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Adaptations of large marsupials to survival in winter snow cover: locomotion and foraging.

Running head: Adaptations of marsupials to snow

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Abstract: The small extent of seasonally snow-covered Australian mountains means that there has not been a great selective pressure on the mammalian fauna for adaptations to this environment. Only one large marsupial, the common wombat (*Vombatus ursinus* (Shaw, 1800)), is widespread above the winter snowline. In the past 20 years, with snow depth and duration declining, the swamp wallaby (*Wallabia bicolor* (Desmarest, 1804)) has become more common above the winter snowline. The red-necked wallaby (*Macropus rufogriseus* (Desmarest, 1817)) is common in alpine Tasmania where seasonal snow cover is neither as deep nor as long-lasting as on the mainland, but has only been recorded regularly above the winter snowline in the mainland Snowy Mountains since 2011. This study examines morphological

aspects of locomotion of these three herbivorous marsupials in snow. The wombat is the best adapted to snow, with quadrupedal gait and an expanded home range allowing it to locate and feed on the same plant groups as it does at lower elevation. Wallabies are poorly adapted to locomotion in snow but the browsing *W. bicolor* is able to maintain its dietary habit by feeding on exposed shrubs in deep snow, whereas *M. rufogriseus*, which depends more on grazing, appears constrained to areas where snow is shallow.

Keywords: common wombat, *Vombatus ursinus*, swamp wallaby, *Wallabia bicolor*, red-necked wallaby, *Macropus rufogriseus*, alpine, gait, foot loading

Introduction

In Australia, seasonal snow cover is rare. On mainland Australia the area above the winter snowline, where snow lies for a minimum of one month per year (Costin 1957) is 2170 km² (Green and Stein 2015). The largest extent of this is in the Snowy Mountains (36°25'S, 148°21'E), which has 1310 km² of largely contiguous snow cover (Green and Stein 2015) that normally lasts at the alpine treeline for about 150 days per year. In the Snowy Mountains, average winter snow density, air temperature and the snow/ground interface temperature are generally higher than found in seasonally snow covered areas of the northern hemisphere, falling outside the ranges of values for the four main snow classes: tundra, taiga, alpine and maritime (Sturm et al. 1995; Sanecki et al. 2006). Sanecki et al. (2006) therefore suggested an additional

classification of 'warm-temperate-tropical snow', also known as 'Australian snow' (Bormann et al. 2013), the term used throughout this paper. The Snowy Mountains has high insolation with winter daytime temperatures frequently above freezing and night-time temperatures $< 0^{\circ}\text{C}$ leading to melt-refreeze metamorphism. Australian snow mid-season densification rates ($1.77 \times 10^{-3} \text{g/cm}^3/\text{day}$) are generally higher than those at northern hemisphere sites with maritime snow ($1.3 \times 10^{-3} \text{g/cm}^3/\text{day}$), taiga ($0.6 \times 10^{-3} \text{g/cm}^3/\text{day}$) and tundra ($0.2 \times 10^{-3} \text{g/cm}^3/\text{day}$) and are only matched by spring densification rates, for example, $2.0 \times 10^{-3} \text{g/cm}^3/\text{day}$ in Western USA (Bormann et al. 2013). Snow hardness influences two animal activities in different ways, whereas travel over the snow surface is made easier on hard snow, foraging for vegetation beneath the snow is made more difficult.

With seasonal snow cover confined to only 0.03% the area of mainland Australia, animal adaptations to snow would be expected to be rare. However, typical mammalian adaptations to seasonal snow cover do occur, particularly in the small marsupials that remain active within the subnivean space. The mainland dusky antechinus (*Antechinus swainsonii* (Waterhouse, 1840)) undergoes autumnal mass loss, an adaptation to existence beneath the snow, previously only found in Rodentia and Soricidae (Green 2001), while the agile antechinus (*Antechinus agilis* Dickman, Parnaby, Crowther and King, 1998) is active but undergoes daily torpor (Wallis 1977). The mountain pygmy-possum (*Burramys parvus* Broom, 1896) avoids winter activity by hibernating (Dimpel and Calaby 1972; Fleming 1985). Large mammals that live above the snow include two arboreal marsupial species (families Phalangeridae and Pseudocheiridae) and within the Snowy Mountains four species of

large ground-dwelling marsupials (Green and Osborne 2012). Of the four, the common wombat (*Vombatus ursinus* (Shaw, 1800)) is the only one found regularly in winter up to the alpine treeline and no large native mammals extend above this. Three macropodid species can be found above the winter snowline (1500 m) but one, the eastern grey kangaroo (*Macropus giganteus* Shaw, 1790), is rarely found in winter and then usually in a distressed state and is not considered further during this study.

There probably has not been great selective pressure for adaptations to a snow-covered environment in these four species, all of which have a contiguous distribution down onto the surrounding tableland, 1000 m in elevation below the treeline.

However, with global warming, one prediction, born out by observations over recent years (see Green and Pickering 2002), is that wallabies on the mainland will move to higher elevations with the decline in snow cover. In the central Snowy Mountains there has been a 39% reduction in the integrated snow profile in 60 years due to climate change. This is a combination of a decrease in the maximum depth of the snowpack by 44.8 cm and a shortening of the average duration of the snowpack by 18.5 days (Sánchez-Bayo and Green 2013). This reduction in depth of snow cover has favoured the ingress of non-migratory marginally occurring sub-alpine species (Green and Osborne 2012). The swamp wallaby (*Wallabia bicolor* (Desmarest, 1804)) only became common above the winter snowline in the mid 1990s (Green and Osborne 1998, 2012). Winter observations of swamp wallabies with pouch young (personal observation) suggest that this species at least is resident and breeding above the winter snowline to an elevation of 1650 m. The red-necked wallaby (*Macropus rufogriseus* (Desmarest, 1817)) has only become common above the winter snowline since about

2011 (personal observation) but is found to the highest accessible elevations in alpine Tasmania where deep seasonal snow cover is rare.

Large native mammals in Australian snow are all marsupials. Unlike many boreal mammals that wade through snow (Jacobsen 1973, Mattfeld 1974, Parker et al. 1984), marsupials travel on the snow surface so that their foot loading and the hardness of the snow surface are crucial to their ease of movement. Unlike the quadrupedal wombat, the Macropodidae are characterised by their in-phase bipedal hopping, which, although not restricted to macropodids, is generally confined to mammals that have a mass less than 1 kg (Bennett 2000). The second gait that macropodids adopt at low speed is the pentapedal gait (Dawson and Taylor 1973). In this gait, the paired front limbs and tail support the animal's mass, much like a tripod, as the hind limbs are swung forward, with the tail also providing propulsive force (O'Connor et al. 2014). This unique combination of gaits means that the way in which macropodids move on snow bears little relationship to modes of locomotion studied in the northern hemisphere. The fact that the two species of wallabies have shifted their elevational range upwards at a time when snow depth and duration are declining (Green and Osborne 2012) suggests that, compared to the wombat, they are not well adapted for life in the snow. This study therefore set out to answer two questions: what is the foot loading of the common wombat, swamp wallaby and red-necked wallaby and how is their locomotion in snow affected by gait?

Methods

Study area

The Snowy Mountains have an approximate north-south orientation with a highest elevation of 2228 m at Mt. Kosciuszko. To the north and west the land drops very steeply to 400 m above sea level, whereas the land surface to the east and south descends gradually in a series of steps to the lower Monaro tableland which lies at about 900 m above sea level. A true alpine zone lies above the alpine treeline at about 1900 m that sits within the worldwide thermal treeline limits of 6.4 ± 0.7 °C (SD) for soil temperature (Körner and Paulsen 2004; Körner 2012). The treeless vegetation of the alpine zone consists of rolling hills characterized by herbfields and heathlands. The subalpine zone lies between the alpine treeline at its upper limit and the timberline (the upper limit of closed montane forest) at its lower limit and broadly correlates with the winter snowline (Costin 1957). The subalpine zone on mainland mountains is characterized by the presence of woodlands dominated by snow gum (*Eucalyptus niphophila* Maiden & Blakely), wet and dry heathlands and sod tussock grasslands. Below this is the montane zone which is often marked by the change from snow gum woodland to tall eucalypt forest.

Snow

In the Snowy Mountains the Spencers Creek snowcourse at 1830 m elevation in an area of heathland and open woodland close to the alpine treeline is the longest running data set for snow cover having been measured weekly throughout the snow season from 1954 to the present by the Snowy Mountains Hydro-electric Authority, (now Snowy Hydro). The snowcourse is broadly representative of the surrounding area and it is used as the standard snowcourse for interannual comparisons (Slatyer et al. 1984). From these readings the weekly depth and duration of snow were obtained as well as

snow density to 2006. Linear regression was used to determine the relationship between the mean July snow density and year and was performed in the statistical package STATISTICA.

For the present study, snowpack density was measured with a Federal Snow Sampler (Carpenter Machine Works, Seattle, WA, USA). A snow penetrometer (Snowmetrics, Fort Collins, CO, USA) was used to characterise layering within the snowpack. An animal snow penetrometer was constructed along similar lines but with a head made to the shape and size of a wallaby foot to determine whether the configuration of the wallaby foot (long and narrow) resulted in a different penetration pattern.

Morphometrics

From 2002 to 2015, in winter when road traffic is heaviest because of access to ski fields, fresh road-killed wombats and wallabies were collected along the Kosciuszko Road from the entrance to Kosciuszko National Park (900 m elevation) to Perisher Valley ski resort (1720 m elevation). The road passes through 11.2 km of montane woodland and then 10.5 km of subalpine woodland, grassland and heath. Because of low ambient temperatures, animals that were killed generally remained either chilled or frozen overnight and therefore, when weighed the following morning, were still essentially fresh. Females that carried pouch young were weighed with and without the young. Animals that had been lying for too long for measurements of their mass to be reliable, either due to dehydration or decomposition were not weighed, neither were animals whose mass was reduced by the effects of vehicular impact or

subsequent scavenging. Animals were weighed using a 100 kg Salter clock-face scale to a precision of 250g (Salter Housewares Ltd, Tonbridge England). Body mass data were collected for 15 female and 20 male wombats, 13 female and 19 male red-necked wallabies and 8 female and 24 male swamp wallabies.

Symmetry of paired feet was assumed, so one hind and one front foot were removed from animals. Feet are not furred and were imaged along with a scale; the area of the whole foot was then measured on the printed picture using a planimeter. For wallabies on a hard surface the arched metatarsal bones keep the mid-region of the hind foot clear of the ground. For calculating the contact area of a macropodid foot Bennett (1999) measured areas only of the forefoot (the foot pad anterior to this arch) and the heel pad. However, in snow the arch also comes into contact so the whole foot pad was measured. When hopping, the mass bears down on the whole foot on landing but on taking off the wallaby rises onto the forefoot, hence, the forefoot was also measured separately and its area as a proportion of the whole foot was calculated. For wallabies the tail was flexed until the ventral surface touched the calcaneum (heel). The distal portion of the tail was then removed at this point, measured as a proportion of the length of the whole tail and the area of the distal portion of the tail which was potentially mass-bearing during locomotion was then measured as for the feet. Comparison of body mass and foot loading between sexes and species were performed using Student's *t*-test in the statistical package STATISTICA.

Chest height was measured from the wall of the chest at the junction with the leg to the back of the heel pad of the manus (front foot) for wombats only. This is slightly more than the chest height of a standing animal, but as road killed animals were used it was an easily replicated measure. Chest height was not measured for wallabies because of their upright gait that made such a measurement redundant to an understanding of their movement in snow.

Animal movement in snow

Tracks of animals moving on the flat were measured opportunistically over a number years in snow of varying depths. At each track the step or hop length, foot penetration and snow characteristics were measured. The presence and depth of a hard layer in the snow was found by careful probing with an avalanche probe or ruler. When walking, wombats placed their hind foot in the same place as the fore foot, so the distance between prints on one side was measured as was sinking depth. For wallabies the species was recorded if possible, also recorded were the gait (bipedal or pentapedal). For the bipedal gait ($n=104$) the length of hop and the depth of sinking at the juncture of the forefoot and heel were recorded. In the pentapedal gait ($n=17$), the depth of penetration of the tail and the length of the imprint of the tail on the snow where it was not dragged were also measured. Linear regression was used to determine the relationship between hop length and depth to a hard layer and was performed in the statistical package STATISTICA.

Results

Snow

Based on the mean July snow density there has been no significant trend in snow density among years over the past 60 years ($r=-0.054$, $P=0.70$). Snow density throughout the snow profile in the Snowy Mountains lies above 0.3 g cm^{-3} for much of the snow season and increases over the season (Fig. 1). Snow densification occurs rapidly. On 25 June 2014 after a fresh snowfall, the snow profile showed 43.8 ± 12.3 cm ($n=5$) of new snow sitting on a hard layer of approximately 120 N that marked the previous snowpack surface (Fig. 2a). After five days of metamorphism, a hard snow layer averaging 210.5 ± 56.7 N was found at 21-45 cm below the snow surface for five profiles. Figure 2b shows one of five profiles in which the hard layer of approximately 175 N was found at 26-37 cm below the snow surface.

Insert Figs. 1 and 2 hereabouts

Morphometrics

Mass

There was no significant difference in body mass in the Snowy Mountains between male and female wombats (Table 1). For both sexes combined, wombats in the Snowy Mountains weighed on average 31.4 ± 4.4 kg. There was a significant difference in the Snowy Mountains between male and female red-necked wallabies ($t=2.850$, $P<0.01$).

There was no significant difference in the Snowy Mountains between male and female swamp wallabies (Table 1).

Foot loading

In a stationery wombat, foot loading for four feet averaged $178 \pm 17.4 \text{ g cm}^{-2}$ ($n=32$) (Fig. 3). Females had a significantly higher ($t=2.380$, $P<0.05$) foot loading ($186.5 \pm 15.1 \text{ g cm}^{-2}$) than males ($172.6 \pm 16.9 \text{ g cm}^{-2}$). The figure for one female, with the addition of her pouch young, rose from 197.7 to 216.3 g cm^{-2} . Chest height in adult wombats averaged $142.2 \pm 32.1 \text{ mm}$ ($n=19$). In the quadrupedal gait wombats, like domestic dogs (*Canis lupus familiaris* L., 1758), would exert a vertical acceleration of approximately 2.5 g (Cavagna et al. 1977), translating to a foot loading for four feet of 445 g cm^{-2} .

In the normal travelling gait macropodids use in-phase bipedal hopping with the whole surface of the hind feet supporting the mass when sinking into the snow on landing. In a stationery red-necked wallaby standing on two feet, foot loading for males was $136.0 \pm 19.0 \text{ g cm}^{-2}$ ($n=20$) and for females $119.1 \pm 19.6 \text{ g cm}^{-2}$ ($n=13$), a significant difference ($t=2.400$, $P<0.05$). However, if the females had been carrying a 1.5 kg pouch young the foot loading would be $133.3 \pm 20.1 \text{ g cm}^{-2}$, a figure not significantly different from males. For swamp wallabies there was no significant difference between foot loading for males $124.2 \pm 18.9 \text{ g cm}^{-2}$ ($n=24$) and females $122.2 \pm 14.4 \text{ g cm}^{-2}$ ($n=8$). With the addition of a 1.5 kg pouch young the foot loading would be $134.0 \pm 15.1 \text{ g cm}^{-2}$, a figure still not significantly different from males. In the Snowy Mountains overall there was no significant difference between foot loading

in swamp wallaby ($123.7 \pm 17.7 \text{ g cm}^{-2}$) and red-necked wallaby ($130.2 \pm 20.3 \text{ g cm}^{-2}$). Both wallaby species had significantly lower foot loadings for two feet than wombats for four feet, 31% less in the case of swamp wallaby ($t=12.436$, $P<0.0001$) and 27% less for red-necked wallaby ($t=10.161$, $P<0.0001$) (Fig. 3). When stationary, wallabies use the hind feet and tail. This increases their supporting surface by approximately 75 %.

The measurements above were for a static load. During motion in the in-phase bipedal gait, although the whole of the foot bears the mass of the animal on landing, the mass transfers onto the forefoot immediately before take-off. The area of the forefoot as a percentage the whole foot was $51.5 \pm 2.4\%$ for the red-necked wallaby and $55.1 \pm 3.1\%$ for the swamp wallaby. As a consequence, forefoot loading in swamp wallaby ($236.07 \pm 23.1 \text{ g cm}^{-2}$) was significantly less ($t= 2.3289$, $P<0.05$) than for red-necked wallaby ($272.1 \pm 42.4 \text{ g cm}^{-2}$).

The foot loading recorded here for wallabies (Fig. 3) was based on the full plantar surface area. When hopping, this full plantar surface also bears the mass of the wallaby on landing. However, on take off, the approximate halving of the contact area of the foot with the ground, combined with the five-fold increase in the ground-reaction force because of the vertical component of the hop, results in pressures about an order of magnitude higher for hopping than when standing at rest (Bennett 1999). Hence foot loading when hopping for swamp wallaby would be approximately 1180 g cm^{-2} and red-necked wallaby 1360 g cm^{-2} .

In the pentapedal gait, in which the load on the mass bearing surfaces is relatively static, there was no significant difference in the supporting surface area of the combined tail and two front feet compared to the two hind feet for either species of wallaby; the ratio of surface areas of tail plus two front feet compared to two hind feet for swamp wallaby was 1.02:1 and for red-necked wallaby was 0.97:1. The mean length of tail imprints in snow was 34.2 ± 5.7 cm; these could not be assigned to species so length of the distal section of the tails of all wallabies measured were combined and resulted in a mean of 37.4 ± 7.0 cm. Pes (hind foot) length for swamp wallaby was 225 ± 12.5 mm and for red-necked wallaby was 231.1 ± 15.9 mm.

Insert Fig. 3 hereabouts

Animal movement in snow

Hops

Insert Fig. 4 hereabouts

Easy movement (defined as a regular spaced hop that is continuous without faltering due to sudden sinking into deeper snow) by wallaby species on flat snow averaged

136.3 $\pm$ 10.3 cm hop length with a sinking depth of 19.9 $\pm$ 3.9 cm. In the bipedal gait there was a slightly negative but non significant correlation ($r^2 = 0.0202$; $P = 0.08$) between hop length and depth to a hard layer (Fig. 4) but a significant positive correlation ($r^2 = 0.6998$; $P < 0.0001$) between sinking depth and the depth to a hard layer of snow. In the pentapedal gait there was a slightly positive but significant correlation ($r^2 = 0.2726$; $P = 0.03$) between hop length and depth to a hard layer and also a significant positive correlation ($r^2 = 0.7282$; $P < 0.001$) between sinking depth and the depth to a hard layer of snow (Fig. 4).

Insert Fig. 4 and 5 hereabouts

Of the wallaby trails measured opportunistically, one which is representative of the different gaits is illustrated. The wallaby measured close to the ram penetrometer site on 30 June 2014 moved bipedally sinking a little over 10 cm with the snow beneath the foot being compressed onto the hard layer (Fig 5). Its hop length increased to close to 150 cm until, with the hard layer at 35 cm subsurface, it sank 29 cm (Fig. 5). At this point it changed to pentapedal gait, reducing its hop length, which reduced penetration into the snow back to about 10 cm. After the hard layer again approached the surface the wallaby changed back to bipedal gait, increasing hop length with foot penetration once again compressing the snow onto the hard layer (Fig. 5).

Discussion

Gait

Quadrupedal – Wombats

The common wombat is the only large marsupial in Australia found above the winter snowline with a quadrupedal gait. The wombat can move all four feet independently, hence at low speeds it can minimise snow penetration by moving one foot at a time carefully packing the snow down with each step (Triggs 1988). Foot loading in mammals generally increases with body mass. However, although wombat mass is only 30-35 kg their foot loading averages approximately 180 g cm^{-2} and can go as high as 200 g cm^{-2} with the addition of the mass of pouch young. This is similar to that of the much larger caribou (*Rangifer tarandus* (L., 1758)) (Telfer and Kelsall 1984). However, because Australian snow has higher densities than are general in boreal climates and because the wombat's gait results in a lower ground-reaction force than for hopping wallabies, movement over snow is not greatly impeded.

Bipedal-pentapedal – Wallabies

The measurement of foot loading for wallabies is complicated by the variety of gaits and the actions within a gait so that there is almost a continuum of increasing load-bearing surface area in response to increasing sinking depth. A hopping macropod spends approximately 75% of the hop period in the air compared to 0-15% of the step period in a trotting quadruped (Cavagna et al. 1977). As a result, unlike the quadrupedal gait of wombats exerting a vertical acceleration of approximately 2.5 g, in the bipedal hopping gait for the red-necked wallaby, this figure is 3.0-5.0 g for speeds of $<10 \text{ km h}^{-1}$ (Alexander and Vernon 1975). Because of an approximate

halving of the contact area of the foot as the wallaby raises itself onto the forefoot, foot loading when hopping for wallabies is 2.5-3 times that of wombats in the quadrupedal gait.

The threshold for easy movement by a wallaby in snow on the flat, i.e. the ability to maintain a hop length of >135 cm, is around 20 cm sinking depth (Fig 4) or close to the pes length of the wallaby. This may be related to the fact that in the hopping motion, the pes is flexed on deceleration, storing elastic energy in the Achilles tendon (Cavagna et al. 1977). This energy storage saves approximately 40% of the energy required for locomotion (Alexander and Vernon 1975) and to recover this energy, thus maximising hopping efficiency, the body must rise to the approximate length of the pes (Cavagna et al. 1977), which in the wallabies measured was 22-23 cm. Snow sinking depth deeper than about 20 cm would, therefore, require greater vertical displacement adding to the energy cost of hopping. In an environment of reduced food availability winter energy conservation is important (Marchand 1996) and the energetic cost of extra snow depth is high. For example, in deer an increase in sinking depth from 35cm to 50 cm leads to a doubling of the net cost of locomotion (Mattfield 1974). No studies of energy expenditure by wallabies in snow have been conducted, but the observed difficulties of wallabies in deep snow suggest the energy cost in such situations is high.

At low speeds both wallaby species can move in a pentapedal gait, in which they use their hind feet and front feet and their tail as a fifth limb. Because the aerial

component of the hop is removed in this gait, vertical acceleration is reduced and they can minimise snow penetration. The forces exerted in this pentapedal gait are essentially close to the static load and equally distributed between the plantar surface area of the hind feet and the combined area of two front feet and the distal part of the tail. For example, the wallaby in Figure 5 was able to maintain a hop length >125 cm, until, with the hard layer falling to 35 cm below the surface, its penetration into the snow reached 29 cm and it changed to pentapedal locomotion which reduced its hop length by 35% and its foot penetration by 40%, without reaching the hard layer below the snow surface. At this speed and gait, when ground reactive forces (the forces exerted by the ground on a body in contact with it) are relatively low (Bennett 1999) the wallaby was not sinking deeply (Fig. 5). However, this gait is inefficient for travel, with an increase in speed being achieved by stride frequency rather than stride length, increasing the energetic cost to four times as much as a mammal running on four legs (Dawson and Taylor 1973). By contrast the change to a bipedal hop, hence a longer stride length allows greater speed and can lead to an actual reduction in energetic cost as speed increases (Dawson and Taylor 1973). Hence the wallaby resumed the bipedal hop as the depth to the hard layer was reduced. Travel in the pentapedal gait, except when foraging, is less common than the bipedal gait with the option of not traveling at all in deeper snow being preferred.

Locomotion of any kind becomes constrained when the animal sinks deeply regardless of movement. In early season snow density typical of freshly fallen Australian snow of 0.14 g cm^{-3} the ram penetrometer tube alone (static load of 1 kg) penetrated $31.4 \pm 2.6 \text{ cm}$ of snow, the wallaby foot version (weighted appropriately for

a wallaby) penetrated 37.2 ± 3.8 cm onto a hard layer at 38.4 ± 3.9 cm. Falls of fresh snow of this depth (>30 cm) can impede locomotion, with wallabies incapable of maintaining a sequence of hops and falling as they attempt locomotion (personal observation). In still deeper fresh snow, wallabies seek shelter and then tend not to move until snow densification makes travel easier. In such a situation in a resting posture wallabies can further increase their contact area by resting on hind feet and tail, thereby nearly doubling their mass-bearing area.

Coping with snow

The major factor limiting the distribution of the wombat in the Snowy Mountains is maximum snow depth, with areas of snow consistently >100 cm deep avoided by foraging wombats (Matthews et al. 2010). The snow in boreal regions is sufficiently light and thin that many mammals sink through to the ground and wade through snow, e.g. white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) and elk (*Cervus elaphus canadensis* Erxleben, 1777) (Jacobsen 1973, Mattfeld 1974, Parker et al. 1984). However, apart from these 'waders' that penetrate the snow to the ground surface, in terms of locomotion the total snow depth is not important for animals but only the depth of less dense non-supportive snow in the upper snow profile, through which the animal sinks to snow of a supporting density or hardness (Bunnell et al. 1990). Melting, refreezing, and settling of Australian snow leads to a rapid increase in mechanical strength of the snowpack and its load-bearing capacity and even on moderately compacted snow wombats may travel for many kilometres before returning to a burrow (Green 2005; Matthews and Green 2012). However, after early snowfalls, wombats are commonly

observed labouring in deep un-compacted snow, forcing their body through the snow until furrows are formed that allow free movement (Green and Osborne 2012). This activity would have a high energetic cost.

The most effective winter energy conservation measure, found in all boreal deer is a voluntary reduction in activity (Marchand 1987). In adverse weather conditions the wombat has the advantage of being able to retreat to the more thermally favourable environment of a burrow and may not emerge from its burrow for a number of nights (personal observation). It neither stores fat nor enters torpor but has a field metabolic rate amongst the lowest for mammals, far lower than predicted for herbivorous mammals (Evans et al. 2003). Wallabies use shrubs for cover and following deep, low density snowfall, evidence of heavy browsing of shrubs in a confined locality with heavy trampling of the snow and one wallaby track in and out suggests that wallabies also remain immobile until the snow hardens.

Foraging

As elevation increases, plants become smaller and become less available as snow depth increases. The larger home range of the wombat at high elevations in a complex terrain and hence varying snow depth allows wombats to fulfil their nutritional requirements with no great change to their grazing habit, specifically the types of food taken does not change with grass still dominant (Matthews and Green 2012; Green et al. 2015). The browsing swamp wallaby has little need to change its diet, feeding on shrubs that project above the snow (Green et al. 2014) and so long as snow is hard

enough it may, like the wombat, cover sufficient territory to gain access to sources of food. Here too its lower forefoot loading relative to that of the red-necked wallaby may be advantageous. The first species to drop out on an elevational gradient is the red-necked wallaby (Fig. 6), which is generally a grazer with a limited shift towards intake of browse at higher elevation (Green et al. 2014). Above the snowline, therefore, red-necked wallabies appear to spend the winter confined to small areas where snow cover is light (personal observation), possibly because of easier access to smaller ground cover plants.

Changes in snow and colonization by wallabies

The major changes in the snow of the Snowy Mountains over the time period that swamp wallabies and later red-necked wallabies have become established has been a reduction in depth and duration of the snowpack. The occupation of areas above the winter snowline by red-necked wallabies has been the most recent (2011) and most marginal shift in elevational range. This followed a time period from 2000-2010 when satellite-based remote sensing (Moderate resolution Imaging Spectroradiometer – MODIS) showed a statistically significant decline in snow cover which included changes in snow cover area, melt date and season duration with a significant decline above 1500 m elevation (Bormann et al. 2013). However, even in areas of marginal snow, high mortality of red-necked wallabies has been reported in infrequent deep snow in Tasmania (J. Kirkpatrick, personal communication) and in Britain due to snow cover for three months in the winter of 1962-63 (Gilmore 1977). It is likely that establishment of wallabies at higher elevations in the Snowy Mountains has been due to the shallower snow at the winter snowline in the case of red-necked wallabies and

the very early densification of Australian snow that possibly allows swamp wallabies to cover larger distances in search of browse made more accessible by shallower snow. Whilst the wombat may be able to survive short early winter periods of deep unconsolidated snow by remaining in its burrow, wallabies do not have this energy saving mechanism and whilst they may continue to push occupation to higher elevations, it appears that the infrequent deep unconsolidated snow will keep a check on their populations.

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Table 1. Mean body mass of male and female common wombat (*Vombatus ursinus*), red-necked wallaby (*Macropus rufogriseus*) and swamp wallaby (*Wallabia bicolor*) together with sample size in parenthesis.

Species	Male mean mass $\pm$ 1 SD	Female mean mass $\pm$ 1 SD
Common wombat	31.6 $\pm$ 3.2 kg (<i>n</i> =20)	32.4 $\pm$ 3.6 kg (<i>n</i> =13)
Red-necked wallaby	17.2 $\pm$ 4.8 kg (<i>n</i> =20)	13.1 $\pm$ 2.6 kg (<i>n</i> =11)
Swamp wallaby	17.2 $\pm$ 3.5 kg (<i>n</i> =24)	15.7 $\pm$ 1.8 kg (<i>n</i> =8)

Figure Captions

Fig. 1. Seasonal changes in snow density at the Spencers Creek snowcourse over the period 1954-2006.

Fig. 2. Ram penetrometer record for 25 June 2014 (a) and 30 June 2014 (b). The snow between these two dates had compressed under the influence of drizzle and the surface hardened by freezing and then re-covered with fresh snow.

Fig. 3. Foot loading (g cm^{-2}) for red-necked wallaby (*Macropus rufogriseus*) and swamp wallaby (*Wallabia bicolor*) (on two feet) and common wombat (*Vombatus ursinus*) (on four feet).

Fig. 4. Relationship between hop length and the depth to a hard snow layer for bipedal gait (diagonal crosses) and pentapedal gait (filled circles) and the relationship between sinking depth and the depth to a hard snow layer for bipedal gait (upright crosses) and pentapedal gait (open circles).

Fig. 5. A part of a trail of a wallaby hopping on level ground with a hard layer (ram hardness R of ~ 210 N) at varying depth beneath the snow surface. Diamonds = hop length with gait, triangles = sinking depth and squares = location of the hard layer.

Fig. 6. Highest elevation occupied by three large marsupial species, red-necked wallaby (*Macropus rufogriseus*), swamp wallaby (*Wallabia bicolor*) and common wombat (*Vombatus ursinus*), together with their mode of locomotion and feeding habit relative to August snow depths from below the winter snowline to near treeline. Snow depth was measured on two transects for different projects, one consisting of a single pole at each elevation from 1350-1650 m elevation (crosses) and a second transect with between 12 and 66 poles at each elevation from 1525-1825 m (diamonds with SD).

Fig. 1. Seasonal changes in snow density at the Spencers Creek snowcourse over the period 1954-2006.

137x122mm (300 x 300 DPI)

Fig. 2. Ram penetrometer record for 25 June 2014 (a) and 30 June 2014 (b). The snow between these two dates had compressed under the influence of drizzle and the surface hardened by freezing and then re-covered with fresh snow.

119x69mm (300 x 300 DPI)

Fig. 3. Foot loading (g cm⁻²) for red-necked wallaby (*Macropus rufogriseus*) and swamp wallaby (*Wallabia bicolor*) (on two feet) and common wombat (*Vombatus ursinus*) (on four feet).

131x150mm (300 x 300 DPI)

Fig. 4. Relationship between hop length and the depth to a hard snow layer for bipedal gait (diagonal crosses) and pentapedal gait (filled circles) and the relationship between sinking depth and the depth to a hard snow layer for bipedal gait (upright crosses) and pentapedal gait (open circles).

157x137mm (300 x 300 DPI)

Fig. 5. A part of a trail of a wallaby hopping on level ground with a hard layer (ram hardness R of ~210 N) at varying depth beneath the snow surface. Diamonds = hop length with gait, triangles = sinking depth and squares = location of the hard layer.

139x108mm (300 x 300 DPI)

Fig. 6. Highest elevation occupied by three large marsupial species, red-necked wallaby (*Macropus rufogriseus*), swamp wallaby (*Wallabia bicolor*) and common wombat (*Vombatus ursinus*), together with their mode of locomotion and feeding habit relative to August snow depths from below the winter snowline to near treeline. Snow depth was measured on two transects for different projects, one consisting of a single pole at each elevation from 1350-1650 m elevation (crosses) and a second transect with between 12 and 66 poles at each elevation from 1525-1825 m (diamonds with SD).

116x87mm (300 x 300 DPI)