Herbivores in alpine herbfields: will wombats shift to higher altitudes with climate change?

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ABSTRACT

Shifts in the geographic range towards higher altitudes are anticipated for many species in south-eastern Australia in response to future climate warming. This is particularly the case for the Snowy Mountains, where a substantial reduction in the snow cover is expected to have a major impact on the distribution of species. A number of large marsupial herbivores occur at lower subalpine elevations, and a shift in their distribution to higher altitudes due to climate change will result in increased grazing of the vegetation of the alpine area. Common wombats *Vombatus ursinus* were chosen as a model species for examining range shifts because they are common in subalpine areas, but rarely occur above the tree line in the alpine zone. Changes in wombat habitat over time were predicted using a rule-based modelling approach that incorporates resources important to wombats as well as changes in snow depth with climate change. These models predicted a 16% increase in the area of suitable wombat habitat across the study area by 2050. This increase was largely within higher subalpine altitudes. Thus, shifts in wombat distribution in the Snowy Mountains with climate change are likely to occur at higher subalpine altitudes as a filling process within the extent of occurrence, rather than an expansion beyond the range boundary into the alpine zone.

Key words: climate change, range shifts, rule-based modelling, snow, *Vombatus ursinus*

Introduction

Mountain ecosystems are particularly sensitive to climate warming because of the low temperatures to which species have become adapted (Pauli *et al.* 2007). There are about 11 major high-mountain ecosystems in the world, including the high mountains of temperate and Arctic Eurasia and North America, Hawaii and Tenerife, Africa, South America, Australasia and Antarctica (Wardle 1989). There is now general agreement that temperatures have increased in these mountain and snow-covered environments, particularly during spring (Foster 1989; Beniston 1997; Brown 2000; Inouye *et al.* 2000; Pauli *et al.* 2007). For example, recent climate warming in the European Alps has been twice as high as the global average (Pauli *et al.* 2007). However, in Australia, temperature appears to have increased marginally over 35 years at high elevation sites (above 1000 m) but not at lower elevations (Hennessy *et al.* 2003).

The implications of climate warming for snow-covered ecosystems include changes to the timing, depth, internal structure and extent of seasonal snow cover (Jones *et al.* 2001). The latest report by the Intergovernmental Panel on Climate Change states that in both the northern and southern hemispheres, mountain glaciers and snow cover have declined on average since the 1960s and snow cover is projected to contract further (IPCC 2007). Contrary to these findings, Brown (2000) reported an increase in snow cover over North America during the past century, which was linked to a concurrent increase in

precipitation (Inouye *et al.* 2000). In the Swiss Alps, the depth and duration of snow showed no long-term trend over 50 years, but declined during a period of warming from the mid-1980s onwards (Beniston 1997). These trends reveal that regional climate factors appear to play a significant role in climate change effects. For example, large variability in annual snowfall in the Swiss Alps is related to the North Atlantic Oscillation (NAO) which influences temperature and precipitation (Beniston 1997). In Australia, large variability in snow depth from one year to the next is thought to be associated with the El Niño Southern Oscillation (ENSO) (Osborne *et al.* 1998). Despite a high inter-annual variability in maximum snow depth in Australia (Hennessy *et al.* 2003), there has been a long-term decline in overall snow cover (measured as metre-days of snow) since 1954 (Green 2006).

Climate change effects on snow cover also influence the timing or seasonality of snow. There is evidence for declines in late season snow characteristics in North America, Eurasia and Australia with reduced snow accumulation and snow depths during spring months (Brown 2000; Hennessy *et al.* 2003). Green (2006) also noted that the earliest thaw in the 50-year snow record in Australia was in 1999, despite the 1990s having had generally more snow cover than the 1980s. These observations indicate that the greatest influence of climate warming on snow characteristics may be at the end of the snow period.

Climate predictions for the Australian Alps

The Australian Alps is also experiencing climate change (Nicholls 2005), and comprise the highest parts of the Great Dividing Range and the associated mountains in the southeast of the continent, incorporating all of the mainland's snow country (Costin 1989). This area is relatively small, covering just 0.02% of the Australian mainland, and the alpine zone is restricted to a narrow altitudinal band of about 400 m above the treeline (Green 1998), yet it supports a wide range of important biota (Pickering et al. 2004). Snow is a defining feature of the faunal composition in both the alpine and subalpine environments of the Australian Alps (Green and Osborne 1998). The duration, depth and density of the snow cover dictate available habitat and food resources and opportunities for breeding (Green and Osborne 1998). Consequently, any change to the snow cover is likely to have a major impact on the fauna in this ecosystem.

The Office of Environment and Heritage (NSW) and the University of New South Wales developed preliminary climate change forecasts at a regional scale using interpolated climate projections based on the IPCC's A2 emissions scenario (DECC 2008). Regional projected climate in 2050 for the Alps is for warmer minimum and maximum temperatures (1 – 2.5 degrees), substantial decreases in winter rainfall and snow (10 – 50%) with less variability than the 20th century, small declines in spring and autumn rainfall (5 – 20%) and increases in summer rainfall (20 – 50%) (DECC 2008; undated). These figures are consistent with projections of temperature rises in global mountain systems by Nogués-Bravo et al. (2007). They predicted temperature under four emissions scenarios (A1F1, A2, B1, B2) and found for Australian mountains increases of 1.3 - 2.0 degrees in 2055 and 1.9 - 3.7 degrees by 2085. The magnitude of these temperature trends was not as large as other high mountain ecosystems of the world, but within Australia, these temperature increases in the mountains are significantly greater than trends in the lowlands.

Hennessy et al. (2003) simulated future snow conditions in the Australian Alps using two scenarios of projected temperature and precipitation. However, the high impact scenario (2050 temperature: + 2.9 degrees, precipitation: - 24.0%) is most consistent with recent projections (DECC 2008), and this predicts large reductions in the extent, depth and duration of the snowcover by 2050. The total area with at least one day of snow cover was projected to decrease 39% by 2020 and 85% by 2050 under the high impact scenario. At the local level, snow depth profiles for Mt Perisher (1835 m) show declines from the present average maximum depth of 160 cm to 90 cm in 2020, and less than 20 cm in 2050 under the high impact scenario. Snow duration at this site also declines from 131 days to 125 days in 2020 and 30 days in 2050 under this scenario. Further, the elevation of the snowline at Mt Kosciuszko on 1 September (i.e. late winter) is predicted to rise from 1460 m at present to 1625 m by 2020 and approximately 2000 m by 2050 under the high impact scenario. These changes are due to more precipitation falling as rain, rather than snow, and higher rates of ablation, particularly during spring, as the climate warms.

Ecological consequences of climate warming

Numerous studies have described changes to ecological systems in line with the type and magnitude of changes that would be expected a priori under a climate warming scenario (Hughes 2000; McCarty 2001; Parmesan and Yohe 2003; Root et al. 2003). While some have showed no response by species, or responses that are counter to predictions of climate warming, the majority showed overwhelming support for climate change effects (McCarty 2001; Parmesan and Yohe 2003; Root et al. 2003). Further, the ecological effects have been more prominent, as expected, at higher latitudes in the northern hemisphere where temperature changes are largest (Root et al. 2003). Although it is not possible to provide a causal link between these observed ecological changes and climate change, failure to act on such consistent patterns could have serious implications for conservation (McCarty 2001).

There have been numerous reviews published recently on the ecological consequences of climate warming (e.g. Kapelle et al. 1999; Hughes 2000; Shaver 2000; McCarty 2001; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Schmitz et al. 2003; Helmuth et al. 2005) and climate processes, such as the NAO and ENSO (e.g. Post et al. 1999; Ottersen et al. 2001; Stenseth et al. 2002). Most describe changes to four major levels of ecological organisation: life history or phenological changes; shifts in geographic range; changes to the composition of communities; and alterations to ecosystem dynamics. The first two, in particular, have been well documented for a range of species in different environments, including mountain environments (e.g. Inouye et al. 2000; Green and Pickering 2002 cited in Green 2006; Walther et al. 2002; Pickering et al. 2004; Green 2004, 2006; Pauli et al. 2007; Erschbammer et al. 2009). Of concern to many ecologists are potential shifts in the range of common native and exotic species, and their impact on more sensitive species in high alpine areas (e.g. Green 1998; Walther et al. 2002; Beniston 2003).

Potential impacts from range shifts of herbivores to higher altitudes

Under a climate warming scenario, the movement of species from lower elevations is expected to occur faster than at higher elevations (Walther et al. 2002), and mobile animals will shift distribution more rapidly than plants (Martin 2001). Thus range shifts of grazing species to higher altitudes may alter the composition, cover and biomass of alpine plants because herbivores can exert considerable pressure on the flora of mountain ecosystems (del Moral 1984; Leigh et al. 1987; Bridle and Kirkpatrick 2001). Changes to vegetation have been observed when grazing is either added or removed from the system. This has been evident in many locations with both the introduction and removal of domestic or feral herbivores, such as cattle and horses (e.g. Wardle 1989; Wahren et al. 1994; Beever et al. 2008). In Australia, some dominant or co-dominant herbs in the tall alpine

herbfields of the mainland are subordinate species in the tall alpine herbfields of Tasmania. This difference in species composition has been attributed largely to differences in grazing pressure by rabbits and native herbivores (wallabies and wombats), since these herbivores are present year-round on the tall alpine herbfields in Tasmania, but are largely absent from high altitude sites on the mainland (Bridle and Kirkpatrick 2001).

The paucity of vertebrate herbivores at high altitude sites on the Australian mainland is probably related to the presence of snow, with many species showing a decline in numbers with increasing altitude (Pickering *et al.* 2004). They include the following native species: common wombat *Vombatus ursinus*, eastern grey kangaroo *Macropus giganteus*, red-necked wallaby *M. rufogriseus* and swamp wallaby *Wallabia bicolor*, and introduced species: rabbit *Oryctolagus cuniculus*, hare *Lepus europaeus*, pig *Sus scrofa*, horse *Equus caballus*, fallow deer *Dama dama* and sambar *Cervus unicolor*. Therefore, in terms of future climate change predictions, it is important to understand whether upward range shifts of these species are likely to occur with reductions in the snow cover, or whether other environmental factors constrain their present range.

Case Study: Modelling potential range shifts of common wombats in the Snowy Mountains

The common wombat is a large, herbivorous marsupial (average 26 kg) that occurs throughout south-eastern Australia, including Tasmania (McIlroy 2008; Triggs 2009). Wombats are nocturnal, and emerge from their burrow to feed just after dusk. In the Snowy Mountains, common wombats occur in woodlands and forests at elevations where snow covers the ground, although they are rarely observed above the treeline into the alpine zone (Green and Osborne 1994). In the 1950s, Costin (1954) thought that wombats were restricted to lower subalpine levels near the winter snow line. Similarly, during the 1970s and 1980s, wombats were not observed in surveys at high altitude sites (Green 2004). However, there is some evidence that wombats have shifted to higher altitudes in recent years, possibly as a result of poor snow years (Green 2004). Sign of wombats has been observed as high as Mt Townsend (~ 2200 m a.s.l.) in spring (K. Green pers. comm., November 2009), and a shallow burrow was found at 2050 m a.s.l. in summer, but it was not used during winter (Green 2005). These descriptions of changes in the occurrence of common wombats in higher areas make them an ideal species for examining range shifts with climate change. Thus, the objective of this study was to develop a predictive model of wombat distribution under future climate scenarios of reduced snow cover in the Snowy Mountains.

Data collation and predictive modelling approach for wombats

This study builds on data and modelling approaches from recent ecological studies of wombats in the Snowy Mountains, which are summarised as follows:

1. Wombat movements and space use were examined in the Snowy Mountains during 2008 – 2009 (Matthews 2011). Home ranges were larger in the Snowy Mountains than in other parts of the species' range, and increased significantly with altitude. Wombats remained in their non-winter home range area during winter, but home range size contracted, and core areas of the range tended to shift to more northerly aspects, corresponding with locations of shallower snow. Movement rates and the distances travelled each night were also reduced during the winter period, particularly for individuals at higher altitudes where the snow was deeper.

2. The foraging behaviour of wombats was examined by following the tracks of individuals in the snow (Matthews 2010). Wombats inhabiting the snow-covered area were capable of digging through the snow to reach ground-based vegetation on which they feed. However, wombats were more successful feeding where the snow was shallower (Fig. 1), and deeper snow altered their foraging behaviour, including changes in their movement path and their diet. When snow depth increased, wombats found sites where the snow had melted around the base of trees or rocks and the snow was shallower to dig through to reach grasses, or they switched to feeding on shrubs that protruded from the snow. Wombats are unlikely to be able to persist on a diet entirely of shrubs, so grasses must be accessible in part of the wombat's home range, and this was shown to be limited where snow depths are consistently greater than 100 cm.
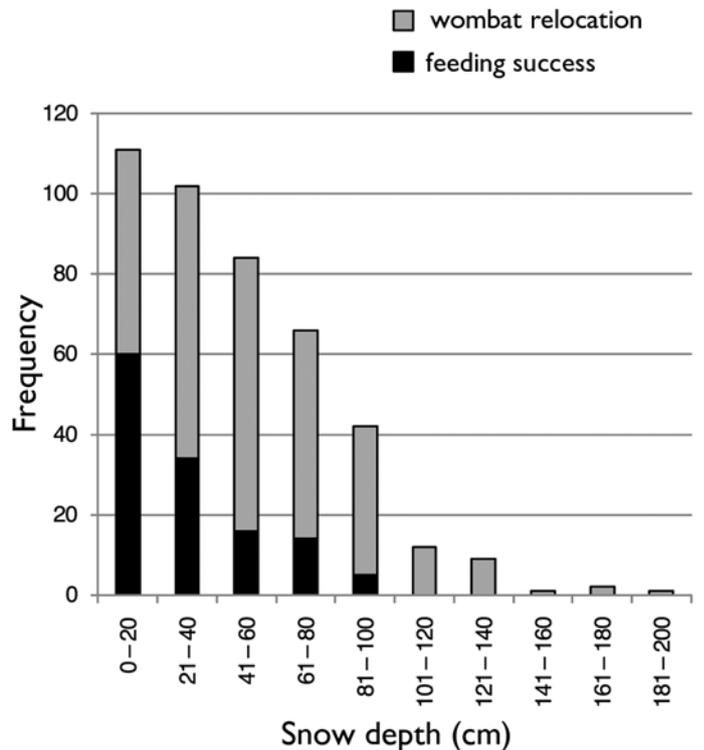

Figure 1. Frequency of observed successful feeding sites over a range of snow depths where wombats were relocated by snow tracking (data from Matthews 2010). Wombat relocation is a point along the track where the wombat moved but did not feed. The maximum snow depth at successful feeding sites was 100 cm.

3. Matthews *et al.* (2010) used logistic regression models to examine the influence of snow and habitat predictors on the occurrence of wombats in the subalpine zone. The variables selected for inclusion in candidate models for winter were maximum snow depth, topographic relief, percentage cover of grasses, herbs, litter, burnt grasses and burnt shrubs, soil bulk density, and distance to water. Maximum snow depth was found to be the most influential variable in the distribution of wombats, but the top winter models included multivariate combinations of maximum snow depth with other habitat covariates. Of these other habitat variables, topographic relief was found to be particularly important (being included in three of the four top AIC ranked models). Topographic relief was positively related to wombat occurrence, with the predictor fitted as a piecewise linear form in the models. Fig. 2 shows how the response curve for topographic relief is positively related to wombat presence above a threshold of 120 m. It allowed the suggestion to be made that high-relief terrain would provide wombats with greater opportunity to access more favourable sites in winter because of the variability in altitude, snow depths and shelter sites.

4. In a separate study of resource selection within the home range of wombats, Matthews (2011) examined which resources were important to wombat survival in the subalpine zone. Wombat location information was combined with a number of topographic, vegetation, fire history and other habitat features to generate predictive models of resource selection. Using AIC model selection techniques, the best global model showed that wombats selected mid-elevations, mid-slopes, drier soils, and locations closer to roads and to water courses, and avoided areas with a high proportion of grassland (or conversely, selected areas of subalpine woodland). This predictive model was then used to map habitat suitability over the landscape in five classes of relative probability of use. Extrapolating beyond the current range of the population, this predictive map showed that the majority of the alpine zone is presently unsuitable for occupation by wombats.

Thus, the main conclusions from these studies, which have a bearing on wombat spatial patterns in the study area, were:

1. Wombats have the physical capability to disperse, but home ranges need to be established in areas that are suitable for winter occupation.

2. Successful foraging can only occur in snow depths less than 100 cm.

3. At the landscape scale, rugged terrain provides a diversity of habitats for wombats to exist in areas where the maximum snow depth is greater than 100 cm.

4. Within the home range, wombats select resources based on topographic, vegetation, landscape and soil attributes, and these features, selected within the subalpine zone, do not necessarily occur in the alpine zone.
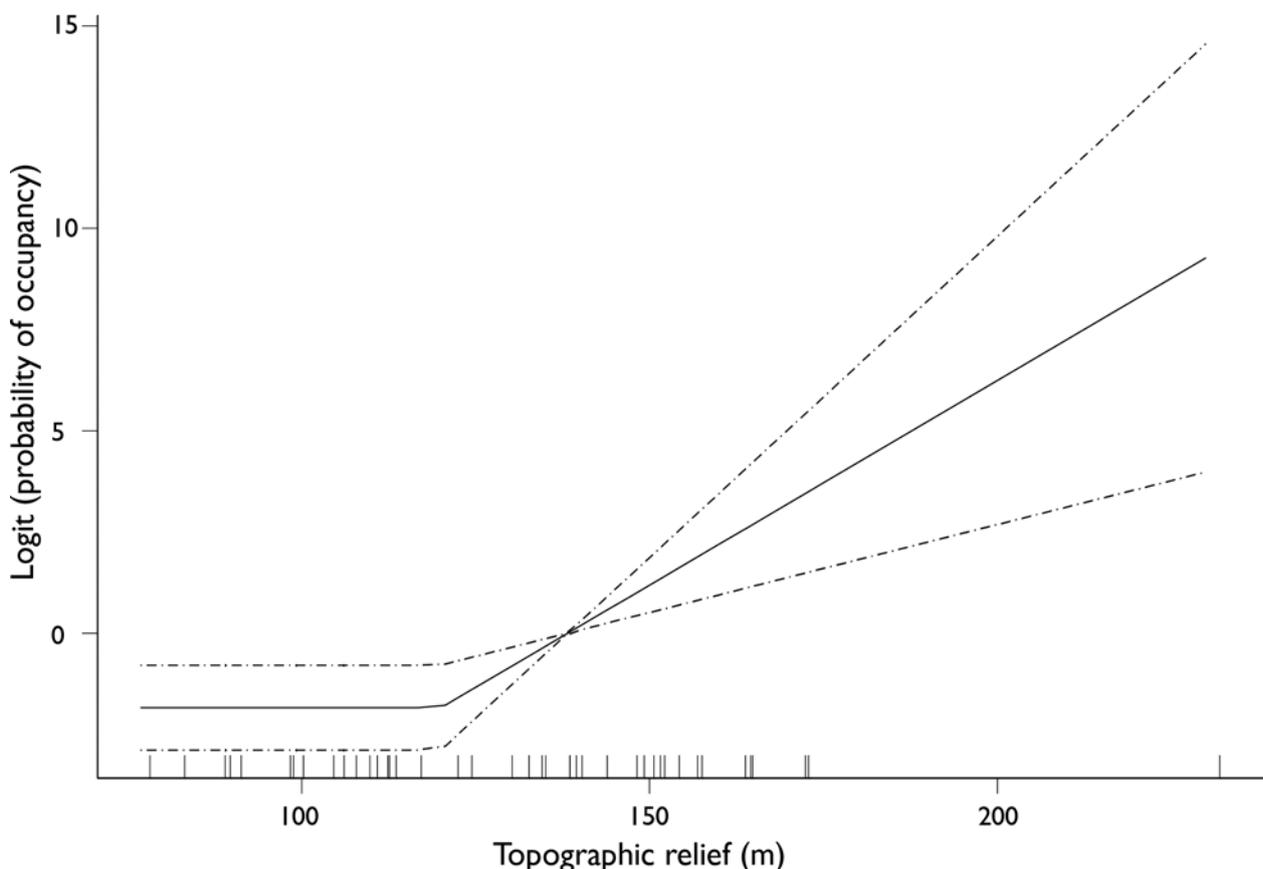

Figure 2. Partial plot of the relationship between the probability of wombat occupancy in winter and topographic relief (data and methods from Matthews *et al.* 2010). Dashed lines represent 95% confidence intervals around the fitted response shape. Tick marks on x axis indicates sample points.

The combination of these ecological conclusions, numerical outputs from logistic models of wombat occurrence, and a suitability map of wombat habitat based on patch-scale resource selection in the subalpine zone (Matthews 2011), provide the basis for predictive modelling under future snow-depth scenarios.

Snow depth data

Snow depth maps obtained from CSIRO (Hennessy *et al.* 2003) provided coarse-grain (2.5 km²) predictions of snow depth over the study area. Simulated regional patterns of maximum snow depth were mapped for the present, 2020 and 2050. Mapped predictions were made for both the low- and high-impact scenarios of projected temperature and precipitation, but only the high-impact scenario maps were used in this study.

Rule-based model

To produce a predictive model to examine changes in wombat spatial patterns over the study area, a rule-based modelling approach (e.g. Schadt *et al.* 2002) was used to incorporate snow depths and habitat attributes that are important to wombats. Using a rule-based approach, verbal rules, which are closely related to the ecological requirements of a species, are replaced by equations in the mapping process. In this study, habitat suitability was based on the following rules:

1. Snow depth must be less than 100 cm, to allow successful foraging by wombats (Matthews 2010);

2. Topographic relief must be higher than 120 m (i.e. the threshold for wombat occurrence; Matthews *et al.* 2010) if snow depth is 100 – 200 cm, to allow wombats access to sites of shallower snow;

3. Habitats must have the necessary resources (resource selection function (RSF) categories 4 or 5; Matthews 2011), to allow wombats to establish a home range.

These rules were implemented in ArcGIS v. 9.2 (ESRI Inc.) to predict locations of suitable wombat habitat at present snow depth levels, and at two times in the future under the high-impact scenarios of snow depth in 2020 and 2050 (Hennessy *et al.* 2003).

Rule 1 was applied using the snow depth maps obtained from CSIRO (Hennessy *et al.* 2003). Rule 2 was applied using a relief map that was derived from a 25 m digital elevation model (DEM) and calculated the difference in altitude within a 500 m radius of each cell. Rule 3 was applied using the habitat suitability (RSF) map (25 m resolution) derived in Matthews (2011) and estimated by the exponential model,

$$w(x) = \exp\,(0.0527003(\text{Elev}) - 0.0000161(\text{Elev}^2) + 0.0974323(\text{North}) + 0.1086489(\text{Slope}) - 0.0031245(\text{Slope}^2) - 0.0009692(\text{Dwater}) - 0.0017377(\text{Droad}) - 0.0651041(\text{CTI}) - 0.5254448(\text{Grass}).$$

where Elev = elevation in metres, North = relative northness, Slope = slope in degrees, Dwater = distance to water in metres, Droad = distance to road in metres, CTI = compound topographic (wetness) index, and Grass = proportion of area containing grassland within 100 m. A full description of each of these raster layers is provided in Matthews (2011).

Thus, each of the predictive wombat habitat maps (present, 2020 and 2050) was derived from one of the snow depth maps, a relief map, and the habitat suitability (RSF) map. The cell size and alignment of each grid map was matched using Spatial Analyst before calculation of the predictive map. The predictive map was then derived using the map calculator function in ArcGIS to combine each grid map using formulas based on the above rules (see Fig. 3 for a flow chart of the modelling process).
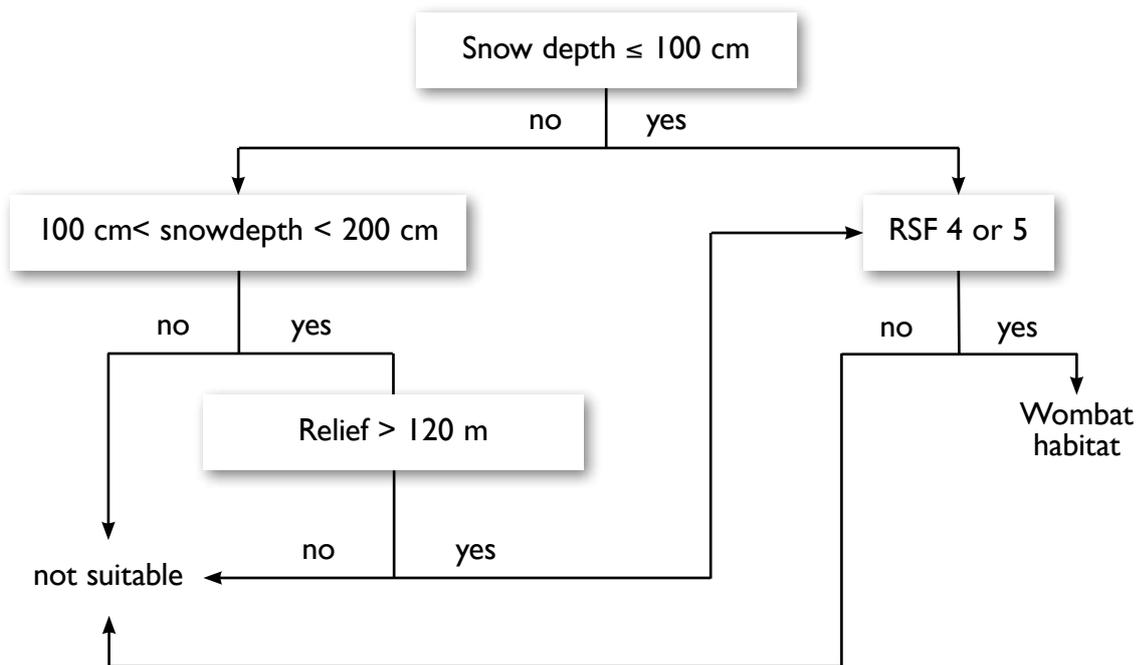

Figure 3. Flow chart of the process used to build predictive maps of wombat habitat using a rule-based formula. RSF = resource selection function.

Case study results

The successive application of these rules resulted in the predictive habitat maps shown in Fig. 4. They show an 11% increase in the area of suitable wombat habitat across the study area by 2020, and a 16% increase by 2050 (Table 1). This increase was largely within higher subalpine altitudes, particularly around the resort areas of Perisher, Smiggin Holes and Blue Cow, and on both sides of the Kosciuszko Road between Perisher and Charlotte Pass. In contrast, just 158 of 1847 ha of additional wombat habitat area in 2050 is in the alpine zone.

The 2050 predictive map reflects the habitat suitability (RSF) map (Matthews 2011) because by then the area is no longer constrained by snow depth. This habitat suitability (RSF) map is the product of patch-scale resource selection by wombats in the subalpine zone, extrapolated beyond the present range of the population, to predict the distribution of suitable habitats if snow conditions were homogenous across the study area. When snow depth declines, conditions in the alpine zone become more similar to present conditions in the subalpine zone, and thus wombat habitat suitability can be predicted by present resource selection models.
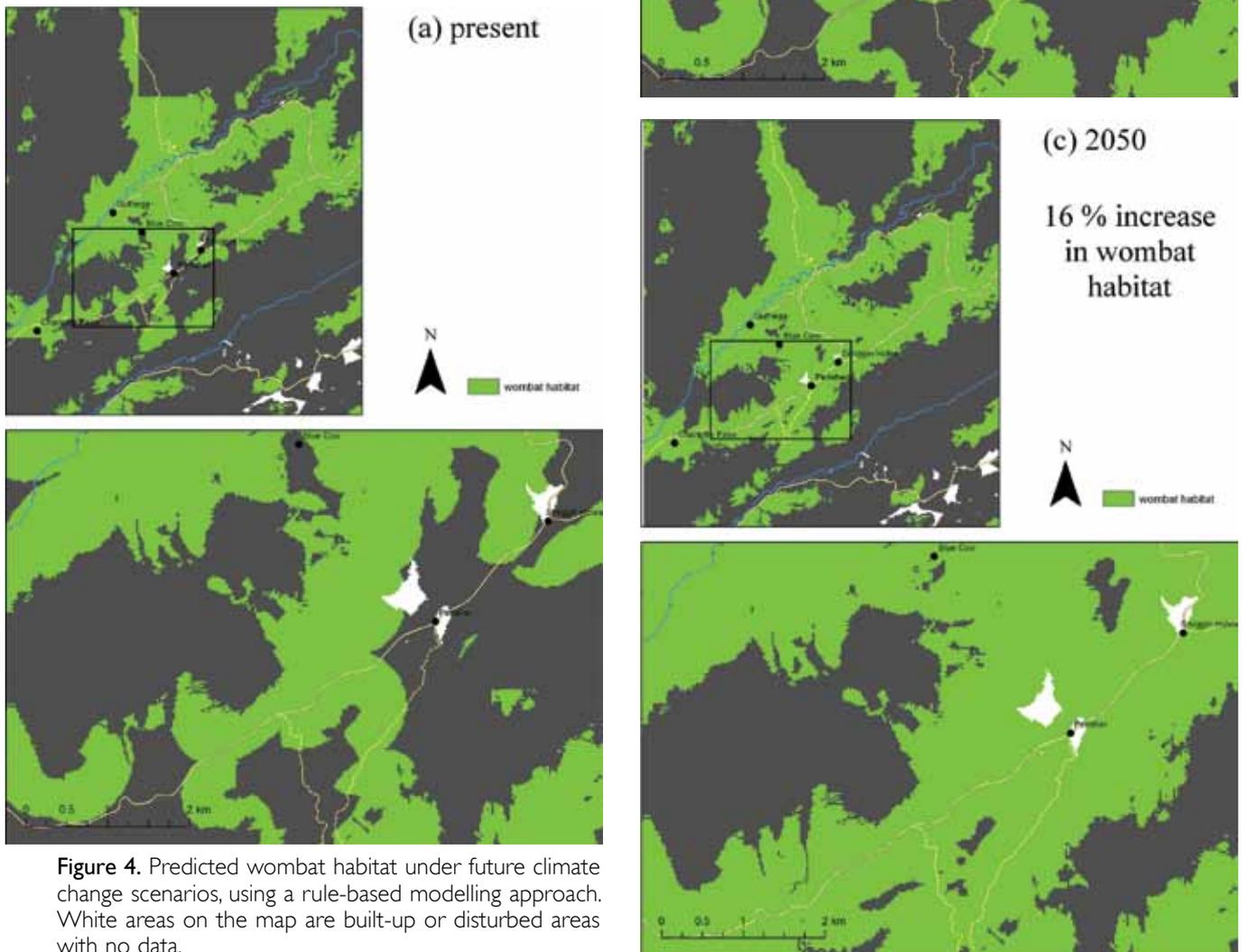

(a) present

(b) 2020

11 % increase in wombat habitat

(c) 2050

16 % increase in wombat habitat

Figure 4. Predicted wombat habitat under future climate change scenarios, using a rule-based modelling approach. White areas on the map are built-up or disturbed areas with no data.

Table 1. Summary of predicted wombat habitat area under high-impact climate scenarios (after Hennessy *et al.* 2003). The study area domain is depicted in Fig. 4.

Climate scenario	Habitat area (ha)	Additional area (ha)	Percent increase
Present	11899	-	-
2020 (high)	13222	1323	11%
2050 (high)	13746	1847	16%

Discussion

Predicted shifts in wombat range

The predictive maps show that shifts in wombat distribution in the Snowy Mountains with climate change are likely to occur at higher subalpine altitudes through a 'filling' process (Gottfried *et al.* 1999), rather than a broadscale upward expansion beyond the treeline into the alpine zone. Thus, the density of individuals is likely to increase at the range boundary as the area of available habitat increases, and conditions for foraging become less harsh. While changes in numbers may also occur within currently occupied habitats, as the quality of those habitats improve (Johnson and Seip 2008; Jarema *et al.* 2009), these results also show how wombat numbers might change with increases in habitat area within the extent of occurrence. Recent observations of wombats in higher areas, where they were not seen during the 1970s and 1980s (Green 2004), indicates that these changes are already occurring.

In contrast to the subalpine zone, it appears that the alpine zone has little suitable habitat for wombats both now, as well as under future climate scenarios. This study examined topographical and vegetative features of the environment that would be needed by wombats for food, shelter and reproduction. Although each of these requirements was not examined separately, the model of resource selection at the patch scale indicated that the habitats selected by wombats within the subalpine zone do not occur at higher altitudes. However, new habitats may be used by wombats that expand their range into novel environments (Thomas *et al.* 2001; Kearney *et al.* 2008).

The availability of habitats for burrowing is vital for wombat survival and suitable burrow habitat would need to be available within the alpine zone for wombat occupation within that zone. At higher subalpine elevations, wombats were seen using large rock habitat as burrow sites, digging long, inter-connected tunnels, with multiple entrances, under the boulders. These sites differed markedly from burrows at lower elevations where they were commonly located in hillsides and under tree roots. The conclusion drawn was that wombats may seek alternative burrow locations if their preferred habitat is unavailable. Other burrowing or denning mammals in subalpine and alpine areas use rocks selectively as burrow habitat, and this must confer some advantage in this environment (Bihr and Smith 1998; Ciarniello *et al.* 2005). Further research is needed to identify the characteristics and suitability of rock habitat for burrowing in different seasons, and its availability in the alpine area.

Limitations of the predictive model

There is a number of limitations to these models, particularly in regard to the coarse grain of the snow depth prediction maps. The maps were developed to examine changes in snow depth over the entire Australian Alps, but do not adequately represent snow depths at the scale over which wombats respond to foraging conditions. Nevertheless, they provide broad changes in snow depth over the altitudinal gradient of the study area that will determine whether wombats can establish home ranges within the landscape. Further, these snow depth prediction maps were developed in 1998—the map of 'present' habitat is now 13 years old at the time of writing this paper—so it is likely that the area of presently available habitat is actually greater than that depicted. Further improvements in snow depth data accuracy and currency by climate modellers would improve the results of this approach to modelling wombat habitat.

The habitat maps define areas of suitability, but habitats at higher altitudes are presently not as densely occupied as areas at lower subalpine altitudes. The habitat depicted around Charlotte Pass (Fig. 4) may be suitable for wombat occupation, but wombats have not become established in this area. There is also difficulty in extrapolating these results from the study area to other locations within the Australian Alps, because the predictive model remains to be tested. However, by using a rule-based approach that incorporates ecological processes, such as foraging thresholds, we are confident these patterns will apply elsewhere in Australian alpine areas.

Finally, the models presented here are based on existing vegetation layers, topographic, and other abiotic data, where current and predicted snow cover has been manipulated to form predictions for wombat range shifts. Future climate change will also result in changes in vegetation patterns (Pickering and Armstrong 2003), and concurrent changes in disturbance regimes (e.g. fire – Lucas *et al.* 2007). Therefore, further refinement of this model incorporating data on predicted vegetation changes would provide additional strength to our predictions.

Implications for management

While the alpine zone appears to have little suitable habitat for wombat occupation, a reduction in the snow cover is likely to see a shift in the density of wombats at higher subalpine elevations. The most immediate impact of this change would be an increase in wombat numbers within the resort areas. Thus managers will need to consider the interaction between wombats and human development. Wildlife conflicts with winter recreational activities have been particularly problematic where species have dramatically increased in numbers

(e.g. Bruggeman *et al.* 2006; López *et al.* 2010). Whether these increases are naturally occurring phenomena, or a result of anthropogenic changes in the landscape, decisions about how best to manage the change can be difficult. Bruggeman *et al.* (2006 p.1540) aptly wrote that "managers now face the increasing challenge of balancing public demand for recreation, while simultaneously preserving wildlife and habitat".

Conflicts between wombats and humans have existed for a long time in farming areas, where wombats have been blamed for damaging fences, and causing erosion and other damage to pastures from their burrowing (Marks 1998; Triggs 2009). Within the ski resort areas, burrows under lodges and other infrastructure do cause problems for managers (e.g. NPWS 2008), as has been the case in Europe with burrowing alpine marmots (López *et al.* 2010), and it might become necessary in the future to exclude them from areas where they could create potential hazards.

Wombats are also regularly killed on the roads (Brown 2001; Ramp *et al.* 2005); road mortality can significantly contribute to local population declines (Roger *et al.* 2011). Wombat-vehicle collisions may increase in the future as more habitat becomes available along the Kosciuszko Road, and as human visitation to the area increases (Pickering and Buckley 2003). Wombats are vulnerable to vehicle collisions because they feed along the roadsides and are often slow to respond to approaching vehicles (Brown 2001) and their dark body colour frequently blends with the background. This presents a hazard to motorists and, if not fatal to the wombat, can cause severe injury.

Changes in the spatial patterns and density of wombats may also alter biotic interactions, particularly with non-native pest species. For example, dogs, foxes, cats and rabbits have been shown to utilise wombat burrows for shelter (McIlroy 1973; Leigh *et al.* 1987; Triggs 2009; Borchard and Wright 2010), and changes in wombat distribution and the creation of new burrows may facilitate changes in these alien invasive species. Foxes are generally not effective predators of adult wombats (Triggs 2009), although concern was expressed about foxes preying on wombats in the winter of 1981 when there was very deep snow cover (Green and Osborne 1994). At that time, it was not known whether foxes were killing or scavenging on wombats that had perished from the harsh conditions, but there was little evidence of wombat being consumed in a dietary study of foxes (Green and Osborne 1981).

Rabbits in subalpine environments are sensitive to snow depth that prevents access to burrows and grasses for feeding (Dunsmore 1974; Leigh *et al.* 1987) and consequently rabbits are limited to areas where there is past or current disturbance, e.g. in areas grazed by stock (Myers and Parker 1965) or around resorts (Ford 2004; Pickering *et al.* 2004). Wombats may facilitate the invasion of rabbits into new areas by creating shelter sites

and keeping access to ground vegetation open (Green and Osborne 1998). Thus, control programs for pest species will need to be vigilant to these potential changes in wombat distribution.

Future research direction

This research examined spatial patterns of the distribution of the common wombat, but changes in their numbers, and an understanding of population dynamics at the range boundary, would be needed to fully examine population shifts and limits to dispersal. Changes in relative abundance may be one of the most dramatic responses to climate change (Shoo *et al.* 2005; Jarema *et al.* 2009), and incorporating ecological dynamics and density-dependence into resource selection functions is emerging as the next important step in forecasting the spatial distribution of animals (McLaughlin *et al.* 2010). Most studies of population dynamics focus on temporal patterns of local populations, with little attention paid to differences across habitats within the species' range (Guo *et al.* 2005), but habitats along elevational gradients provide opportunities to study differences in population demography and dynamics because there is wide range of environmental variability over a small spatial scale (Gillis *et al.* 2005).

Much attention has also been given to threatened species, but changes in the distribution of common and widespread species are also likely (Hughes 2003; Ritchie and Bolitho 2008). Australia's large marsupial herbivores have been relatively neglected in climate change research, but recent evidence suggests that they are vulnerable to climate change effects (Ritchie and Bolitho 2008). Conservation strategies must recognise that changes in the range of any species will have consequences for the ecosystem through various trophic interactions.

Conclusion

This study on one species, the common wombat, is just a start to understanding range shifts and potential ecosystem changes in the Australian Alps. Changes will occur as both animals and plants respond to changes in snow cover, and other environmental change (e.g. increased fire frequency). Our predictive models have shown that shifts in the spatial pattern of wombats will occur mostly through a filling process within the extent of occurrence, rather than an extension beyond their present range boundary. As this study has demonstrated, local ecological studies are important to fill gaps in existing knowledge, and provides baseline information which is required for more integrated and complex ecosystem modelling (Schmitz *et al.* 2003). This combination of intensive field based studies for specific species, and broader landscape ecological modelling, is urgently required to better inform managers of the likely dispersal of expanding species, and impacts on more restricted alpine biota.

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APPENDIX I
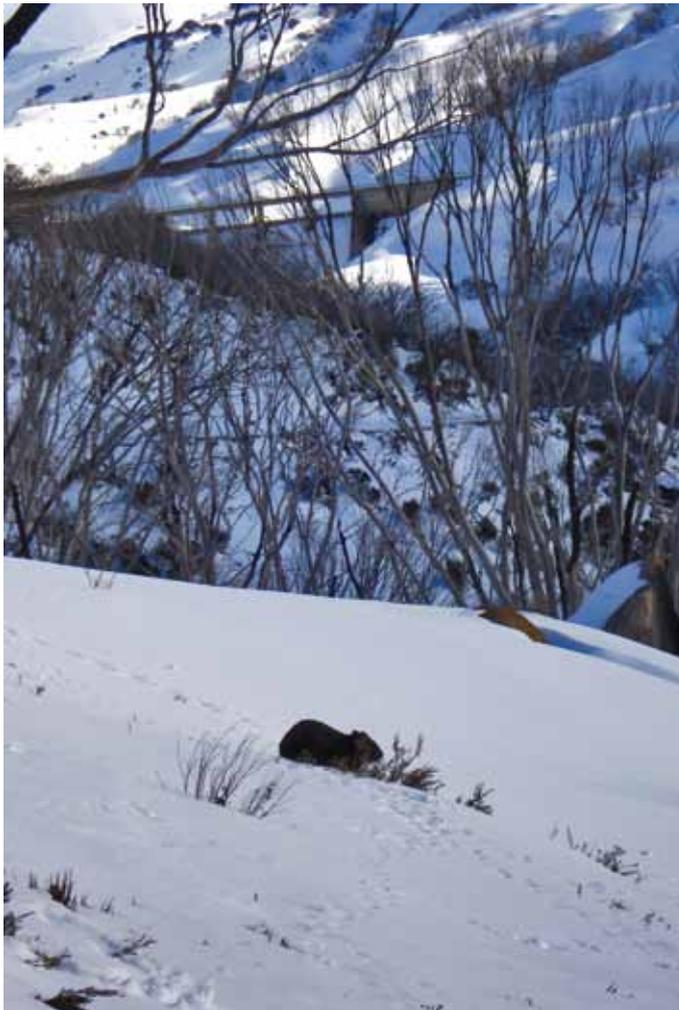
A common wombat near Guthega in the Snowy Mountains. This individual was feeding on shrubs that protruded from the snow.

Photo, A. Matthews.

The foraging location of a wombat that had dug through the snow to feed on *Poa* grasses.

Photo, A. Matthews.

APPENDIX I

This wombat emerged from its burrow during the day to feed on a north-facing slope where the snow had melted.

Photo, A. Matthews.

A collared wombat recovering from anaesthetic at the entrance to its burrow. This site is covered by snow during winter, and the wombat remained in its home range throughout the year.

Photo, P. Barrett.

Wombats are not particularly well-adapted to moving in the snow due to their short stature, but they are good diggers.

Photo, T. Kaminskis.

Wombats are regularly killed on the roads in the Snowy Mountains because they are attracted to the roadside to feed where the snow is cleared.

Photo, A. Matthews.