-tube at each of the 22 sites and compressed a 1 m wide strip of snow in a circle around each of the selected snow-tubes. Snow was compressed by trampling (and excavation where necessary) to destroy layers in the snowpack that might prevent complete compression. The effectiveness of the compression was determined using a Federal Snow sampler (Carpenter Machine Works, Seattle) to check the size of the subnivean space. Following the methods used by (Sanecki *et al.* In Review-b) we used the sampler to drill six holes randomly into the compressed strip. The sampler was drilled until it came to rest on the ground surface, at which point the snow depth was measured. A snow core was then extracted and the difference between snow depth and the length of the core was taken to be the size of the subnivean space. Snow compression was considered complete when the subnivean space was less than 2.5 cm. Both snow-tubes at each site were then surveyed using hair tubes.

To determine whether snow compression around snow-tubes affected the likelihood of detecting small mammals, we used binomial generalised linear models with detections of small mammals as the response variables and snow condition (uncompressed, compressed) as fixed effects.

9.3.4 Fire effects on habitat structure

During January and February 2003, a wildfire burnt 69% of the area above 1500 m in the Snowy Mountains (Green & Sanecki In Review). This provided an opportunity to investigate the effect of the loss of habitat structure, as occurs on new ski slopes, on the development of the subnivean space.

We used sampling sites at elevations between 1600 m and 1800 m asl that had been established for previous studies (Sanecki *et al.* In Review-b; Sanecki *et al.* In Review-c) and randomly selected five burnt and five unburnt replicates of each of the four major habitat types present in the subalpine zone of the Snowy Mountains (wet heath, dry heath, seral woodland, grassland). At each replicate site, the size of the subnivean space was measured at three sampling plots as described above using a Federal Snow sampler.

The effects of burning and habitat type on subnivean space size were investigated using Analysis of Variance; modified snow types were included in the analyses for comparison. Data were log-transformed where necessary to satisfy assumptions of normality.

9.4 Results

9.4.1 Modified snow

Neither subnivean space size nor snow density was significantly different among all modified snow types (Table 9.1). Consequently, data for all modified snow types were combined for further analyses. In many cases, there was no measurable subnivean space under modified snow, rather the snowpack sat directly on the ground. Modified snow was significantly denser than natural snow cover at Spencers Creek during all months except October ($F_{5,122} 62.75$, $p < 0.001$) (Figure 9.2).

Table 9.1 Mean subnivean space size and snow density of modified snow types. Figures in brackets are standard deviations.

	Subnivean space (cm)	Snow density (g cm ⁻³)
Groomed downhill ski slopes	1.6 (1.4)	0.52 (0.03)
Groomed cross-country ski trails	1.1 (1.4)	0.51 (0.06)
Surface ski lift tracks	0.9 (1.5)	0.56 (0.03)
Over-snow routes	1.3 (1.5)	0.49 (0.05)

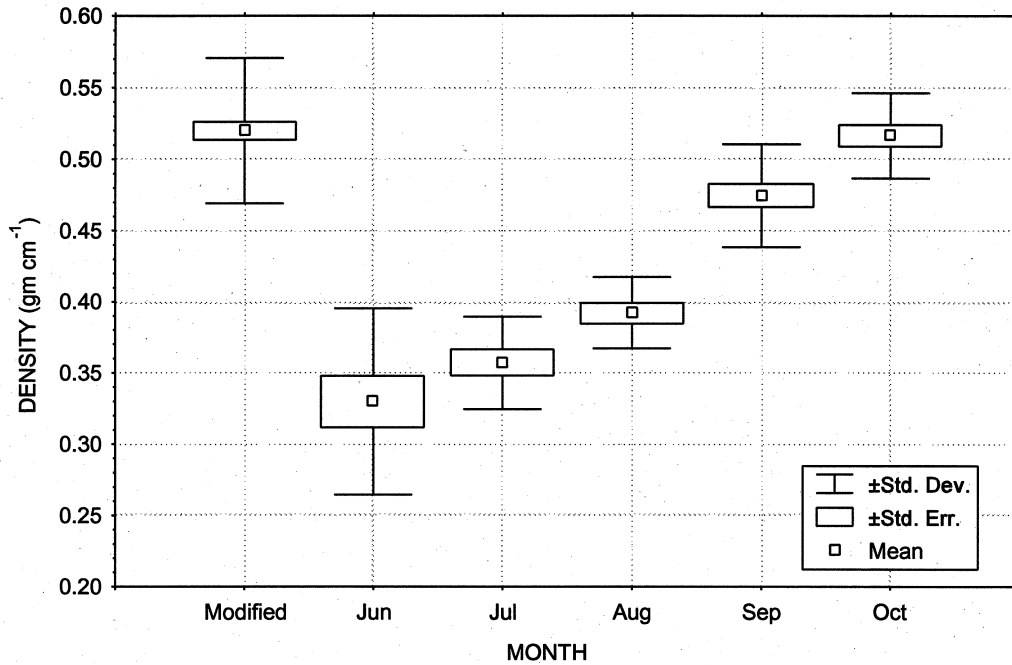


Figure 9.2 Snow density of modified snow in July, including groomed ski trails, over-snow routes, and surface lift tracks in comparison to naturally occurring snow density recorded monthly by Snowy Hydro at Spencers Creek snow course.

9.4.2 The effect of compressed snow

Table 9.2 shows the number of small mammal detections in response to the modification of snow cover. There was no significant difference in the likelihood of detection between treatment (compressed) and control (uncompressed) plots during the first survey (before snow was modified by compression). During the post-compression survey, small mammals were significantly more likely to be detected at uncompressed plots ($\chi^2 = 19.52$ $p < 0.0001$).

Table 9.2 Number of small mammal detections in response to the experimental modification of the snowpack by compression and consequent destruction of the subnivean space.

	<i>R. fuscipes</i>		<i>A. swainsonii</i>	
	Control	Compressed	Control	Compressed
Pre-Compression	3	5	16	15
Post-Compression	5	1	16	4

9.4.3 Effect of habitat structure loss

The subnivean space was significantly smaller at all of the burnt habitats in comparison to the unburnt habitats ($F_{4,238} 331.5, P < 0.0001$). The unburnt habitats showed a gradational decline in subnivean space size (Figure 9.3) with wet heath and dry heath having significantly larger subnivean spaces than other habitats (Table 9.3). Some structural components of wet heath survived burning and enabled a small subnivean space to form (Figure 9.4, Table 9.4), whereas in the other three habitats the space averaged 3.8 cm. Modified snow had significantly smaller subnivean spaces than all burnt habitats.

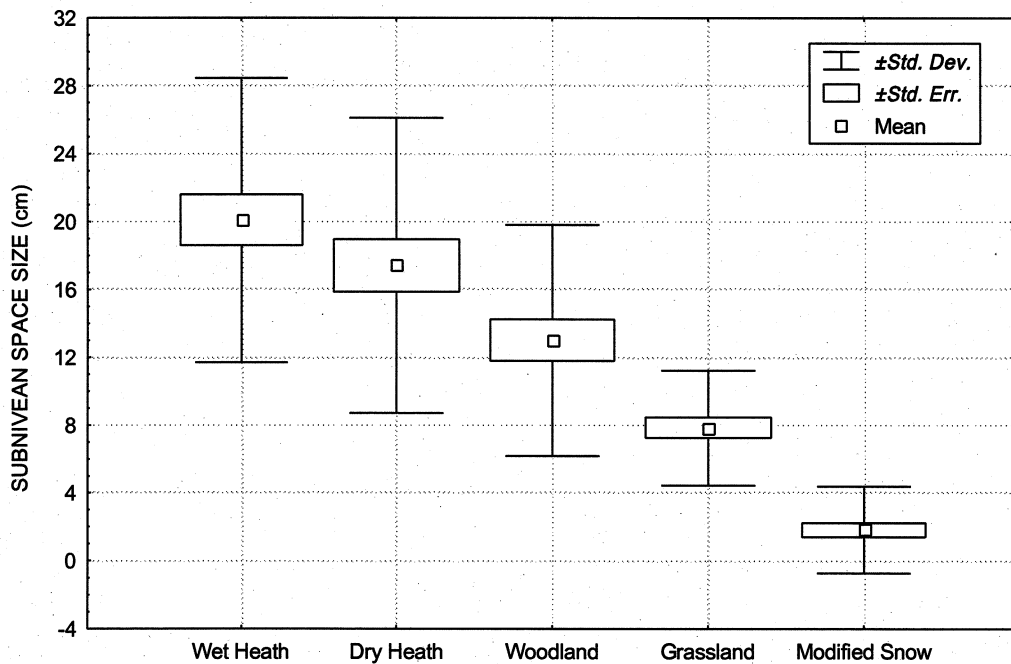


Figure 9.3 Subnivean space size at unburnt habitats.

Table 9.3 Results of pairwise comparisons of subnivean space size among unburnt habitats.

	Wet Heath	Dry Heath	Woodland	Grassland
Dry Heath	NS			
Woodland	<0.0006	<0.0246		
Grassland	<0.0001	<0.0001	<0.0177	
Modified Snow	<0.0001	<0.0001	<0.0001	<0.0001

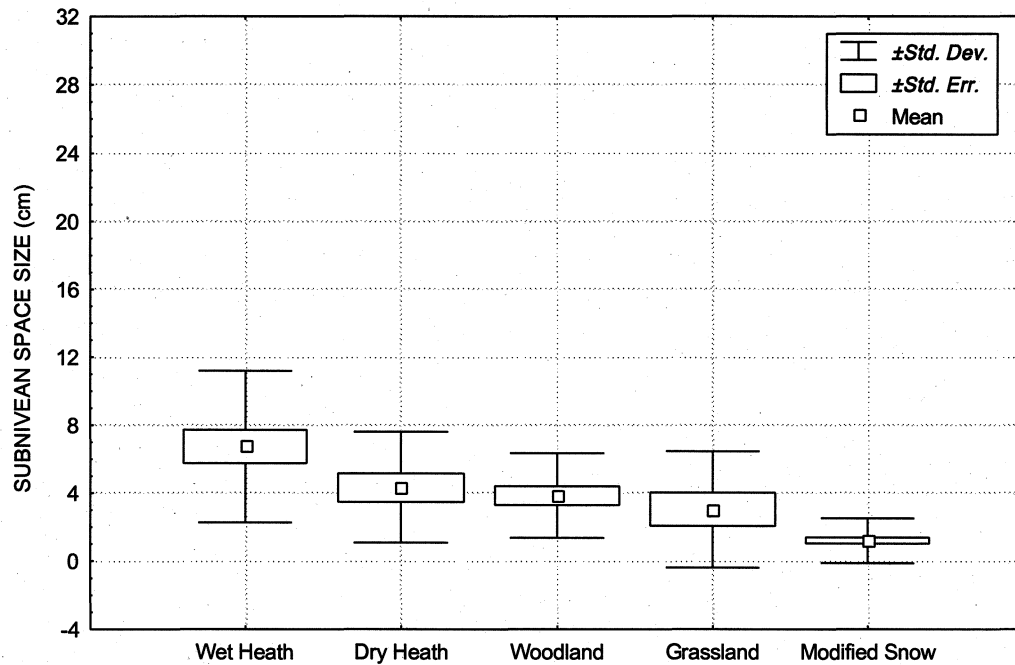


Figure 9.4 Subnivean space size at burnt habitats.

Table 9.4 Results of pairwise comparisons of subnivean space size among burnt habitats, including unburnt modified snow sites.

	Wet Heath	Dry Heath	Woodland	Grassland
Dry Heath	<0.0271			
Woodland	<0.0108	NS		
Grassland	<0.0002	NS	NS	
Modified Snow	<0.0001	<0.0001	<0.0001	<0.0139

9.5 Discussion

Winter-active small mammals are dependent on the formation of a subnivean space, which occurs under Australian snow conditions only if structural features such as vegetation, boulders and microtopography are present (Sanecki *et al.* In Review-b). Therefore, it was not surprising that the destruction of the subnivean space in otherwise suitable habitat significantly reduced the detection rate of *A. swainsonii* and *R. fuscipes* in our study area at Kosciuszko National Park. Both species actively forage in the subnivean space and experience reductions in home range size during winter (Sanecki *et al.* In Review-d). Therefore, further reductions of available habitat by snow compression could jeopardise their ability to survive over winter. Since most recreational use and over-snow activities occur at higher elevations, the impact of subnivean space loss due to compression may be even more detrimental than at lower elevations where there is more extensive subnivean space development and patchy snow permits small mammals to use both the supranivean and subnivean environments (Sanecki *et al.* In Review-b).

The maritime and ephemeral snow cover types occurring in Australia (Sanecki *et al.* In Review-a) are characterised by snow density values (and thus physical strength of snow) that are generally greater than those of alpine or taiga snow that occurs overseas (Sturm *et al.* 1995) and increase progressively following deposition (Figure 9.2) (Ruddell 1998; Sanecki *et al.* In Review-a). The ability of the snowpack to resist compressive forces is therefore lower during the early part of the winter. If early snow falls are accompanied by strong winds, snow will fill between shrubs from the ground level and thus initially inhibit the formation of the subnivean space. If this snow cover is then compacted, a high-density snow layer is formed in contact with the ground. This inhibits subsequent formation of a subnivean space. By contrast, under still conditions, snow may be more readily intercepted by vegetation enabling a subnivean space to form almost immediately; if the snow binds with the vegetation before compaction, the subnivean space may not be as readily destroyed (G. Sanecki pers. obs).

The capacity of snow modification activities to destroy the subnivean space once it is formed is affected not only by the compressive force that is applied to the

snow and the snow's ability to resist this force, but also by the strength and complexity of the underlying habitat that supports the snowpack (Sanecki et al. In Review-b). The removal of vegetation structure in the 2003 fires had a significant effect on the development of the subnivean space (Figures 9.3 and 9.4). This effect could be considered analogous to the impact caused by human activities that reduce or remove the structural elements of habitats, in particular supergrooming. Supergrooming involves the removal of all woody vegetation as well as other features such as microtopography and boulders, all of which are important structural components of small mammal habitats (Sanecki et al. In Review-b). Therefore, it is likely that supergrooming has even more extreme impacts than fire on habitat integrity during the nival period. This is suggested by the fact that wet heaths, which are often associated with higher microtopographic relief because they tend to occur in drainage lines, had significantly larger subnivean spaces than the other habitats, even after burning had removed the vegetation.

Snow modification has effects on the integrity of vegetation that may compromise its long-term ability to sustain a subnivean space. In areas of shallow snow, vegetation protruding through the snowpack may be broken by the movement of vehicles, machinery or skiers (Forbes 1992; Emers et al. 1995), while vegetation under deeper snow cover may be crushed as the snowpack above it is compacted (Mosimann 1985). Erect woody plants are the most vulnerable to damage by over-snow vehicles (Neumann & Merriam 1972; Emers et al. 1995), but other plant communities also suffer adverse effects (Greller et al. 1974; Foreman et al. 1976; Keddy et al. 1979).

The thermal conductivity of snow is directly related to its density (Halfpenny & Ozanne 1989), consequently a snowpack that has been compacted has less thermal buffering capacity than unmodified snow (Singh 1999). Under Australian snow conditions, winter-active small mammals appear to favour areas of thermal instability where winter temperatures can fall well below freezing (Sanecki et al. In Review-c). Therefore, changes in the subnivean environment during winter as a result of increased thermal conductivity of snow are likely to have little direct impact on these species. However, this may not be the case for the mountain pygmy-possum *Burramys parvus* which experiences periods of

torpor throughout the winter months; any changes to thermal regimes may be detrimental to its survival (Walter & Broome 1998). On a global basis, thermal effects of snow modification on small mammals need to be considered in the context of the ecology of each species and the prevailing climatic and snow cover conditions.

9.5.1 Management implications

The activities associated with ski resort development and snow-based recreation often represents the most intensive examples of human-induced changes to snow-covered ecosystems. Our findings suggest that there need not be a conflict between winter recreation and the over-winter survival of small mammals, provided appropriate consideration is given to ski slope development. For the most part, slopes consisting of grassland or herbfield habitats with little microtopography have limited habitat value for small mammals throughout the year (Sanecki *et al.* In Review-b), and if snow modification is focused on these slopes, the negative effects on small mammals will be minimised. In particular, supergrooming should be limited to sites of low habitat value.

Shrubby habitats on mid to upper slopes, such as dry heaths and woodlands, are not high quality nival habitats because the development of the subnivean space in these habitats is naturally limited (Sanecki *et al.* In Review-b). These suboptimal winter habitats are still utilised by small mammals during the non-nival period and are probably important in providing additional foraging areas and facilitating breeding and dispersal activities (Carron 1985). Managers should be aware that any deliberate or incidental damage to these habitats as a result of snow modification may reduce the capacity for these habitats to support small mammals during the non-nival period.

High quality nival habitats for small mammals include boulderfields, wet heaths and areas of high microtopography such as drainage lines in which small mammal activity is focused during the nival period (Sanecki *et al.* In Review-d). From a management perspective, it is these habitats that should be identified and protected, as it seems probable that these act as winter refugia and as population sources. We recommend that no snow modification be permitted in high quality small mammal habitats and where necessary fencing be used to protect them.

Grooming and movement of oversnow vehicles over important habitats should only occur once snow cover has attained sufficient strength to resist compression of the subnivean space. The connectivity of high quality habitats should also be maintained.

Subsequent to the 2003 fires, many unburnt high quality habitats now occur within, or in the vicinity of, ski resorts due to the concentration of firefighting activities on the protection of ski lodges in Kosciuszko National Park. These remnant habitats are vulnerable to disturbance due to heavy usage of snow near resorts and require active measures to ensure their protection. Their management presents particular challenges, since impacts may not only be the result of management decisions by resort operators, but also of unstructured activities (snow play) which are difficult for managers to monitor or control.

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10 CONCLUSION

10.1 Conclusion

The work undertaken for this thesis represents the first attempt anywhere in the world to describe and quantify the distribution and behaviour of winter-active small mammals in relation to snow cover and the development of the subnivean space. Although the fauna described in this thesis are unique to Australia, the findings of this study have a broader relevance to researchers working in areas around the world that are subject to the seasonal accumulation of snow cover, particularly in areas with comparable climatic conditions.

The findings of this study are also relevant to colder regions which may be subject to milder climatic conditions with continued global warming. Nival areas at higher latitudes, such as the taiga and higher alpine zones, may in time, with global warming, be subject to snow cover that is more characteristic of nival areas at lower elevations and latitudes, such as in Australia.

Australian snow cover is maritime at higher elevations (above about 1700 m asl in the Snowy Mountains) and ephemeral at lower elevations and on higher abating aspects (Chapter 4). To date, most research in subnivean ecology has emanated from boreal regions which are dominated by taiga and alpine snow classes, while maritime snow is the least extensive class and ephemeral snow by its nature occurs sporadically (Sturm *et al.* 1995). Therefore, conclusions based on research in boreal zones are unlikely to be applicable to Australian snow conditions. The role of depth hoar in the development of the subnivean space is a case in point.

Depth hoar is considered by some workers in boreal zones to be crucial in permitting small mammals to exist in the subnivean space (Pruitt 1978, 1984; Halfpenny & Ozanne 1989), although, to date, no studies have shown conclusively that this is the case. Depth hoar does not occur in the Australian Alps (Chapter 4), yet a subnivean space forms and small mammals are able to survive there because of the presence of suitable structures that support the snowpack (Chapter 6). It appears that a subnivean space can form as a result of *two quite different processes, which could be termed 'passive' and 'active'*. In the passive process, the snow density increases as a result of metamorphism (Chapter 2) until it has sufficient structural capacity to maintain a subnivean

space in conjunction with competent structures. The active process refers to small mammals having the ability to tunnel through low density snow cover such as *depth hoar and thus actively "make" their own subnivean space*. In the absence of empirical evidence regarding the role of depth hoar in subnivean ecology, the relative importance of the two processes on a global scale is unknown. In Australia, the passive process is dominant and in this study there was no evidence of the active process occurring.

Rattus fuscipes and *A. swainsonii* have wide distributions; indeed snow-free areas constitute the bulk of their geographic ranges (Chapter 3). Both species are able to tolerate thermally variable climates (Chapter 7), which is not surprising since temperature extremes are experienced in other regions where they occur. For example, annual minimum and maximum temperatures at Perisher Creek (elevation 1735 m) are -19.5°C and 30.0°C respectively, while corresponding temperatures at Tumut where both species are also common (elevation 305 m) are -7.8°C and 42.8°C. Although somewhat milder, monthly minimum temperatures at Tumut are still below 0 °C for 9 months of the year (Bureau of Meteorology).

Thermal stability and the relatively mild temperatures in the subnivean space are viewed as imparting significant benefits for small mammals (Coulianos & Johnels 1962; Happold 1998). However, the findings of this study indicate that these considerations need to be taken in an appropriate context. First, thermal stability is only useful to small mammals if a suitable subnivean space exists (Chapters 6 and 7). Second, comparisons between air temperatures and those occurring in the subnivean space are misleading, because temperatures at ground level are greatly modified by structures such as vegetation, whether or not snow is present (Geiger 1950). Third, small mammals in thermally unstable locations, where snow cover was not complete or long lived, derived considerable thermal benefit from daytime temperatures that were often considerably higher than the constant 0-1 °C experienced by animals in the subnivean space, even in mid winter (Chapter 7). Overall, however, the fact that there is no significant shift in diurnal activity patterns of either *R. fuscipes* or *A. swainsonii* during the nival period (Chapter 8) suggests that the temperatures to which they are exposed are within the tolerance limits of these species.

In the subalpine zone, the nival distributions of both *R. fuscipes* and *A. swainsonii* are related to snow type: ephemeral snow restricts winter activity to a much smaller degree than deep maritime snow, which reduces small mammal detections despite the presence of shrubs capable of supporting a subnivean space (Chapter 6). The situation is likely to be even less favourable for small mammals in the alpine zone because the predominant vegetation formations are herbfields (Chapter 3) which have a subnivean space of only 1.10 ± 0.86 cm (G Sanecki and K Green, unpublished data). Where heathland habitats occur in the alpine zone, reduced plant growth due to the short growing season is likely to result in low-growing shrubs incapable of supporting the snow cover. It seems probable that at elevations above 1800 m asl in the Snowy Mountains, the distributions of both species are confined almost exclusively to boulderfields.

The findings of this study suggest that at higher elevations, high quality habitats act as refugia from which small mammals re-radiate following the nival period into habitats that are otherwise unsuitable for overwintering due to the lack of subnivean space (Chapter 6). There was no direct evidence that small mammals perish in suboptimal nival habitats, but the absence of detections in these habitats for up to four weeks after snowmelt strongly suggests that this is the case (Chapter 6). If nival refugia act as sources for recolonisation of habitats used during the non-nival period, it is likely that both *R. fuscipes* and *A. swainsonii* experience annual genetic 'bottlenecks' whereby the gene pool shared by survivors in each refugium is different from those of surrounding populations. Thus, snow cover could prove to be the major influence on metapopulation dynamics of at least some species in alpine and subalpine areas. This might provide an interesting avenue for future research.

The main impact of human activities on winter-active small mammals arises from the compression of snow and consequent destruction of the subnivean space, and the modification and loss of habitat structure that is crucial to the development of the subnivean space (Chapter 9). As the area available for foraging decreases during winter (Chapter 6), the home ranges of both *R. fuscipes* and *A. swainsonii* contract dramatically into high quality habitats and overlap to a greater extent (Chapter 8). Although there would appear to be a certain level of resource partitioning between these species that may reduce

competition, both species are dependant on the development of the subnivean space. Beyond some threshold the reduction of the extent of the subnivean space extent would jeopardise the over winter survival of individuals or even entire populations. The situation may be somewhat different for the broad-toothed rat *Mastacomys fuscus* which is relatively inactive during winter (Bubela *et al.* 1991). While this species may not require access to extensive foraging areas, it is particularly vulnerable if destruction of the subnivean space occurs in the vicinity of its communal nest sites (Chapter 3).

The negative effects of snow compression on the insulating properties of snow are more relevant to boreal snow conditions where continuous nival temperatures are far lower than any recorded in Australia (Formozov 1946). Maritime snow is, by its nature, relatively dense (Chapter 4) and thus has a comparatively high thermal conductivity. Nevertheless, subnivean temperatures remain stable even under relatively shallow snow provided cover is continuous, and in any case there is no evidence that *R. fuscipes* and *A. swainsonii* are adversely affected by fluctuating nival temperatures (Chapter 7). This may not be the case for the mountain pygmy possum *Burramys parvus* which is dependent on the maintenance of a thermally stable hibernaculum (Walter 1996).

To ensure the continued survival of small mammals in nival areas, management practices should have, as their primary objective, the conservation of high quality habitats containing suitable structures to facilitate the formation and maintenance of the integrity of the subnivean space (Chapter 9). Achieving this objective does not necessarily mean that conflict with recreational users is inevitable, provided that the requirements of subnivean fauna are well understood and taken into account. If winter recreation is well managed and contained within limited areas then their overall impact is likely to be minimal in the Australian Alps. However, if climate change causes shrinkage of snow covered areas and there is increased competition for the diminishing resource between wildlife and recreational users, resolving conflicts will become increasingly problematic.

Average global surface temperatures have increased by $0.6 \pm 0.2^{\circ}\text{C}$ since 1900, and the current rate of warming is perhaps greater than at any time in the past 1000 years (IPCC 2001); the rate of change in global temperature since 1976 is about three times that of the past century (WMO 2004). The years 1995-2004

included the warmest 10 years on record, with 1998 the warmest year since 1861 (WMO 2004). While no consistent declines in snow cover were evident in the Snowy Mountains between 1910 and 1991 (Duus 1992), more recent analyses indicate that alpine temperatures have increased since 1962 and snow depths may have declined slightly since 1957 (Hennessy *et al.* 2003). Wide interannual variability in precipitation and subsequent snow cover, resulting from the generally low elevation of the Australian Alps interacting with very sensitive atmospheric conditions (Davis 1998), makes it difficult to discern long-term trends in past data. However, models of future snow cover conditions in Australia are unanimous in predicting a decline in the extent and duration of snow cover over the next 20-70 years (Galloway 1988; Whetton *et al.* 1996; Whetton 1998; Hennessy *et al.* 2003).

Reduction of snow cover is likely to benefit *R. fuscipes* and *A. swainsonii* by enabling the expansion of populations at higher elevations into nival habitats currently unavailable due to a lack of subnivean space. As the tree line ascends, areas currently supporting alpine vegetation will be invaded by subalpine shrubby species (Hughes 2003), potentially increasing the extent of habitats capable of supporting a subnivean space.

Mastacomys fuscus nests on the ground surface in the nival period and in underground burrows when snow is absent (Bubela *et al.* 1991; Green & Osborne 1994), which suggests that shallow and short-lived snow cover may expose the species to an increased risk of predation (Green 2002). Present distribution suggests that declining snow cover will be detrimental in the long term because, although *M. fuscus* occurs outside the major nival areas of Australia (Wallis 1992; Green & Osborne 2003), these populations are at lower densities and are not able to colonise areas with wet ground in winter because of their dependence on burrowing in the absence of snow cover under which to construct above-ground nests (K. Green unpublished data). The impact of decreasing snow cover on this species is, however, difficult to assess.

On the other hand, the prospects for *B. parvus* are bleak. This species requires boulderfields in areas with reliable snow cover (Mansergh & Broome 1994; Brereton *et al.* 1995); as the snowline moves to higher elevations and snow cover becomes more sparse, the extent of suitable habitat must decline. *Burramys*

parvus was once more widespread throughout south-eastern Australia, but since the last glacial period its distribution has contracted and it now occurs in isolated patches of habitat in alpine and subalpine areas (Mansergh & Broome 1994).

Despite the practical difficulties of working in nival environments, it is essential that research into these areas continues. The investigation of snow/fauna interactions probably represents the best opportunity for monitoring the ecological effects of global warming, because changes in the characteristics and distribution of snow are likely to be reflected rapidly in the ecology of nival areas, whereas climate change may take longer to become evident in more temperate regions.

10.2 References

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