

The persistence of common wombats in road impacted environments

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The persistence of common wombats in road impacted environments



Erin Roger

PhD thesis

School of Biological, Earth and Environmental Sciences
University of New South Wales

August 2009

“We treat the attrition of [wildlife] lives on the
road like the attrition of lives in
war: horrifying, unavoidable, justified.”

Barry Lopez, *Apologia*

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There is growing global concern over the influence of road development on the conservation of biodiversity and on the functioning of ecosystems. Published reviews in the field of road ecology have identified that most research has examined the effects of roads linearly and have advocated for research at landscape scales. Among the many effects roads have, one of the most significant is the loss of animal life resulting from collisions with vehicles. Despite this, little is known of what toll this has on animal populations and how these impacts vary with scale. This stems from the perception that impacts are localised and that animals killed are typically considered common, and therefore not of great conservation concern. This thesis challenges this notion by showing that the impacts of fatalities can affect populations at landscape extents and that commonness is not a barrier to localised extinction risk. To achieve this I focus on the common wombat; an example of a common species for which road impacts have never been previously examined. Chapter 1 provides an overview of the importance of scale in quantifying road impacts and the debate surrounding common species persistence in road environments. Chapter 2 assesses habitat use of wombats in a road environment at a local scale. Results suggest that wombats select for roadside habitat and as a result populations could be under threat. Chapter 3 is a predictive model of wombat road fatalities which demonstrates the importance of incorporating habitat use in predictive fatality modelling. Through use of a spatially explicit population viability analysis, Chapter 4 demonstrates that roads, in conjunction with other threats can affect the persistence of a common species at a local scale. Chapter 5 is a landscape extent assessment of wombat habitat use, finding that increased effort should be employed in evaluating how reserves confer resilience to species from the impacts of roads and that habitat quality can dictate road-based fatality rates. Chapter 6 summarises the research presented in the thesis and suggests direction for future work, particularly the importance of evaluating the interplay between susceptibility and abundance on species vulnerability in road environments.

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Preface

These theses consists of four stand-alone papers (chapters two to five) that have either been published, accepted, or are currently in review. Therefore each chapter is self contained and some repetition occurs. Because each chapter is a stand-alone journal article, the tables and figures are not sequentially numbered throughout the thesis, rather each chapter is presented as it would appear as a published journal article. I have also kept journal specific formatting for each chapter. The chapters that have been published are identical to the published version with the exception of some of the figures which I have changed from their printed black and white version to colour. To prevent unnecessary duplication a single reference list is provided at the end of the thesis formatted in the style for Biodiversity and Conservation.

This thesis is a compilation of my own work, with guidance from my supervisors Daniel Ramp and Shawn Laffan. Apart from the contributions of my co-authors outlined below I conceptualised my research, conducted all data analysis and wrote and illustrated the manuscripts. I also generated all maps and photographs included in this thesis. My co-authors proof-read and edited the final manuscript versions as is required for publications. The contributions of my co-authors are detailed below.

Chapter 2: Roger, E., S. W. Laffan, and D. Ramp. 2007. Habitat selection by the common wombat (*Vombatus ursinus*) in disturbed environments: Implications for the conservation of a 'common' species. *Biological Conservation* 137, 437-449.

S.W. Laffan assisted with GIS analysis and GIS layer generation. He also gave conceptual advice and guidance in his function as my supervisor.

D. Ramp wrote the GAM script and provided advice and assistance with modelling within the program R. He also contributed significant intellectual input and general guidance in his function as my supervisor.

Chapter 3: Roger, E., and D. Ramp. 2009. Incorporating habitat use in models of fauna fatalities on roads. *Diversity and Distributions* 15, 222-231.

D. Ramp wrote the GAM script and provided advice and assistance with modelling within the program R. He also contributed significant intellectual input and general guidance in his function as my supervisor.

Chapter 4: Roger, E., Laffan, S.W., and Ramp, D. (accepted 05/01/2010) Road impacts a tipping point for wildlife populations in threatened landscapes. *Population Ecology*.

S.W. Laffan assisted with GIS analysis and spatial analysis results. He also gave conceptual advice and guidance in his function as my supervisor.

D. Ramp wrote the GAM script and provided advice and assistance with modelling within the program R. He also contributed significant intellectual input and general guidance in his function as my supervisor.

Chapter 5: Roger, E., Ramp, D., Bino, G., Laffan, S.W. (in review) Rethinking the impact of roads on common species persistence. *Landscape Ecology* (submitted 10/08/09).

D. Ramp wrote the GAM script and provided valuable advice with modelling within the program R. He also contributed significant intellectual input and general guidance in his function as my supervisor.

G. Bino developed the predictive and dependent layers for the GIS analysis and refined the modelling process. He also gave conceptual advice and guidance.

S.W. Laffan gave conceptual advice and guidance in his function as my supervisor.

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My gratitude goes, as ever, to a great many people for their peerless support and patience. I am greatly indebted to Daniel Ramp for introducing me to the field of road ecology. His support, vision and mentorship meant a great deal to me throughout my PhD (even if it did involve extensive modelling). I would also like to thank Shawn Laffan for taking me on as a student halfway into my candidature. I am grateful for his enduring patience with my lack of patience in all things GIS, and for his approachability and friendship throughout this process.

Throughout this project I had help from many people. I would like to thank Jo Caldwell for collecting the majority of the road-kill data and for her thoughtful responses when I asked how the wombats were doing. Thanks to Alison Fitch for agreeing to genotype my DNA samples and to Jen Sinclair for her monumental help in analysing the results. Thanks also to David Alder and John from the Goobarragandra Heritage Trust Foundation for collecting wombat tissue and hair samples for me. Thanks to the Kosciuszko National Park Tumut Park Office for allowing me to conduct field work in the park, providing me with GIS layers and for rescuing me from a near four-wheel drive disaster on top of the Blowering Cliffs. Thank you to all the volunteers who helped with field work for my project: Joanna Bagniewska, Franziska Boemka, David Croft, Jenny Hans, Maureen Roger and Dave Wheeler. Thank you also to Jacqui Marlow, who is an inspiration in her relentless pursuit of a more compassionate world.

I cannot imagine going through this process without my friends. Thank you to Alex James who sat across from me and was my rock. Thank you to Gilad Bino for the advice on all things ecological and technical and for being the first half of team GE. I am grateful to Chris Hellyer, Therese Kenna, Tom Mullaney and Fiona Thomson for all

the support. Thank you to the entire Samuels crew past and present for all the advice, laughs and friendship. I absolutely could not have done it without you.

Thank you also to Dave Wheeler for making this all possible. I will be forever grateful for his exceptional patience in enduring flies, snakes and brambles in the field and for his companionship, emotional and financial support. Finally, thank you to my family for proving that arms can extend across oceans. To Geo, Jen, Dad and Mom, thanks a million times over for everything. It is incredibly reassuring to know there is a team of people who believe in you and are unwavering in their support.

Abstract

There is growing global concern over the influence of road development on the conservation of biodiversity and on the functioning of ecosystems. Published reviews in the field of road ecology have identified that most research has examined the effects of roads linearly and have advocated for research at landscape scales. Among the many effects roads have, one of the most significant is the loss of animal life resulting from collisions with vehicles. Despite this, little is known of what toll this has on animal populations and how these impacts vary with scale. This stems from the perception that impacts are localised and that animals killed are typically considered common, and therefore not of great conservation concern. This thesis challenges this notion by showing that the impacts of fatalities can affect populations at landscape extents and that commonness is not a barrier to localised extinction risk. To achieve this I focus on the common wombat; an example of a common species for which road impacts have never been previously examined. Chapter 1 provides an overview of the importance of scale in quantifying road impacts and the debate surrounding common species persistence in road environments. Chapter 2 assesses habitat use of wombats in a road environment at a local scale. Results suggest that wombats select for roadside habitat and as a result populations could be under threat. Chapter 3 is a predictive model of wombat road fatalities which demonstrates the importance of incorporating habitat use in predictive fatality modelling. Through use of a spatially explicit population viability analysis, Chapter 4 demonstrates that roads, in conjunction with other threats can affect the persistence of a common species at a local scale. Chapter 5 is a landscape extent assessment of wombat habitat use, finding that increased effort should be employed in evaluating how reserves confer resilience to species from the impacts of roads and that habitat quality can dictate road-based fatality rates. Chapter 6 summarises the research

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Chapter 1

Introduction

Few attempts have been made to associate the impacts of roads with landscape extent species responses. This thesis addresses this knowledge gap by evaluating how the impacts of roads affect populations at local and landscape scales. To accomplish this, I focus on the common wombat (*Vombatus ursinus*), a common species that is frequently hit on roads. In this chapter I describe the impacts of roads on wildlife at both landscape and local spatial scales. I also discuss perceptions of commonality, and how abundance does not preclude species from the threat of localised extinction. Finally, I provide information on common wombat biology and the study area, and outline how the chapters are linked to provide an evaluation of the impacts of roads on common wombats at multiple spatial scales.

Roads as a key threatening process

There is growing concern over the influence of road development on the conservation of biodiversity and the condition of ecosystems globally (Forman et al. 2003). Roads pervade most ecosystems and are increasingly recognised as a key threatening process (Sherwood et al. 2002; Forman et al. 2003). The ecological impacts of roads can occur far from the road edge, up to one or two kilometres (Forman 2000). This road environment is often also termed the ‘road effect zone’ (Forman and Alexander 1998). As a result of the road effect zone, roads can have multiple abiotic and biotic effects; affecting microclimate, wind flow, water run-off and facilitating the dispersal of both plants and animals (see reviews by Forman et al. 2003; Seiler 2003; Coffin 2007). For wildlife, roads can also have numerous impacts on populations. They can alter

population structure, by causing road avoidance in some species (Jaeger et al. 2005) and isolate individuals from resources and mates (Gerlach and Musolf 2000). Perhaps most obviously roads cause fatalities of animals as a result of collisions with vehicles (Ramp et al. 2005; Roedenbeck et al. 2007; Bissonette and Adair 2008; Fahrig and Rytwinski 2009; Roger and Ramp 2009). These impacts raise serious concerns about the stability and sustainability of wildlife populations in road-affected environments (Roedenbeck et al. 2007; Grilo et al. 2009). With road networks rapidly expanding, there is a pressing need to assess the conservation implications of the impact of roads on wildlife on multiple spatial scales.

Scale

To date, the majority of research has investigated the impacts of roads on wildlife locally (Jones 2000; Ramp and Ben-Ami 2006; Roedenbeck et al. 2007; Fahrig and Rytwinski 2009). Local scale assessment is critical and has demonstrated that road fatalities have the capacity to severely impact local populations (Haines et al. 2006; Ramp and Ben-Ami 2006). Research has demonstrated that certain morphological and or biological traits can disproportionally impact species (Trombulak and Frissell 2000; Grilo et al. 2009), and that predictive fatality models are useful in identifying hotspots where animal mitigation efforts would be most effective (Malo et al. 2004; Ramp et al. 2005). In turn, this has provided sufficient evidence to merit the implementation of mitigation techniques to reduce road fatalities (Jaarsma et al. 2006; Bissonette and Adair 2008; Grilo et al. 2009). In combination, this evidence has been crucial in establishing the ecological effects of roads on wildlife as a primary consideration in regional road construction planning (Bond and Jones 2008).

However, localised studies are limited in their ability to extrapolate findings over larger spatial extents (Roedenbeck et al. 2007). As a result, the majority of concern

surrounding the impacts of roads on species persistence (as opposed to population persistence locally) continues to be focussed on threatened species (Forman et al. 2003). Broad scale studies are important because some species may appear to be persisting in road impacted environments when investigated at smaller spatial extents but could be suffering broad scale range reductions as a result. Key questions remain, such as how long fatality rates are sustainable until species persistence at larger landscape scales is affected.

Landscape extent impacts of roads on populations

Resource distribution is a key motivation behind animal movement in road environments, yet resources have not properly been integrated into our understanding of wildlife populations adjacent to roads (Martin et al. 2007). Animals are attracted to road environments for a variety of reasons: snakes and other ectotherms are attracted to the warm surface, some birds use roadside gravel to aid their digestion of seeds and some mammals are attracted to roadside salts, while browsing herbivores are attracted to the dense vegetation of roadside edges (Forman et al. 2003). Largely missing from the road ecology dialogue has been the implication for species if roads act as attractive sinks (Delibes et al. 2001). Attractive sinks can arise when human modification of the environment causes formerly reliable cues to result in poor selection decisions (Igual et al. 2007). Fundamental to the source-sink model is that sink populations can persist when replenished by continuing immigration from source populations, offsetting high rates of local mortality (Kreuzer and Huntly 2003; Hargrove et al. 2005). However, over time, source populations can become depleted if mortality and attraction to the sink area is high. Source-sink dynamics suggest roads can have a much wider influence on susceptible species, effectively drawing individuals that are attracted to road environments from surrounding areas (Roger and Ramp 2009).

Theoretical and empirical studies suggest that species susceptibility to roads interacts with species use of habitat, morphology, foraging behaviour, and flight response when determining the general level of impacts on species from roads (van Langevelde and Jaarsma 2004; Ford and Fahrig 2007; Lee and Croft 2008; Fahrig and Rytwinski 2009). These characteristics can be attributed to a range of species (Fahrig and Rytwinski 2009), including common species, and are crucial in determining the effects of roads on species persistence. It is likely that roads may act as a selecting agent for species, leading to decline and extinction in species with traits that confer susceptibility. The key issues for wildlife populations are how individual-based movement decisions change with distance from the road and the implications of these decisions, coupled with fatalities, on the viability of roadside populations.

Persistence of common species in road environments

The ecological importance of common species is due to their two foremost characteristics, they are both abundant and widespread (Gaston and Fuller 2007). Because they are widespread, small proportional reductions in their abundance can impact across large geographical areas (Gaston 2008). Because they are abundant, they usually account for most individuals in an assemblage and often a large proportion of the biomass and function (Pearman and Weber 2007; Gaston and Fuller 2008). Despite evidence of their importance, common species are not typically the focus of conservation even though anthropogenic threats have impacted common species (Gaston and Fuller 2008).

Debate continues over the extent in which road mortality impacts common species persistence in road impacted environments. Forman and Alexander (1998) suggested that the local abundance of a species is linked to its road mortality, with road mortality not a severe enough threat to affect population persistence except in the case

of threatened species. Bennett (1991) concurred, while Mallick et al. (1998) believed that the relationship between population size and road-kill frequency is secure and that one can predict the other. In contrast, Hels and Buchwald (2001) stated that whether or not a population is affected by roads is dependent on what regulating mechanisms are within a population. Taylor and Goldingay (2004) insisted that the variety of species and location covered in literature, supports the idea that there are no geographic and taxonomic restrictions to the effects of road mortality on animal populations.

Central to the debate is the lack of research quantifying landscape extent impacts of roads on common species. Generally, road impacts of common species are viewed as localised, and therefore not likely to impact on species persistence. This is contrary to the reactionary approach taken by management when threatened species are killed, with the threat to species persistence more immediate. Ultimately, conserving wildlife populations in road environments may come down to a trade-off between preventing extinction of threatened species at local extents or trying to prevent population level depletion of common species over larger spatial scales. Evidence for landscape extent reductions in persistence of common species will help determine the amount of effort invested in the latter.

Common wombats as a representative common, wide ranging species

An example of a common species is the common wombat (*Vombatus ursinus*) (Fig. 1). The common wombat is a thickset herbivorous marsupial endemic to temperate Australia. Adults can be more than 1 m in length and weigh between 35-40 kg (McIlroy 1995). Common wombats are generally solitary above ground and are primarily nocturnal, with home range size between 5 and 25 hectares largely dependent on habitat quality (Skerratt et al. 2004a). During the day time they occupy a series of burrows and have been observed to use up to 11 burrows over several months (McIlroy 1973). They

exhibit female biased dispersal, with females thought to disperse into new territories to leave offspring their territory (Banks et al. 2002b). Wombats are protected in all Australian states in which they occur (New South Wales, Victoria, Queensland, Tasmania, South Australia and the Australian Capital Territory), although they remain unprotected in 193 counties in eastern Victoria where they are still regarded as vermin (Triggs 1988).



Figure 1. Common wombats are a large burrowing marsupial endemic to Australia.

Common wombats are both widespread and abundant throughout south-eastern Australia (Fig. 2), however their range reduction is quite broadly described, with no quantitative data detailing where populations exist (Roger et al. 2007). There is some evidence that their distribution has declined in recent years (McIlroy 1995; Buchan and Goldney 1998) but little information detailing over what scale the decline has been observed. Wombats are able to exploit such a large area and varying environments largely because of their low energy requirements and correspondingly low food and water requirements (Evans 2008). Because of their broad niche, common wombats are

thought to be a robust and adaptable species, particularly in human-modified environments (Roger et al. 2007; Roger and Ramp 2009).

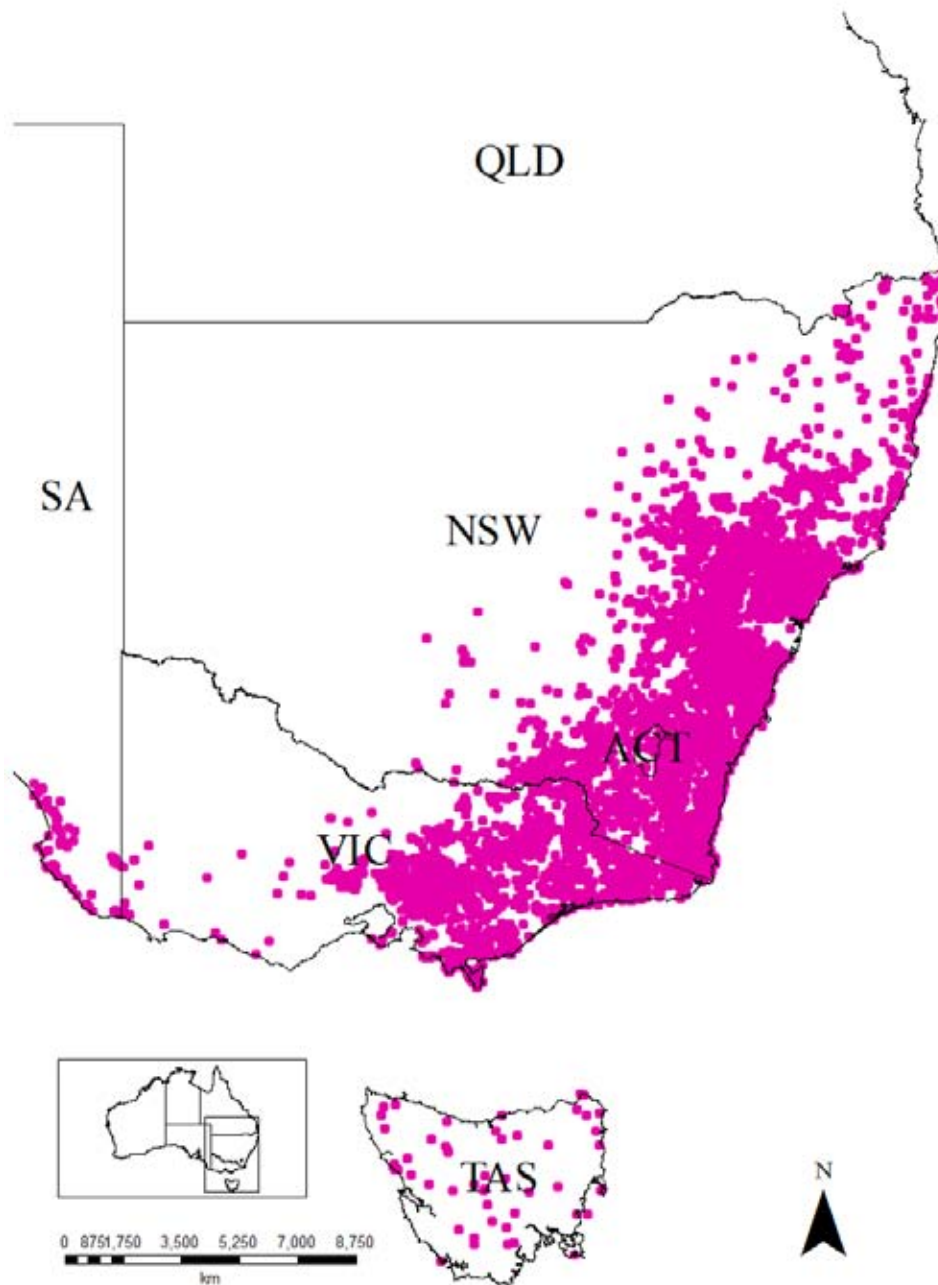


Figure 2. Distribution of the common wombat throughout south-eastern Australia derived from Atlas data. They are found within Queensland (QLD), New South Wales (NSW), Australian Capital Territory (ACT), Victoria (VIC), South Australia (SA) and Tasmania (TAS).

Factors affecting common wombat abundance

Very little research has investigated the complexity of issues surrounding wombats and roads, and what has been recorded has been mainly subjective. Triggs (1988) observed that even after a road has been established wombats will continue to cross it as though it is another open space in the forest, often utilising the roadsides to graze. Brown (2001) found that the locations of wombat road fatalities were not evenly distributed along a road, rather distinct clumping of fatalities was observed. This suggests that wombats use regular crossing points and that predictive models may be useful, particularly those which incorporate habitat use.

When modelling wombat fatality hotspots, Ramp et al. (2005) found that the southern oscillation index, distance to water, and elevation were negatively associated with wombat fatalities; slope, sinuosity, and distance to town were positively associated with fatalities (Ramp et al. 2005). Sinuosity contributed the most explanation to the predictive model. This suggests that the often cited indifference of wombats to oncoming vehicles may indeed make them more susceptible to collisions when drivers do not have as much vision of the road ahead and have less time to take appropriate action to prevent the collision.

Catling and Burt (1995), through observation, link the susceptibility of a wombat to vehicle collisions with severe infection of sarcoptic mange. Sarcoptic mange is prevalent in common wombat populations throughout Australia (Skerratt 2001) and is caused by a parasitic mite of the skin (*Sarcoptes scabiei*). Wombats that are severely infected with sarcoptic mange change their behaviour from nocturnal to diurnal and may lose their sight and hearing (Skerratt et al. 2004b) (Fig. 3). Animals are also likely to be in poor body condition as the infected individuals have higher energy requirements (Skerratt et al. 2004b). Skerratt (2001; 2004b) identified factors that increase the risk of

wombats being severely affected by mange. Factors included high densities of wombats, poor or limited habitat quality and the spread of the disease through burrow sharing by foxes.



Figure 3. Female and joey affected with sarcoptic mange. Notice the severe hair loss and the thick crust around the eyes and ears of the joey.

There is considerable debate as to what percentage the common wombat contributes to the feral animal diet. In areas where predators have access to carrion, the proportion of the diet attributed to common wombats may be considerable. May and Norton (1996) suggest that roads may also facilitate the ingress of feral predators into areas thought not to be accessible to them. Corbett (1995) found that common wombats dominate the dingo's diet at higher altitudes in eastern Australia. Green and Osborne (1979) found the remains of common wombats in 2.7 % of fox scats above the winter snowline in New South Wales during the months of November and December. In all other months of the study remains of the common wombat were absent from fox scats.

There are a number of other factors that may affect common wombat abundance in an area. These include land clearing, intentional killing of 'pest' wombats and unintentional poisoning of wombats through feral baiting. Wildfire, floods and drought can also affect common wombat abundance (Triggs 1988).

Study Area

With the exception of chapter five which covers the state of New South Wales, all research was conducted within the region surrounding Kosciuszko National Park (Fig. 4). Kosciuszko National Park is the largest National Park in New South Wales and covers approximately 6980 km² and is nationally recognized as a UNESCO Biosphere reserve (Scherrer and Pickering 2005). Located in the south-eastern corner of the Australian mainland between latitudes (35° 20' S and 37° 02' S) and longitudes (138° 50' E and 148° 02' E), the National Park includes a wide diversity of habitats, including alpine and wilderness areas (Scherrer and Pickering 2005). There are a total of 10 major road corridors within the National Park with a total length of 380 km. Most visitors to the National Park utilize roads within this zone (DECC DECC 2009).



Figure 4. Location map and study area showing the study section of the Snowy Mountains Highway between the townships of Tumut and Talbingo, within Kosciuszko National Park south-western New South Wales, Australia.

The area within the park surveyed for this study is in proximity to the townships of Tumut (35° 19' S, 148° 14' E) and Talbingo (35° 34' S, 148° 18' E). This area includes a 40 km segment of the Snowy Mountains Highway that partitions the study site into east and west sections. The western side of the highway is dominated by the Blowering Reservoir which sits at the base of the Snubba Range. The topography of the site consists of low undulating rolling hills with moderate relief ranging from 400 m at the reservoir foreshore to 600 m at the peaks of the hills to the east (Dehaan et al. 2007) (Fig. 5).



Figure 5. The area is bound in the west by the Blowering Reservoir while the east is characterised by grassy south-west facing slopes of pasture and remnant native forest. The Snowy Mountains Highway runs through the site fragmenting the foreshore area from the slopes.

Flora

The study area is dominated by cleared land, moist and dry forest. Most of the pre-European dry sclerophyll forest along the Blowering Foreshore has been cleared for grazing with only small, isolated patches remaining. Cleared land is dominated by grasses and include: kangaroo grass (*Themeda australis*), plume grass (*Erianthus ravennae*), and red leg grass (*Bothriochloa macra*). Blackberry (*rubus fruticosus*) is also common and occurs as patches up to 4 m high along gullies and at the edge of roads and woodlands (Dehaan et al. 2007). The wooded areas of the study area generally consist of dry sclerophyll forest composed of blackwood (*Acacia melanoxylon*), kangaroo apple (*Solanum aviculare*) and silver banksia (*Banksia marginata*).

Fauna

The area supports a diverse range of fauna from many taxonomic groups. Large mammals include four species from the family Macropodidae: the common wallaroo (*Macropus robustus*), red-necked wallaby (*Macropus rufogriseus*), eastern grey kangaroos (*Macropus giganteus*) and the swamp wallaby (*Wallabia bicolor*). Other mammals include: the common wombat (*Vombatus ursinus*), short-beaked echidna (*Tachyglossus aculeatus*) and the common brushtail possum (*Trichosurus vulpecula*) (Jaremovic and Croft 1991; Lindenmayer et al. 1999; Roger et al. 2007). Smaller mammal species are well represented and include the house mouse (*Mus musculus*) and feathertail glider (*Acrobates pygmaeus*). By far the most numerous are the avifauna and include: the wedge tailed eagle (*Aquila audax*), galah (*Eolophus roseicapilla*), emu (*Dromaius novaehollandiae*), crimson rosella (*Platycercus elegans*), superb fairy wren (*Malurus cyaneus*), and the kookaburra (*Dacelo novaeguineae*) (DECC DECC 2009).

There are several introduced species within the study area. These include pigs (*Sus scrofa*), dingos/wild dogs (*Canis lupus*), red foxes (*Vulpes vulpes*), cats (*Felis catus*) and rabbits (*Oryctolagus cuniculus*) (Dehaan et al. 2007). Eradication programs are employed to control the numbers of some introduced species, namely trapping and shooting of pigs, 1080 baiting of wild dogs and foxes, and endemic infection of rabbits with calicivirus.

Climate

The climate is temperate, with mean monthly rainfall from 46-104 mm and mean annual total rainfall from 782-1250 mm. Daytime temperatures in summer generally exceed 25°C. Night time temperatures in summer are mild with a mean of approximately 10°C. During winter, daytime conditions are mild, reaching a mean of 13°C, while night time conditions are relatively cool, averaging around 2°C (Fig. 6). The mean annual temperature ranges from 11.2-14.4 degrees Celsius (Australian Bureau of Meteorology records for Tumut Plains).

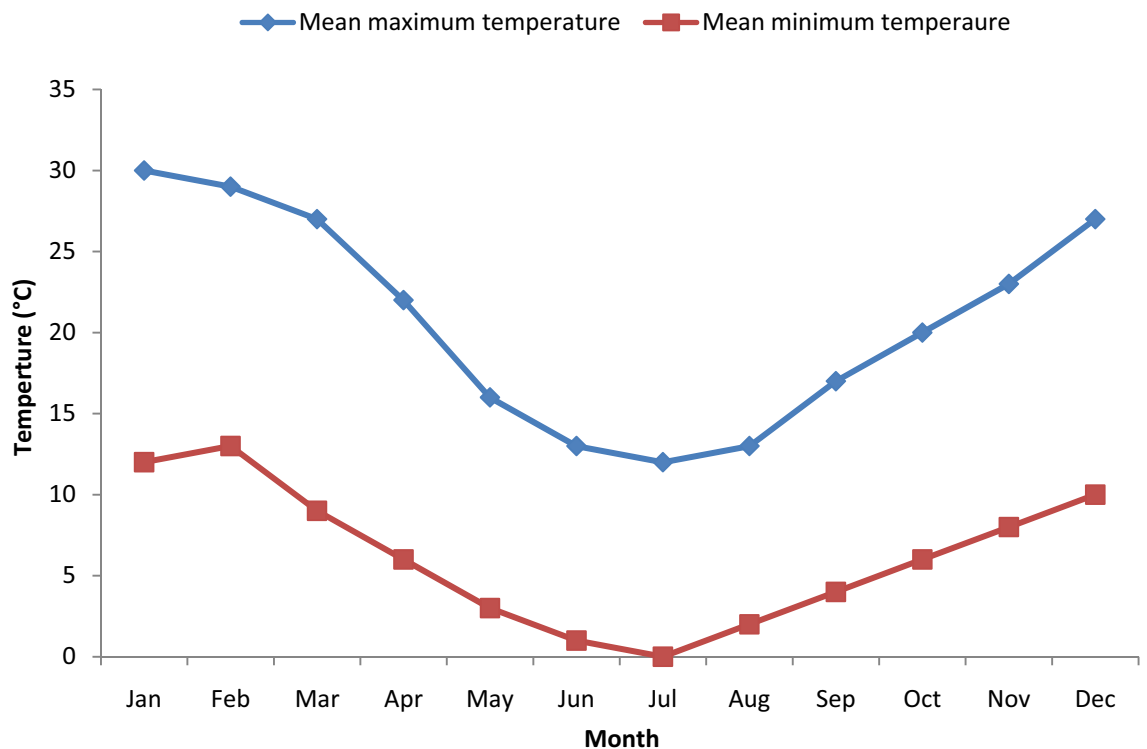


Figure 6. Mean temperature for Tumut, NSW (January 1990 to January 2008) (Australian Bureau of Meteorology records for Tumut Plains).

Research Approach

The research approach that was undertaken is outlined in the following pages. It was designed to approach several of the ecological topics discussed above and illustrate that road impacts can affect populations at multiple spatial scales and that commonness is not necessarily a barrier to localised extinction risk. Specific details are contained within each chapter's introduction.

Chapter 2 is a habitat suitability model for a local population of common wombats, and uses burrow location as the basis for ecological modelling. The objective was to identify landscape features that may be used to predict the presence of wombats. Findings challenge the perception that wombats are common and not in need of monitoring and suggests their adaptation to modified landscapes comes at a considerable cost. The work has been published in *Biological Conservation*.

Chapter 3 incorporates habitat use of common wombats in predictive modelling of five years of fatality locations. The objective was to provide an example of the benefits of incorporating spatially-explicit information of habitat use in the modelling of animal-vehicle collisions. The final predictive model had high discriminatory power and highlights the importance of incorporating variables which describe habitat use by fauna for improved predictive modelling. This work has been published in *Diversity and Distributions*.

Chapter 4 is a common wombat population viability analysis within a 750 km² area. The objective was to explore the impact of various threats on wombat population persistence. Estimates of current threatening processes suggest a rapid decline in populations adjacent to roads. Results highlight the importance of thinking about road impacts in conjunction with other threats. This work has been accepted to *Population Ecology*.

Chapter 5 quantifies common wombat habitat use at large spatial scales. The objectives were to investigate how roads affect the persistence of common species over large spatial extents and evaluate how effective reserves are at enhancing resilience. This chapter emphasizes the need for increased effort to be expended in evaluating how reserves confer resilience to species from the impacts of roads. This work has been submitted to *Landscape Ecology*

Chapter 6 summarises the main findings of the research presented in this thesis, the implications of this research, and suggests potential avenues for future research.

Chapter 2

Habitat selection by the common wombat (*Vombatus ursinus*) in disturbed environments: implications for the conservation of a common species

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Key words: Habitat suitability, Modelling, Spatial analysis, Road-kill, Common species, *Vombatus ursinus*

ABSTRACT: The construction of habitat models is a repeatable technique for describing and mapping species distributions, the utility of which lies in enabling management to predict where a species is likely to occur within a landscape. Typically, habitat models have been used to establish habitat requirements for threatened species; however they have equal applicability for modelling local populations of common species. Often, few data exist on local populations of common species, and issues of abundance and habitat selection at varying scales are rarely addressed. We provide a habitat suitability model for the common wombat (*Vombatus ursinus*) in southern New South Wales. This species is currently perceived as abundant throughout its extensive range across temperate regions of eastern Australia, yet little factual survey data exist and populations appear under threat. We use wombat burrows to reflect habitat selection and as our basis for ecological modelling. We found that environmental variables representing proximity to cover, measures of vegetation and proximity to watercourses are important predictors of burrow presence. Extrapolation of habitat models identified an abundance of habitat suitable for burrows. However, burrows in many suitable areas were abandoned. Our estimate of the population size was similar to the total annual mortality associated with road-kill. Theoretically, given the availability of suitable habitat, common wombat populations in the region should be thriving. It seems likely that this area once supported a much higher number of wombats; however limiting factors such as road mortality and disease have reduced the populations. The persistence of wombats in the study region must be supported by migration from other populations. Our findings challenge the perception that wombats are currently common and not in need of monitoring, suggesting that perceptions of abundance are often clouded by socio-political motives rather than informed by biological and ecological factors.

1. Introduction

Human mediated disturbance represents the most profound change to landscapes around the world, yet the ecological consequences for many species are not well understood. As human disturbance continues to degrade and fragment ecosystems, conservation biology must increasingly aim to identify and preserve suitable habitat needed to sustain species (Foley et al. 2005; Wilson et al. 2005). Habitat models are often utilised to achieve this, and can provide managers with the ability to predict where a species is likely to occur within a landscape (Warren et al. 2005; Dayton and Fitzgerald 2006; Rotenberry et al. 2006). Typically, habitat models have been used to establish habitat requirements for rare or threatened species (Reading et al. 1996; Ben Wu and Smeins 2000; Gibson et al. 2004; Santos et al. 2006; Seoane et al. 2006). Threatened species warrant this attention due to the more immediate risk of loss of diversity (Soulé et al. 2005); however it is also important to preserve local biodiversity, including local populations of common species, that may become threatened in the near future.

Species are generally perceived as common if they have extensive ranges and are abundant, although it is often hard to establish accurate assessments of abundance. Often, few data exist on local populations of common species, and issues of abundance at varying scales are rarely addressed. In the absence of monitoring, managers are only able to be reactive to decline, rather than proactively preventing decline. Recent evidence suggests that even common species can become susceptible to localised population extinction. Ramp and Ben-Ami (2006) found that the long term viability of a population of the common swamp wallaby (*Wallabia bicolor*) was in steady decline from the threat of roads, competition by rusa deer (*Cervus timorensis*) and predation by red foxes (*Vulpes vulpes*). There have been documented regional declines of once prevalent common herbs (*Trillium camschatcense*) (Tomimatsu and Ohara 2006) and

local declines of widespread vertebrate species like the ubiquitous northern dusky salamander (*Desmognathus fuscus fuscus*) (Bank et al. 2006), as well as more historic examples like the near extinction of the American Bison (*Bison bison*) and the extinction of the passenger pigeon (*Ectopistes migratorius*), both of which occurred virtually simultaneously (Farrow 1995).

In Australia, an example of a common species where few data exist is the common wombat (*Vombatus ursinus*). Included in the suborder Vombatiformes, wombat ancestors were once a diverse and dominant group with diversity peaking during the late Pliocene and Pleistocene, with many forms larger than the current extant species (Woolnough and Steele 2001). However, five of the seven known families within this suborder are now extinct; with only the koala (*Phascolarctos cinereus*) and three species of wombat surviving. Of the three species, the southern hairy-nosed wombat (*Lasiorhinus latifrons*) is restricted to fairly small fragmented areas, and listed as vulnerable, the northern hairy-nosed wombat (*L. krefftii*) is listed as critically endangered, with only the common wombat typically perceived as common and wide ranging. Yet, despite the perception of commonness driven by its extensive range, there is evidence that its distribution has been reduced since European arrival, particularly in western Victoria, southern Queensland, and northern South Australia (Triggs 1988; McIlroy 1995; Buchan and Goldney 1998). This recognised range reduction, however, is quite broadly described, with no real data detailing where local populations exist, over what scale the decline has been observed, or what factors have contributed to their decline.

The contraction of common wombat populations from former ranges does suggest that a number of factors may be affecting common wombat abundance at a local population level. Most evident are the numerous wombat fatalities from collisions with

vehicles on highways (Ramp et al. 2005). Sarcoptic mange, caused by a parasitic mite of the skin (*Sarcoptes scabiei*), has been identified as the most significant infectious disease affecting the common wombat (Hartley and English 2005). It is thought to limit the activity of mature wombat gonads, thus affecting wombat reproduction (Skerratt et al. 1999), and is in most cases fatal. Feral animals such as wild dogs and foxes have also been shown to prey on common wombats (Newsome et al. 1983; Corbett 1995; Banks 1997). Licenses are also issued by state agencies permitting wombat destruction on the grounds of them being nuisance animals, with claimants stating undue property damage.

In the present study we used wombat burrows to reflect habitat selection and as our basis for ecological modelling. Using burrow location data, three sets of habitat models were constructed: a) a habitat suitability model based on the presence-absence of burrows in the landscape; b) a habitat suitability model based on the Getis-Ord G_i^* spatial hotspot clustering statistic and; c) a model of the likelihood of a burrow being occupied or abandoned. The central aims of this study were (1) to assess factors that were important for predicting burrow presence, clustering and occupation and (2) to evaluate the areas within the study area of prime habitat for the species. The common wombat was used as a model species because they have been positively associated with varying habitats (Mallett and Cooke 1986; Rishworth et al. 1995; Skerratt et al. 2004a), suggesting great adaptability and widespread abundance. However, given the advent of several threatening processes that reduce local population numbers, we do not have a clear idea of how large a local population is required to be sustainable, or how individuals are connected throughout the broader landscape. Importantly, we are lacking information as to what landscape features and at what scales of influence may be used to predict the presence of wombats, so that accurate monitoring of populations can begin. To address this, our habitat modelling approach accounts for multiple scales, by

using both landscape-extent and site-extent variables as predictors in our modelling. Habitat modelling will assist with understanding the ecology and requirements of local populations, and indeed the population throughout its range.

In an effort to evaluate our habitat models for this species, the following hypotheses were tested: (1) high habitat suitability is not necessarily indicative of healthy local population numbers; and (2) perceived benefits from living in proximity to humans may result in reduced annual survival and population sustainability.

2. Methods

2.1 Study area

The study was conducted on the Blowering Reservoir foreshores between the townships of Tumut (35°19'S, 148°14'E) and Talbingo (35°34'S, 148°18'E) in Kosciuszko National Park, southern New South Wales, Australia (Fig. 1). The area is bound in the west by the Blowering Reservoir while the east is characterised by grassy south-west facing slopes of remnant pasture and native forest. The Snowy Mountains Highway runs North-South through the site, fragmenting the foreshore area from the slopes. The study area is dominated by cleared land, moist and dry forest, blackberry thickets (*Rubus fruticosus*), patches of bracken fern (*Pteridium esculentum*) and briar bushes (*Rosa rubiginosa*). Hill slopes are dominated by shrubs (*Leptospermum* spp.) and patches of trees (*Eucalyptus* spp.). Introduced grass species are widespread; mostly perennial ryegrass (*Lolium perenne*) and paspalum (*Paspalum dilatatum*). Native grasses such as kangaroo grass (*Themeda australis*) and tussock grass (*Poa* spp.) are also present (Jaremovic and Croft 1991). The area has a temperate climate, with cool wet winters and warm summers, and an average yearly rainfall of 900 mm (Australian Bureau of Meteorology records for Tumut Plains). Common wombats share the open pasture

grazing sites with native and introduced herbivores; namely kangaroos (*Macropus giganteus*), swamp wallabies (*Wallabia bicolor*), emus (*Dromaius novaehollandiae*) and rabbits (*Oryctolagus cuniculus*). The site is representative of many sites across the range of the common wombat, where there is a mix of native forest, human land-use areas, and a multitude of threats. Recognised threats in the region include disease, road mortality, shooting, and predation.

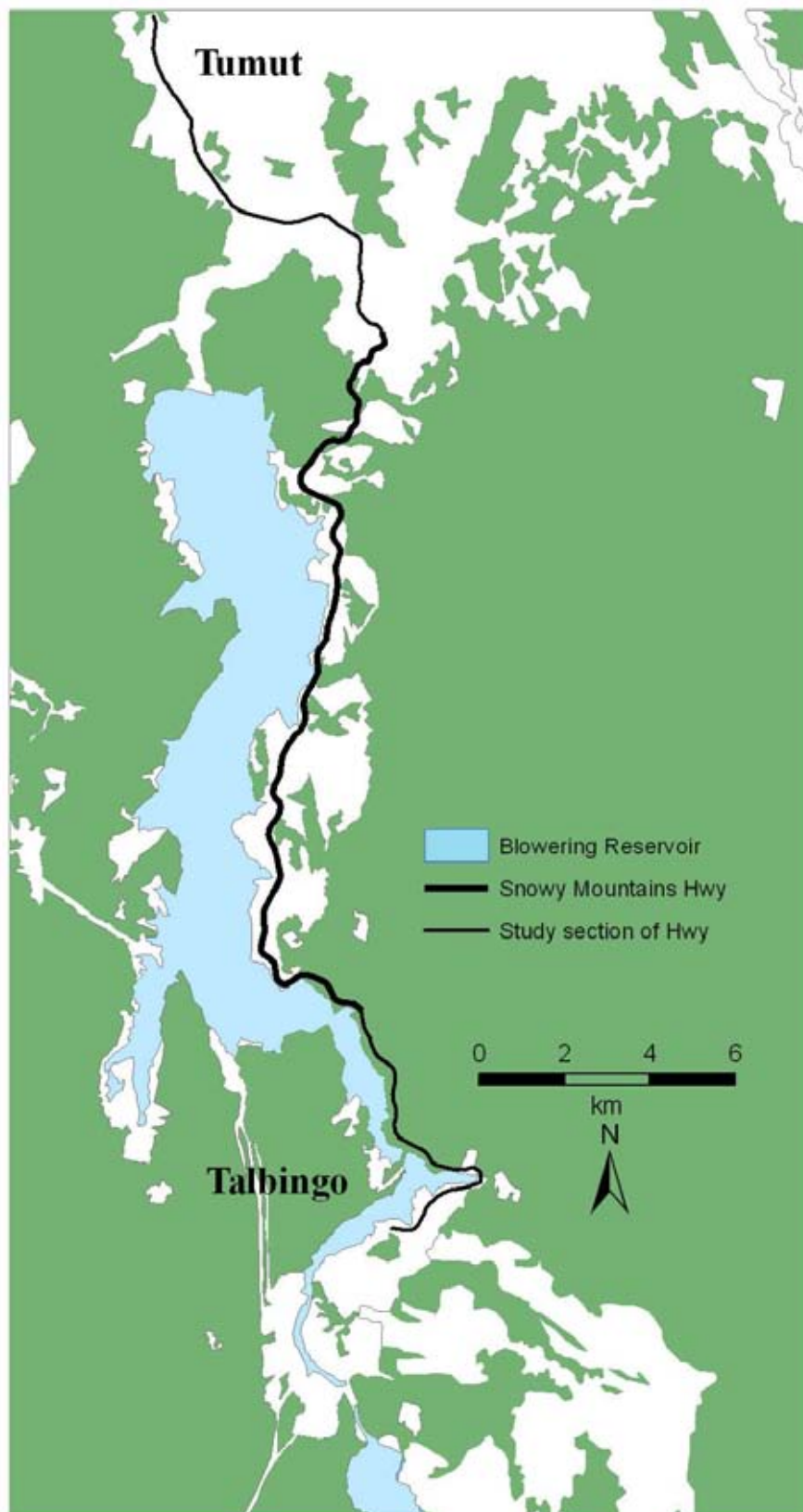


Figure 1. The study area is along the Snowy Mountains Highway, adjacent to Blowering Reservoir. White areas are cleared, green areas are forested.

2.2 Burrow location as presence data

To address the problem of reliability of presence-absence data, we used wombat burrows as a reflection of common wombat habitat selection, rather than species sighting records. An equal number of randomly generated points were used as absences. Burrow location has been shown to represent site selection in other species such as the muskrat (*Ondatra zibethicus*) (Nadeau et al. 1995). Similarly, variations of wombat density have been shown to correlate with the placement of the burrow within a landscape (Downes et al. 1997), presumably because wombats strongly associate burrow construction in relation to physiographic features of the landscape. Rishworth et al. (1995) found a linear relationship existed between the number of burrows present in an area and the mean number of wombats. Wintle et al. (2005a) suggest that presence-absence models are effective, but caution that they often succumb to false negative observation errors in species surveys. The problematic nature of using random absence locations in conjunction with species' sightings has been documented in studies by Ferrier et al. (2002), Elith et al. (2006), and Olivier and Wotherspoon (2006). Because the entire study site was surveyed to the best of our capacity, we were able to be reasonably confident of non-burrow locations when assigning random absences across the area. By choosing to model a fixed location, we were able to ascertain where wombats were actively choosing to construct burrows, and where they were not.

2.3 Data collection

Burrow surveys were conducted daily in June and July 2005 by systematically surveying the entire study area on foot, following Rishworth et al., (1995). East-west aligned transects were traversed by four observers spaced lengthwise 15 to 30 meters apart (depending on visibility due to terrain). Each transect ran from the border of the

reservoir in an easterly direction for an average distance of 1600 m, such that the end points were all latitudinally aligned. Approximately 120 transects per observer were traversed in total, to cover an area of 30 km². Detectability of wombat burrows was shown to be accurate (1 burrow missed for every 30 detected) in subsequent burrow surveys employing a double sampling approach (Pollock et al. 2002) to determine detection probability (E. Roger, unpublished data). Burrow locations were recorded using a global positioning system (GPS) and scored as either abandoned or occupied based on the criteria for major burrows described by McIlroy (1973). Maximum height and width of burrow entrances were measured. Entrance areas greater than 2100 cm² were scored as occupied, while visible signs of occupation such as tracks and presence of scat were also used. When in doubt, small sticks were placed across burrow entrances and checked the following morning for signs of displacement.

2.4 Burrow location model development

2.4.1 Dependent variables

Burrow locations (both occupied and abandoned) were compiled using ArcGIS (ESRI 2007) (Environmental Systems Research Institute, 2006). An equal number of absence points were randomly generated within the entire study area using the Hawth's Analysis Tools add-on for ArcGIS (Beyer 2004). A total of 756 presence-absence data points were used in the analysis.

To identify hotspots of wombat burrows within the landscape, presence-absence points were analysed using the Getis-Ord G_i^* spatial cluster statistic (Getis and Ord 1992; Ord and Getis 1995; Getis and Ord 1996). The G_i^* statistic can detect spatially local clusters that exist despite negative tests for global spatial autocorrelation (Swenson and Howard 2005). It measures the degree of spatial clustering of a local sample based

on how different it is from the mean of the data set (the expected value), expressed as a Z-score. Positive cluster values indicate a local cluster of data values above the mean, while negative cluster values represent a cluster of data values below the mean. In our case, a positive G_i^* value represents a cluster of burrows, while a negative G_i^* value represents a non-burrow area. The extent to which a G_i^* value is greater or less than the mean represents the strength of the spatial clustering in the sample, with values greater in magnitude than ± 2 being significant at approximately the 95% level. The G_i^* statistic was calculated after Laffan (Laffan 2006), using circular radii from 125 m to 12,500 m at 125 m increments, aggregated into a single layer using the radius with the greatest magnitude.

2.4.2 Predictor variables

Potential predictor variables at each burrow location were based on published findings (McIlroy 1973; Catling and Burt 1995; Buchan and Goldney 1998; Walker et al. 2007) but inclusion depended on availability as GIS data layers. Blackberry (*Rubus fruticosus*) was chosen as a predictor variable, as a result of our field observations and those of Triggs (1988). Site-level predictor variables used included: distance to drainage lines (the Blowering Reservoir was not included in the analysis), forest cover and distance to blackberry bush, while landscape-level predictors were: slope, normalised difference vegetation index and hillshade. All environmental variables were stored as raster layers within ArcGIS with a resolution of 25 m.

A raster layer of slope (degrees) was derived from a 25 m resolution Digital Elevation Model (DEM). A hillshade raster, generated within ArcGIS, was used to provide a proxy for relative radiation load. It provides an alternative to aspect, as circular variables like aspect do not behave well in correlative studies (Beers et al.

1966). Raster layers of distance from burrow to the nearest watercourse (m) and the nearest blackberry bush (m) were generated using the Euclidian distance function in ArcGIS Spatial Analyst.

Vegetation community data (Ramp et al. 2005) were derived from 30 m LANDSAT data and used to calculate the proportion of forest cover surrounding each burrow. A circular sampling area based on the average home range of common wombat (Skerratt et al. 2004a) was generated assuming the radius of a circle was equal to the diameter (320 m) of an average reported home range for wombats. The area covered by all forest communities in the study area (moist forest, disturbed forest, severely disturbed forest, moist forest tending to dry and dry forest) was aggregated into a proportion of area covered by forest (following Ramp et al. 2005).

A normalised difference vegetation index (NDVI) image was calculated using an ASTER (advanced spaceborne thermal emission and reflection radiometer) image (15 m resolution, acquired 26 Dec 2000) to provide an index of vegetation greenness within the study area. NDVI was calculated as $(\text{NIR}-\text{VIS})/(\text{NIR}+\text{VIS})$, where NIR is the near infrared light reflected by the vegetation and VIS the visible light reflected by the vegetation (Pettorelli et al. 2006). Negative NDVI values correspond to an absence of vegetation, while higher positive values are associated with greater density and greenness of the plant canopy (Justice et al., 1985). The NDVI values were then converted into a habitat complexity index (NDVI-SD) by taking the standard deviation of values within a 200 m radius. This used the focal statistics within ArcGIS, in the process resampling the ASTER 15 m cell sizes to conform to the 25 m used for the remainder of the data. In the NDVI-SD index, one will obtain higher values for mixed forest and grassland, and lower values for pure forest and grassland.

2.4.4 Burrow location

Burrow location was modelled using binary logistic regression using both occupied and abandoned burrows as presences and randomly generated locations as absences, while burrow hotspots were modelled using Gaussian logistic regression using G_i^* values and associated predictor variables at each location. Generalized Additive Models (GAMs) were constructed for each possible combination of predictors in R (R Development Core Team 2005). Model selection was conducted using bootstrapping and the .632 estimator rule which has been shown to be appropriate when the underlying parameter distributions are unknown (Hastie et al. 2001). Bootstrapping involves resampling the modelling data while the .632 rule pulls the leave-one-out bootstrap estimate down towards the training error rate and therefore reduces upward bias (Rajvong 2005). Bootstrapping has been shown to outperform cross-validation, particularly using the .632 rule (Efron 1983; Efron and Tibshirani 1997), and provides a predictive performance estimate of a model without the expense of collecting a completely new model-testing set (Wintle et al. 2005a). All predictor variables were checked for collinearity. In order to evaluate model performance, two loss functions were employed: misclassification error rate and deviance (only the deviance loss function was used to evaluate model performance for the burrow hotspot model). Loss functions assess the discrimination performance of habitat models derived using regression. Use of the misclassification error rate requires a threshold value to classify the predicted probability as presence or absence. Rather than choosing an arbitrary threshold, a Receiver Operating Characteristic (ROC) curve was used to find the threshold that best discriminates between the sensitivity (probability that a burrow is correctly predicted) and 1 minus specificity (a false positive prediction) (Ferrier et al. 2002).

Following Ramp et al. (2005), final models were obtained by comparing all models subsets for the six predictors and employing the “one standard error rule” to select the best model set. The one standard error rule is often used to find a more parsimonious model than the one with the smallest error rate (Hastie et al. 2001). For the deviance loss function, the deviance per observation was calculated rather than deviance so that it was comparable across different methods. Final model selection was based on comparing the best models (within both loss function groups) that contained the fewest numbers of predictor variables without compromising the predictive capability of the model.

Hierarchical Partitioning was used to lend additional support to the model selection process (Mac Nally 2000; Brambilla et al. 2006). A goodness of fit measure for the entire hierarchy of models using all combinations of predictor variables was calculated using maximum likelihood. The contribution of each predictor to variability in the full model was identified and compared to results from the bootstrapping process.

The relationship between each predictor and the dependent variable was assessed to choose the appropriate degrees of freedom in the model based on ecological validity. Plausibility of response shapes was used to discern the relationship between variables and relationships were either retained as linear or splined with 2, 3, or 4 degrees of freedom.

Prediction values (one for every 100 x 100 m grid cell in the study area) were generated in R. The prediction values with the matching GIS coordinates were then imported into ArcGIS to create a habitat map.

2.5 Burrow occupation

Burrow occupation was modelled using occupied burrows as presences and abandoned burrows as absences. The predictor variables used in the burrow location models were used as well as the site- specific variable, distance to road (m) generated using the Euclidian distance function in ArcGIS Spatial Analyst. Distance to road was chosen as a discriminating variable important for predicting occupied burrows, rather than habitat suitability. Model selection was conducted as described for burrow location.

Table 1.

Model results for habitat suitability. Table presents the number of models within 1SE of the best model and the proportion of models containing the variable within 1SE of the best model for each criterion.

Model	Loss Function	Total # Models	B	F	S	RIV	H	N	Median # variables
Presence-absence	Misclassification error Rate	27	0.66	0.59	0.66	0.55	0.52	0.90	4
	Deviance	57	0.53	0.53	0.53	0.50	0.50	0.53	4
Getis-Ord	Deviance	15	1.00	0.53	0.53	0.53	0.53	1.00	4

Table presents the number of models within 1SE of the best model and the proportion of models containing the variable within 1SE of the best model for each criterion.

Symbols for predictor variables occurring in the model set are distance to blackberry (B), percent forest cover (F), slope (S), distance to river (RIV), normalised difference vegetation index (N), and hillshade (H).

3. Results

3.1 Burrow location

A total of 81 occupied and 297 abandoned burrows were identified in the burrow surveys. Based on previous studies this reflects a total population size in the area ranging from 20 to 40 individuals (McIlroy 1973; Rishworth et al. 1995; Skerratt et al. 2004a). Strong variation of wombat burrow density was found. Burrows were not evenly distributed throughout the landscape, but were clearly clumped. Based on 95%

confidence intervals, occupied burrows were located a mean distance of 409 m from the road (± 55), while abandoned burrows were on average, slightly closer, at a distance of 373 m (± 29) from the road.

The misclassification error rate and deviance loss functions identified 27 and 57 models respectively within one standard error of the best model (Table 1). Discrimination among predictors using the deviance loss function was relatively poor compared to misclassification error. NDVI-SD was selected in 90% of models in the best model set using misclassification error, while hillshade was the least frequent selected predictor at 52%. Although slope was selected in 66% of models using misclassification error, the inclusion of slope contributed very little to the explained variance (Table 2). Aside from slope, there was good agreement among the three methods of model selection on the final model of NDVI-SD, distance to blackberries, the proportion of forest cover and distance to the nearest watercourse.

The final model explained 28.7% of the deviance (Table 3). The probability of a burrow being located in a 25 m cell was negatively associated with distance from blackberries and watercourses (Fig. 2). The probability of burrow presence was greatest when percent forest cover was around 50%, with probabilities declining either side of this mark. For NDVI-SD, the probability of a burrow increased in a linear fashion until NDVI-SD was around 0.1 and then levelled and declined slightly. Hierarchical partitioning indicated that distance to blackberries and NDVI-SD provided the most explanation. Areas scored as most likely to have a burrow were centred in patches of remnant pasture in the foreshore area in close proximity to the highway, while areas least likely to contain a burrow were at the extreme boundaries of the study region in dense native forest.

A habitat map is provided (Fig. 3) for predicted probability of burrow presence throughout the study area.

Table 2.

Variable coefficients, and Z-scores for the three models.

Model	Variable	Coefficient	Independent contribution	Chi-squared	P
Presence-Absence	Intercept	-0.6815			
	Blackberry	-0.0001	30.52		
	River	-0.0046	21.86		
	Ndvi	-0.3413	45.26	70.848	<0.001
	Forest	19.3662	2.34	16.575	<0.001
Getis-Ord	Intercept	3.7492			
	Blackberry	-0.6235	12.84	38.724	<0.001
	River	-0.0043	22.56	8.418	0.005
	Ndvi	-0.0127	56.88	105.296	<0.001
	Forest	-0.2736	1.02	14.010	<0.001
Burrow Occupation	Intercept	-1.4601			
	Forest	1.0838	19.35	3.678	0.055
	Ndvi	-8.4698	19.28	0.097	0.077
	Road	0.0012	24.74	0.001	0.020
	Blackberry	0.8614	26.93	0.004	0.036

Missing Chi-Squared and P values represent variables which were left linear. The independent contribution of each variable was determined through hierarchical partitioning is presented as a percentage of the total explained variance.

Table 3.

Deviance explained by the final model for all three model types using the complete data set.

Model	Final Model	Null	Residual	% Deviance Explained	AUC
Presence-absence	F, 2 + B + RIV + N, 2	1039.7 (df=749)	740.9 (df=742)	28.7	754.9
Burrow clustering	RIV, 1 + N, 2 + B, 2 + F, 2	9452.0 (df=754)	5952.2 (df=746)	37.0	3719.5
Burrow occupation	F, 2 + N, 1 + R, 1 + B, 1	391.3 (df=374)	364.5 (df=368)	14.6	376.6

Symbols for predictor variables occurring in model set are distance to blackberry bush (B), percent forest cover (F), distance to river (RIV), normalised difference vegetation index (N), and distance to road (R).

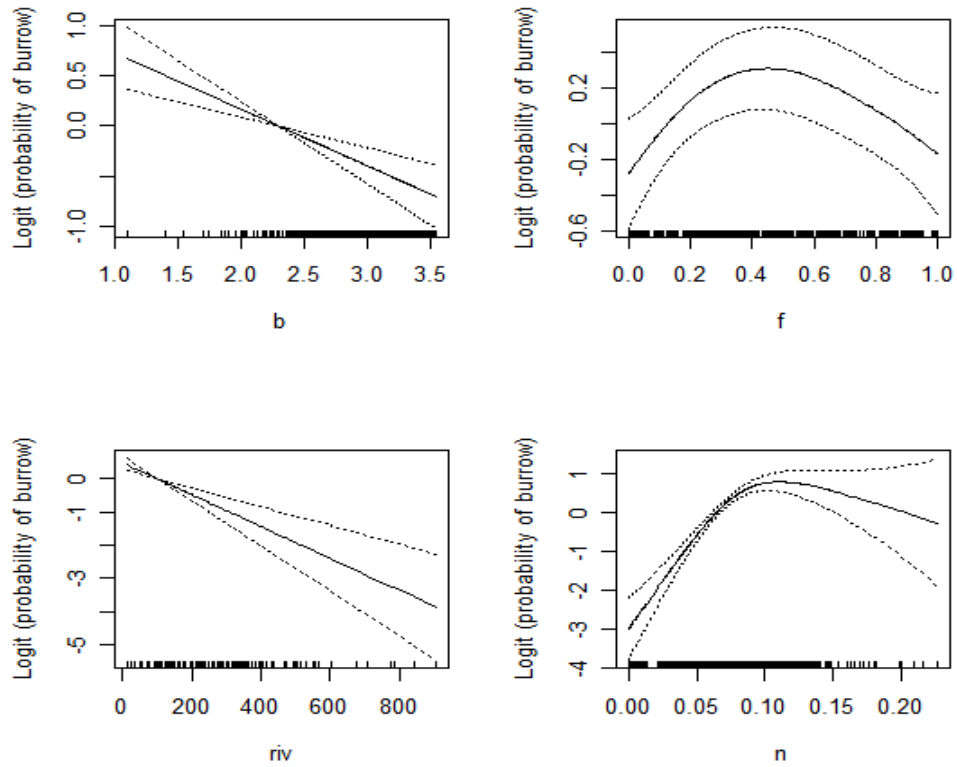


Figure 2. Partial plots of the relationship between the probability of a burrow and the predictor variables included in the final model. The X-axis represents the range of values for each environmental variable [(f) percent forest cover, (b) distance to blackberry, (riv) distance to river, and (n) normalized difference vegetation index]. Probabilities on the Y-axis are plotted in transformed ‘logit’ space, so that they can be interpreted in the same way as linear regressions. Dashed lines represent 95% confidence intervals around the fitted response shape.

3.2 *G-star statistic*

The G_i^* results indicate that there are distinct areas of strongly positive burrow clusters, as well areas with strongly negative burrow absences. Approximately 15% of all cells occur in strong positive (presence) clusters ($G_i^* > 2$), while approximately half of all cells occur in strong negative (absence) clusters ($G_i^* < -2$) (Fig. 4). There are also many spatially distinct, weakly positive ($0 < G_i^* < 2$) and weakly negative clusters ($0 > G_i^* > -2$). Generally, burrow clusters occur within close proximity to the eastern study boundary

and the Snowy Mountains Highway, while large absence clusters occupied the westerly extremes of the study area.

The deviance loss function identified 15 models within one standard error of the best model (Table 1). NDVI-SD and distance to blackberry bush were selected in 100% of models in the best model set, while the remaining four variables occurred at equal frequencies of 53%. The inclusion of distance to watercourse contributed significantly to the variance explained (Table 2). Aside from distance to watercourse, there was good agreement among methods of model selection on the final model of NDVI-SD, distance to blackberries, the proportion of forest cover and distance to the nearest watercourse.

The final model explained 37% of the deviance (Table 3). The probability of a positive burrow cluster being located in a 25 m cell was negatively associated with distance from watercourses (Fig. 5). The probability of a burrow cluster decreased with increasing distance from blackberry until a value of approximately 12 m was met, and then increased sharply, suggesting a positive relationship after a fixed distance. The probability of a burrow cluster was greatest when percent forest cover was around 50%, with probabilities declining either side of this mark. For NDVI-SD, the probability of a burrow increased linearly until the value was around 0.1 and then levelled and declined slightly.

3.3 Burrow occupation

The misclassification error rate identified 51 models within 1 standard error of the best model (Table 4). Discrimination using the deviance loss function was ineffective. Proportion of forest cover was selected in 78% of models and distance to road in 76% of models, while distance to creek was the least frequently selected predictor at 51%. The final model chosen contained the proportion of forest cover, distance to road, distance to blackberry, and NDVI-SD, explaining 15% of the deviance (Table 3). The

likelihood of a burrow being occupied was negatively associated with NDVI-SD, while the probability of an occupied burrow increased with increasing percent forest cover, with probabilities declining slightly at around 60%. The probability of an occupied burrow increased linearly with increasing distance from road, as did distance from blackberry (Fig. 6). Hierarchical partitioning indicated that distance from blackberry and distance to road were the most important explanatory variables (Table 2).

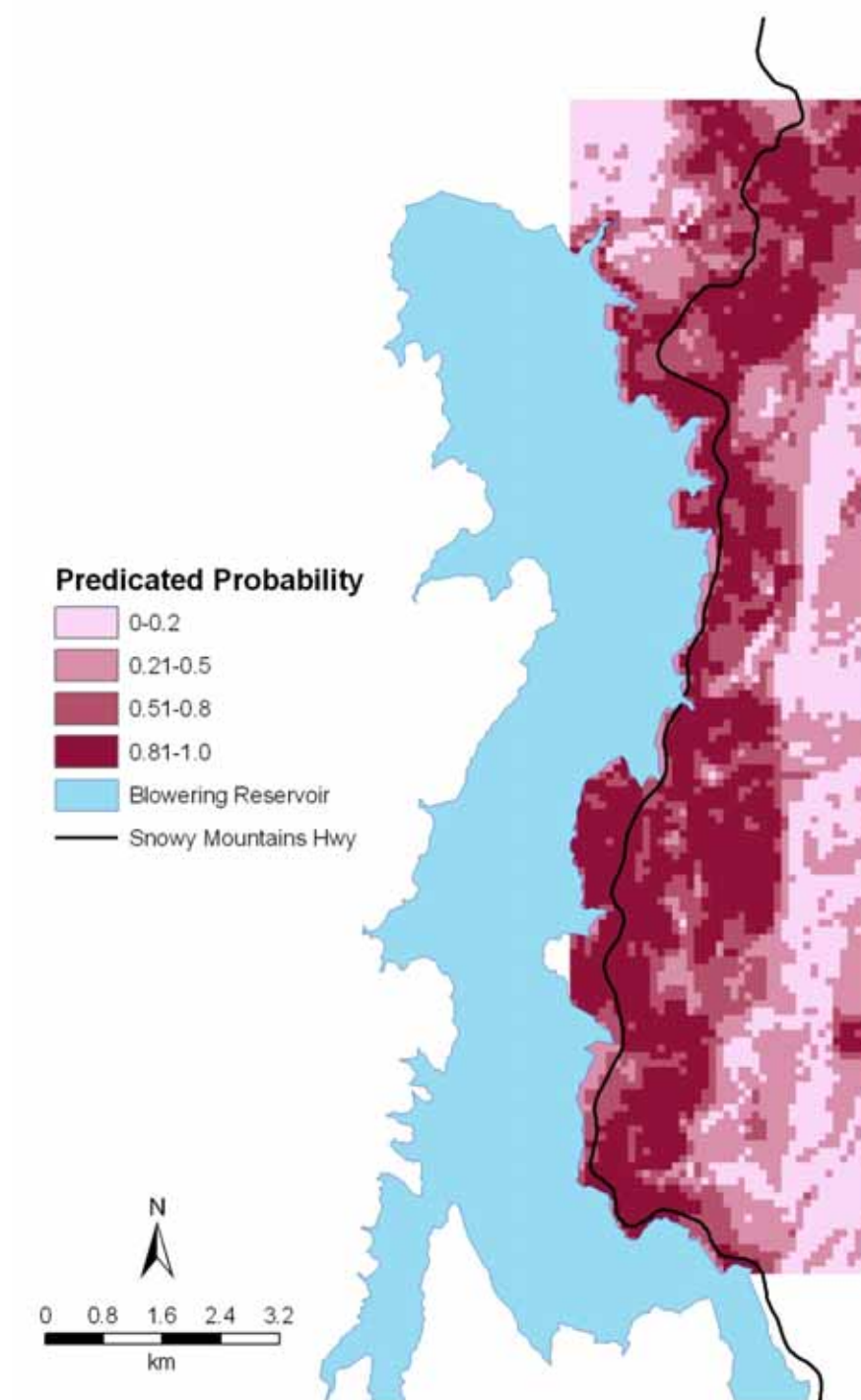


Figure 3. The predicted probability of wombat burrows across the study area.

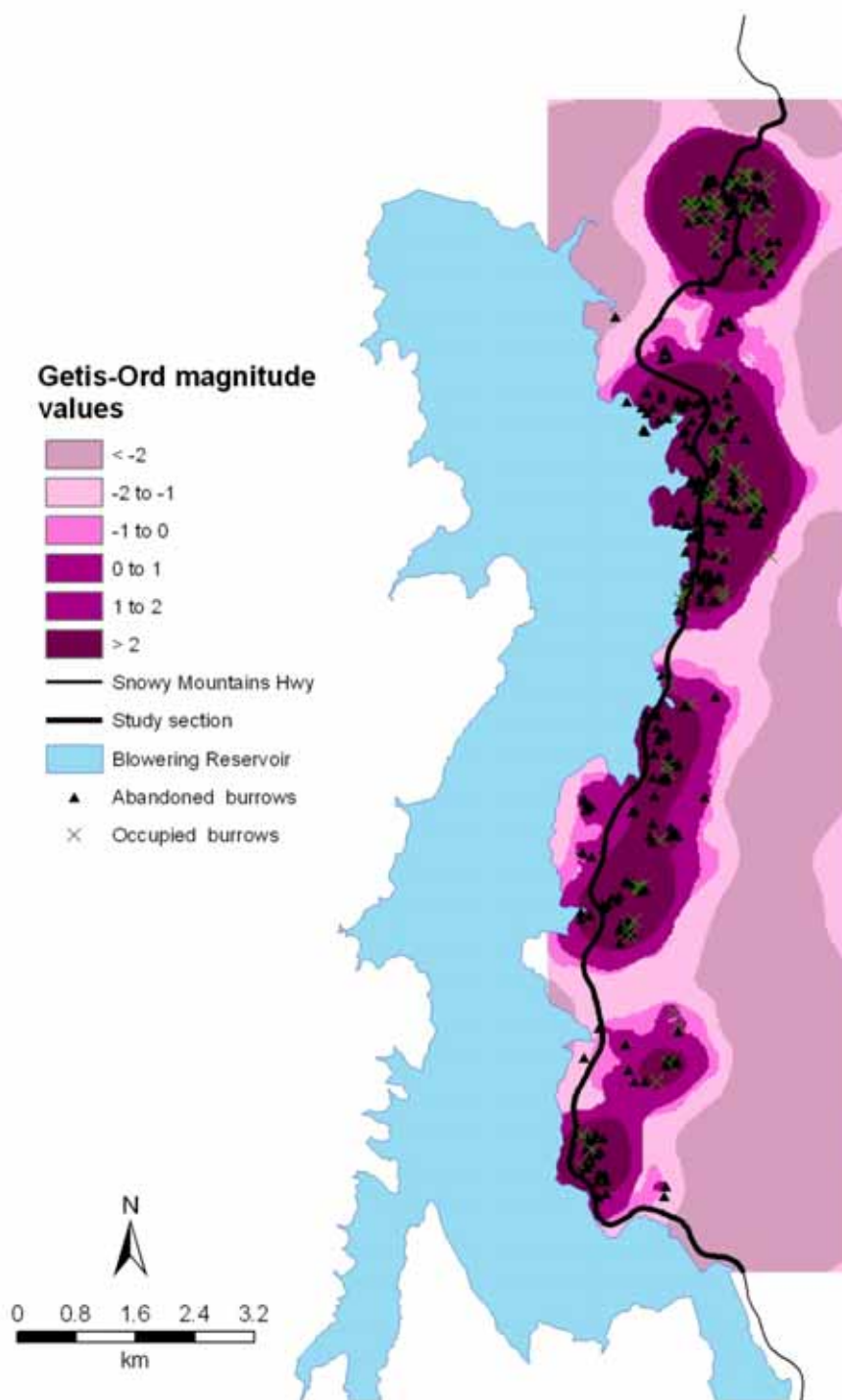


Figure 4. The Getis-Ord values grouped into magnitude classes, values range between <-2 and >2. Occupied and abandoned burrows are overlaid. Also displayed are the Blowering Reservoir and the Snowy Mountains Highway.

4. Discussion

4.1 Burrow distribution and location

The final model included both landscape-level and site-specific variables. Using presence-absence data, burrow probability was highest near blackberry bushes and watercourses (blackberry bushes occur throughout the study area, and are not confined solely to creek areas). This result is supported by previous studies which have observed the association of common wombats with blackberry bushes (Triggs 1988) and Boxthorn shrubs (*Lycium* spp.) (Taylor 1993) and associated burrow presence with riverbanks and gullies (McIlroy 1973; Lunney and O'Connell 1988; Buchan and Goldney 1998).

The positive relationship with NDVI-SD reflects a preference for good foraging habitat near cover as wombats are typically grazers. They typically refrain from burrow construction in barren or rocky areas and in areas of dense leafy vegetation, preferring instead good quality grazing land. Forests selected by wombats in this study generally had an open understorey, with a preference for 50% cover. This is consistent with McIlroy (1973) and Buchan and Goldney (1998) who considered forest cover important for protection from predators and extreme weather. Similarly, Catling et al. (2000), using generalised linear models to analyse the distribution and abundance of ground-dwelling mammals, such as the common wombat, found their models reflected the species' preference for open forests with open grassy understorey and low shrub cover. Taylor (1993) did observe a number of burrows in pasture areas; however these were all associated with Boxthorn shrubs.

The results indicate that burrow locations are clearly clumped. The G_i^* model included the same predictors as the presence-absence model, although the predictive power of the model was greater than the presence-absence model. Similarly, Buchan

and Goldney (1998) found the most important variable for predicting burrow usage was the presence of other active burrows. Their study found that a burrow had a greater chance of being used if it had a large number of active burrows close by.

It is almost certain that the occurrence of wombat burrows is influenced by additional habitat variables not used in our study. The inclusion of soil type and ground litter would have potentially improved the predictive capacity of all models. Buchan and Goldney (1998) observed a strong relationship between burrow location and the distribution of red earth, as opposed to yellow podsolc soil. However, as soil type is strongly correlated with vegetation and with topography, we would have partially accounted for it with these variables. It is also evident from the extent of the species range that wombats are suited to a range of soil types (McIlroy 1973, 1976; Mallett and Cooke 1986; Triggs 1988)

The Blowering foreshore area has been extensively degraded since European settlement: its pastoral history, creation of an artificial lake, construction of a major highway and use as a recreational area for boating and camping. The remnant forest of the study area has been severely degraded, while blackberry bush has invaded most of the cleared land along the foreshore. Although an invasive weed, blackberry bush provides wombats with protection, enabling them to construct burrows in prime grazing areas and to move about freely. The habitat models also indicate that common wombats prefer forest edges with a mix of forest cover and grazing land for burrow placement. The use of the forest edge in this manner often places wombats in direct competition with land-holders on adjacent farms. Buchan and Goldney (1998) reported that land-holders near their study site in the Central Tablelands believed that wombats significantly damaged their property, and there was a general perception of the need to eradicate them. Similarly the New South Wales Department of Environment and

Conservation has issued several licences permitting local land-holders to exterminate wombats on their property (M. Pettit, Department of Environment and Conservation Area Manager, Personal Communication).

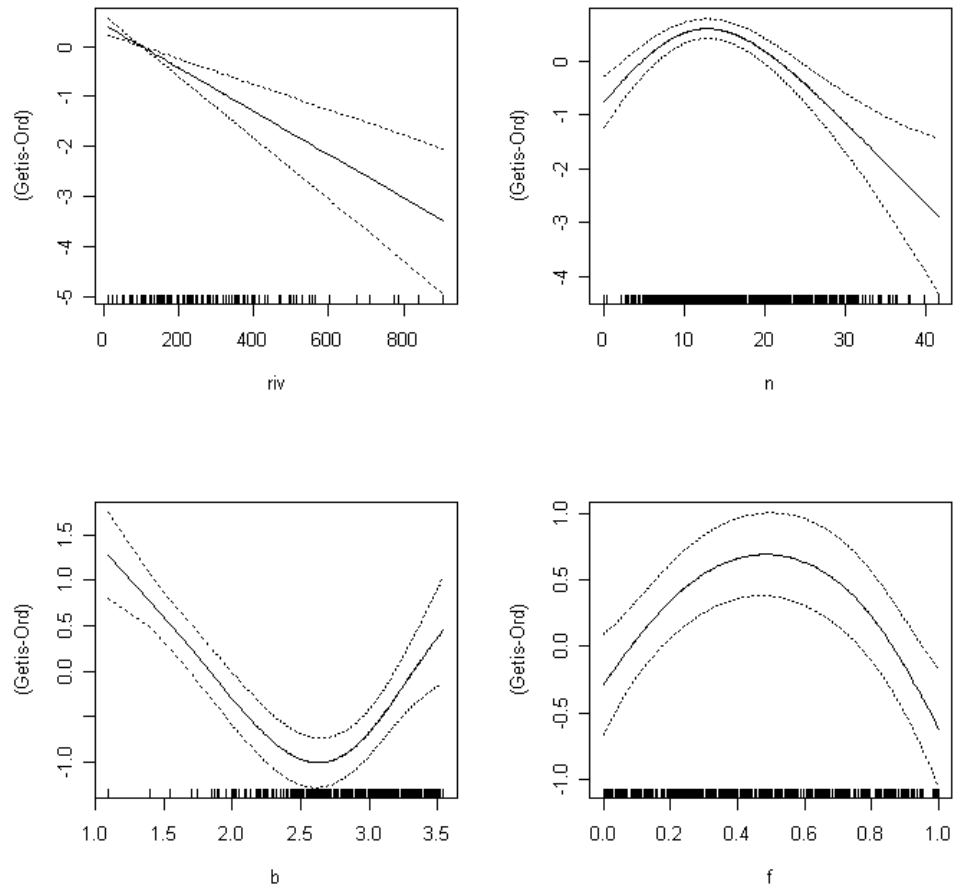


Figure 5. Partial plots of the relationship between the Getis-Ord statistic of positive and negative burrow clusters and the predictor variables included in the final model. The X-axis represents the range of values for each environmental variable [(f) percent forest cover, (b) distance to blackberry, (riv) distance to river, and (n) normalized difference vegetation index]. Dashed lines represent 95% confidence intervals around the fitted response shape.

Table 4.

Model results for burrow occupation model.

Model	Loss Function	Total # Models	B	F	S	RIV	H	N	R	Median # vars
Probability occupation	Misclassification error rate	51	0.61	0.78	0.55	0.51	0.66	0.61	0.76	4
	Deviance	128	0.50	0.50	0.50	0.50	0.50	0.50	0.50	4

Table presents the number of models within 1SE of the best model and the proportion of models containing the variable within 1SE of the best model for each criterion.

Symbols for predictor variables occurring in model set are distance to blackberry (B), percent forest cover (F), slope (S), distance to river (RIV), hillshade (H), distance to road (R), and normalised difference vegetation index (N).

4.2 Burrow occupation

The probability of the presence of an occupied burrow increased with increasing distance from road, presumably because wombats living in close proximity to the highway would be struck by vehicles more often. Burrows further from the highway may be preferred as they would incur fewer disturbances from people and traffic using the foreshore area for recreation. Burrow occupation was also positively associated with percent forest cover. This finding supports our burrow location model and can be interpreted as a reflection of the importance of proximal forest for weather and predator protection. Similarly, Buchan and Goldney (1998) found that burrows were more frequently used when they were situated within a 2 m radius of an overstorey tree; this variable was also significant in their study as a predictor of the frequency of burrow use. The probability of an occupied burrow was also correlated with NDVI-SD. This supports the findings that wombats seek out high quality forage, but actively select areas away from dense foliage. Given the lack of performance of the occupancy model, our results suggest that other factors, such as density dependence, may play more important roles in determining burrow occupation.

4.3 Limitations of burrows as presence data

Although we can be confident that all burrow locations were true presences, we cannot demonstrate undoubtedly that the randomly generated absence points were in fact true absences. However, by choosing to model a fixed location, we were not relying on locations of calls, or species sightings, which can be problematic in their failure to distinguish between where animals forage and the territory they pass through (Burgman et al. 2001; Wintle et al. 2005a; Ray and Burgman 2006). In addition, species sightings and call locations are more subject to false absences that occur when an observer fails to record a resident species (Wintle et al. 2005b). False absences often occur via misidentification of species, adverse weather, and random chance (including temporary absence of wide-ranging species) (Wintle et al. 2005b); use of burrows greatly reduces the risk of these occurring. Burrows are important in driving wombat ecology (Taylor 1993; Walker et al. 2007), such that burrow presence can be thought to not only reflect suitable burrowing conditions but also proximity to optimal foraging habitat. A caveat associated with using burrow locations is that they may not incorporate the true structure of randomness present in the data, as distinct areas of burrow clumping were observed. However, the Getis-Ord spatial clustering model accounts for incidents of spatial autocorrelation. As this and the presence-absence model exhibited similar results, pseudo-replication is not a major concern in this dataset.

4.4 Population sustainability

Extrapolation of the habitat models across the study region identified an abundance of habitat suitable for burrows but the number of occupied relative to abandoned burrows was low. Buchan and Goldney (1998) observed 80% occupancy rates, compared to the 27% observed in this study. Given the availability of suitable habitat the common

wombat populations in the region should be thriving. McIlroy (1973) noted that very high densities of wombats ($0.5 \text{ wombats ha}^{-1}$) could be found in forest that was very close to high quality grazing areas, like the Blowering foreshore. However, given that common wombats are thought to use as many as four burrows on a regular basis (McIlroy 1976) the 81 major burrows likely represent a population of between 20 and 40 wombats. This population size was extremely low, as estimates of mortality from threats would appear to match this population estimate on an annual basis. At least 4 to 22% of the population was infected with the fatal disease sarcoptic mange (based on averages of prevalence reported in Skerratt et al. 2004a), while an average of 28 were killed on the highway each year (Ramp et al. 2005). As common wombats are slow breeders, there is little chance that this mortality was being replenished solely by local reproduction. It is more likely that the habitat of the study region was a sink for populations within the interior of the national park. Given that the majority of the study area has historically supported a large wombat population by providing an abundance of food and shelter, the apparent influx of wombats from surrounding areas (or source populations) suggests that the region is now acting as an ecological trap (Battin 2004). Ecological traps occur when species are unable to accurately identify the suitability of a habitat, perceiving it as good when in fact it is bad (Kokko and Sutherland 2001; Kristan 2003). One would predict that an ecological trap would be associated with changes in the fine-scale distribution of subpopulations, such as increases in the number of isolated or semi-isolated subpopulations. We are currently gathering data to test this hypothesis. Certainly, the identification of source and sink populations becomes crucial for resource managers, who may wish to conserve source but not sink habitats (Runge et al. 2006).

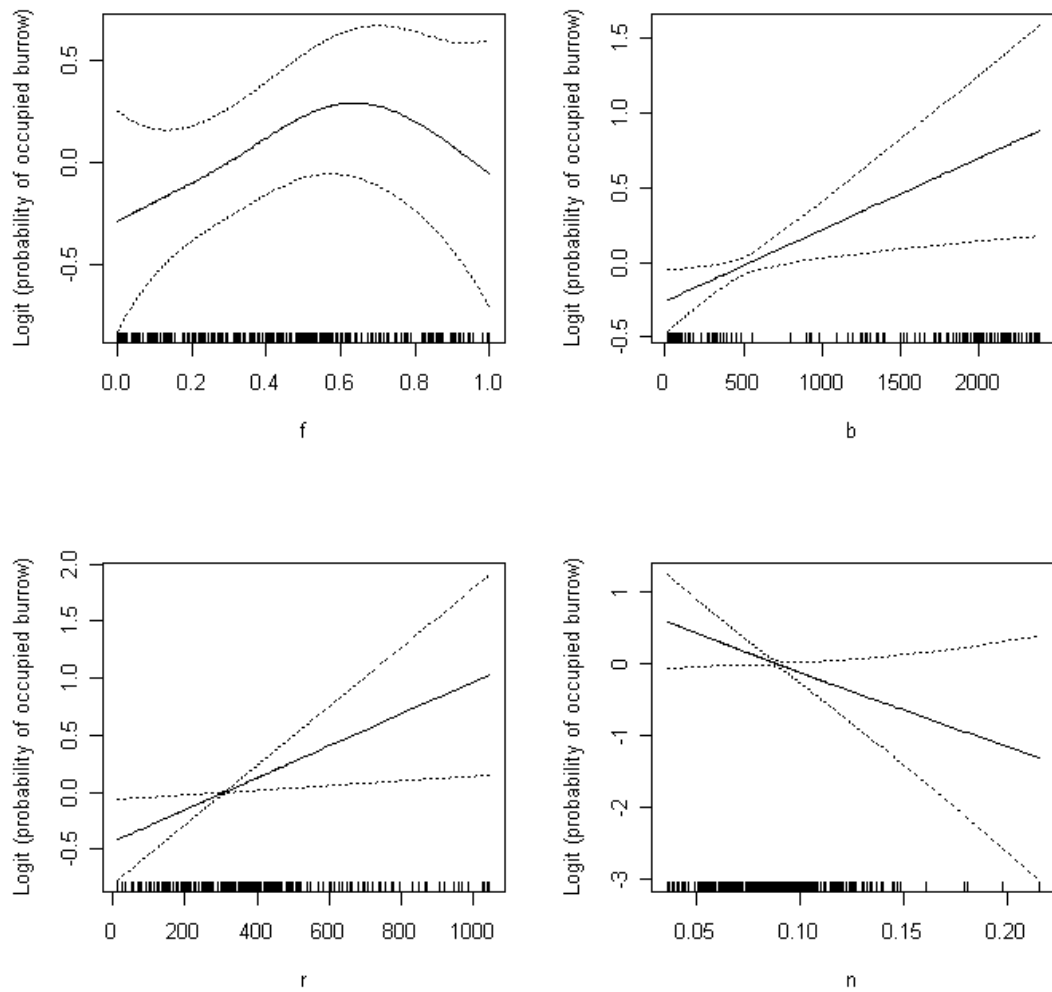


Figure 6. Partial plots of the relationship between the probability of an occupied burrow and the predictor variables included in the final model. The X-axis represents the range of values for each environmental variable [(f) percent forest cover, (b) distance to blackberry, (r) distance to river, and (n) normalized difference vegetation index]. Probabilities on the Y-axis are plotted in transformed ‘logit’ space, so that they can be interpreted in the same way as linear regressions. Dashed lines represent 95% confidence intervals around the fitted response shape.

4.5 Conservation implications

Common wombats play an important role in preserving ecosystem health, as native grazers and as ecosystem engineers (*sensu* Jones et al. 1997), increasing rates of soil turnover, and impacting soil nutrition (Kinlaw 1999). The loss of such a species would have serious environmental implications, and their status as a common, wide ranging

species cannot simply be assumed. Lunney and O'Connell (1988) found that, due to the excessive logging and burning of large forest areas, near Bega, New South Wales, that the common status of large forest herbivores, such as the common wombat and swamp wallaby, could not be guaranteed. Similarly, Buchan and Goldney (1998) noted that common wombats in the Central Tablelands were patchily distributed and appeared to be declining in the region. Little else has been reported on the status of the species, but what is recognised is that there is increasing isolation of populations of common wombats in remnant forest patches scattered over much of the species' former range (Lunney and O'Connell 1988; Triggs 1988). This isolation, in conjunction with other drivers of change, like road-kill, is a major threat to the conservation of local populations (McIlroy 1995; Buchan and Goldney 1998). Our findings suggest that although areas may have an abundance of suitable habitat for wombats, suitable habitat does not necessarily equate with high densities of animals. We suggest that wombats are drawn to cleared areas, and this movement is often to their detriment. Management needs to evaluate common wombat populations in this context, and strive to preserve habitat linked to optimal suitability, while mitigating limiting factors.

Constructing habitat models is an important step in highlighting species relationships with environmental variables to assist in the development of conservation strategies. Localised habitat models are limited to quantifying suitability within the study area, and are often criticised for their limited ability to be extrapolated to larger scales and other populations. Our final models demonstrated how wombat occurrence is influenced by both local and landscape spatial scales, and it is likely that habitat selection processes inherent to the common wombat operate on both spatial scales. Therefore, mechanisms of burrow selection may be similar between locations, despite the broad-scale heterogeneity of wombat habitat, and may enable the application of

predictive models throughout their range. Comparison of historic and current records of common wombat distribution challenges the opinion that common wombats are currently common and suggest that perceptions of abundance are often clouded by socio-political factors rather than informed by biological and ecological factors. Given the risks facing wombat populations, we recommend the expansion of biomonitoring of common wombats along a gradient of human disturbance and land-use areas to determine metapopulation function and localised population decline.

Acknowledgements

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Chapter 3

Incorporating habitat use in models of fauna fatalities on roads

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Key words: Road-kill, habitat use, predictive modelling, spatial analysis, Getis-Ord clustering, common wombats, *Vombatus ursinus*.

ABSTRACT

Aim To highlight the benefit of using habitat use to improve the accuracy of predictive road fatality models.

Location The Snowy Mountains Highway in southern New South Wales, Australia.

Methods A binary logistic regression model was constructed using wombat fatality presences and randomly generated absences. Species-specific habitat variables were included as predictors in the model selection process as well as two spatially-explicit measures of wombat habitat use. Generalized Additive Models (GAMs) were constructed for each possible combination of predictors in R. The final model was selected by comparing all models subsets for the eight predictors and employing the one standard error rule to select the best model set.

Results The final predictive model had high discriminatory power and incorporated both measures of species habitat use, greatly exceeding the variation explained by a previously published model for the same species and road.

Main Conclusions Our findings highlight the importance of incorporating variables which describe habitat use by fauna for predictive modelling of animal-vehicle crashes. Reliance upon models that ignore landscape patterns are limited in their capacity to identify hotspots and inform managers of locations to engage in mitigation.

INTRODUCTION

The adverse impacts of roads on wildlife are well documented (see reviews by Forman et al. 2003; Seiler 2003; Coffin 2007). Although population effects on fauna extend well beyond the boundary of the road (Reijnen et al. 1997; Gaines et al. 2005; Jaarsma et al. 2006; Ramp and Ben-Ami 2006), fatalities of fauna killed in collisions with vehicles on the road itself are of major concern to conservationists and road managers (Forman and Alexander 1998; Trombulak and Frissell 2000). Recently, many quantitative models of animal-vehicle collisions have been developed (Malo et al. 2004; Saeki and Macdonald 2004; Gaines et al. 2005; Jaeger et al. 2005; Ramp et al. 2005; Orlowski and Nowak 2006), with the goal of providing effective mitigation techniques for management (Jaarsma et al. 2007). These probabilistic approaches to predicting locations of animal-vehicle collisions are conducted for two primary purposes: a) to infer those factors contributing to collisions and b) to identify hotspots for targeted mitigation.

Driven by the need to develop feasible models, modelling approaches for predicting fatality locations have typically relied on variables that characterize the road environment; such as road sinuosity, road-verge attributes and spatial and temporal traffic variation (Finder et al. 1999; Taylor and Goldingay 2004; Clevenger and Waltho 2005). Often missing, or at best generic in nature, are species-specific variables that describe how the animals in question utilize the landscape. When included, species-specific variables are often restricted to vague characterizations of landscape utilization (Jaeger et al. 2005), and often multiple species are modelled simultaneously using the same suite of generic variables (Clevenger et al. 2003; Taylor and Goldingay 2004; Ramp et al. 2005). The biological link between these habitat variables and the fauna that are involved in collisions is never explicitly described. This oversight has significant ramifications, as the importance of understanding species-specific distributions in

ecological studies in road environments has been shown for a wide range of species (Forman et al. 2002; Alexander et al. 2005; Lesbarreres et al. 2006; Barnum et al. 2007; Eigenbrod et al. 2008). Although often due to the absence of relevant data, the adoption of species-specific habitat variables within predictive fatality modelling has been slow, despite many models suffering from poor explanatory power.

To highlight the benefit of including species habitat use information in fatality models we chose to model fatalities of common wombats *Vombatus ursinus* using spatially-explicit information on habitat use. As burrow dwelling animals, wombats emerge from their burrow at dusk and re-enter at dawn. They generally have at least four major burrows within their home range (ranging between 5-25 ha), distinguishable by their size (Triggs 1988). High burrow density can be used as a reflection of good wombat habitat, while burrow occupancy rates are a surrogate for estimation of population size.

Although historically considered abundant, few data exist of actual densities and current distribution. The evidence that does exist suggests that the distribution of the common wombat has contracted since European arrival, particularly in western Victoria, southern Queensland, and northern South Australia (Triggs 1988; McIlroy 1995; Buchan and Goldney 1998). The common wombat is impacted by a range of threatening processes, including road-kill, habitat loss, predation, disease and culling (Triggs 1988; Roger et al. 2007). This contraction is alarming as species decline is often first recognised at range extremes (Baldi 1999; Lehman et al. 2006). Much of the current distribution of the common wombat lies in fragmented or disturbed areas (Buchan and Goldney 1998); environments that are often characterized by roads. Their adaptability and preference for human modified habitats has maintained perceptions of their commonality. Common wombats are edge specialists, preferring patchy habitats

with a mix of open and closed forest in proximity to watercourses or drainage lines (Roger et al. 2007). This seeming preference, determined by landscape structure, puts them in direct contact with anthropogenic disturbance.

The persistence of the common wombat is a concern as there are only three extant species of wombat, two of which are threatened. The common ancestors of wombats were once a diverse and dominant group, with many forms larger than the current extant species (Woolnough and Steele 2001). Today, the southern hairy-nosed wombat *Lasiorhinus latifrons* is restricted to small fragmented areas concentrated along the Nullarbor Plain in South Australia, and is listed as vulnerable, while the northern hairy-nosed wombat *L. krefftii* is listed as critically endangered with fewer than 115 individuals located in central Queensland (Banks et al. 2003).

In this paper we provide an example of the benefits of incorporating spatially-explicit information of habitat use in the modelling of animal-vehicle collisions. To do this we chose a road for which a fatality model for common wombats had previously been constructed and where habitat suitability modelling had also been conducted for this species. This enabled us to make a comparative assessment of the increase in value of incorporating habitat use variables in the fatality model. We discuss the importance of our results for management and encourage conservation managers to utilise models that include spatially-explicit information on species distributions that are at an appropriate extent to the fatality locations being modelled.

METHODS

Study area

The study was conducted on the Blowering foreshores between the townships of Tumut (35°19'S, 148°14'E) and Talbingo (35°34'S, 148°18'E) in Kosciuszko National Park,

southern New South Wales, Australia (Fig. 1). The study area of 30 km² is bound in the west by the Blowering Reservoir while the east is characterised by native forest and grassy south-west facing slopes of what was once remnant pasture. The study area is dominated by cleared land, moist and dry forest, blackberry thickets *Rubus fruticosus*, patches of bracken fern *Pteridium esculentum* and briar bushes *Rosa rubiginosa*. Slope areas are dominated by shrubs *Leptospermum* spp. and patches of trees *Eucalyptus* spp. (Jaremovic and Croft 1991). The area has a temperate climate, with cool wet winters and warm summers, and an average yearly rainfall of 900 mm (Australian Bureau of Meteorology records for Tumut Plains). The common wombat shares the open grassy foraging areas with native and introduced herbivores; namely the eastern grey kangaroo *Macropus giganteus*, the emu *Dromaius novaehollandiae* and the European rabbit *Oryctolagus cuniculus*. The windy and single-laned Snowy Mountains Highway (speed limit 100 km h⁻¹) runs through the site separating the foreshore area from the slopes and is a known hotspot for animal-vehicle collisions. An average of 247 cars travel this section of highway each day with peak volumes occurring between 9:00 and 18:00 (Ramp et al. 2005). Traffic volume remains relatively constant throughout the year.



Figure 2. The study area is along the Snowy Mountains Highway, adjacent to Blowering Reservoir. White areas are cleared, green areas are forested.

Data collection

Fatalities of common wombats along the 40 km segment of the Snowy Mountains Highway between Tumut and Talbingo were recorded between 1998 and 2005. Beginning in March of 2002, fatalities were recorded using a hand-held GPS device (Garmin II Plus) following Ramp et al. (2005). The road was travelled twice daily five days per week with carcasses removed from the roadside after recording to avoid double counting. Only fatalities (post March 2002) were used for modelling as prior to this fatalities were not spatially referenced.

Habitat use was determined by recording the location of common wombat burrows in the study area (Roger et al. 2007). Burrow location has been used to represent habitat use in other species such as the muskrat *Ondatra zibethicus* (Nadeau et al. 1995). Similarly, variations of wombat density have been shown to be correlated with the placement of the burrow within a landscape (Downes et al. 1997), primarily because wombats construct burrows in relation to physiographic features of the landscape. Burrow surveys were conducted in June and July 2005 by systematically surveying the entire study area on foot, following Rishworth *et al.*(1995). Transects running east-west were traversed by four observers spaced lengthwise 15 to 30 meters apart (depending on the visibility of terrain). Each transect ran from the border of the reservoir for an average distance of 1600 m. Approximately 120 transects per observer were traversed in total, covering an area of 30 km². Burrow locations were recorded using a global positioning system (GPS) and scored as either abandoned or occupied based on the criteria for major burrows described by McIlroy (1973). Maximum height and width of burrow entrances were also recorded. Entrances greater than 2100 cm² were scored as occupied, and visible signs of occupation were also used, such as tracks and presence of scat. When in doubt, small sticks were placed across burrow entrances

and checked the following morning for sign of displacement. A raster layer of burrow location data (both occupied and abandoned burrows) was then created in ArcGIS 9.1 (ESRI 2007).

Model Development

Dependent variables

Common wombat fatalities were compiled using ArcGIS 9.1. An equal number of absence points were randomly generated on the highway using Hawth's Analysis Tools add-on for ArcGIS (Beyer 2004). Although common wombat fatalities were recorded over the entire 40 km length of the highway, only fatalities recorded on the 15 km length within the study area were used in the analysis in order to match the 30-km² area surveyed for burrows. A total of 208 presence-absence data points were used in the analysis.

Predictor variables

Selected variables were based on a previously developed habitat suitability model that used burrow location to predict habitat use by wombats (Roger et al. 2007). Predictors selected for use in the modelling process included: distance to drainage lines (not including the Blowering Reservoir), forest cover, distance to blackberry bush, slope, normalised difference vegetation index (NDVI), distance to the nearest burrow, burrow occupation and abandonment clustering (Getis-Ord G_i^* statistic) and hillshade (percentage of time spent in topographic shade). All environmental variables were stored as raster layers within ArcGIS with a resolution of 25 m.

Vegetation community data was obtained from 30 m LANDSAT data and used to calculate the proportion of forest cover surrounding each wombat fatality. A circular sampling area based on the average home range of a common wombat (Skerratt et al.

2004a) was generated assuming the radius of a circle was equal to the diameter (320 m). The area covered by all forest communities in the study area (moist forest, disturbed forest, severely disturbed forest, moist forest tending to dry and dry forest) was aggregated into a proportion of area covered by forest following Ramp *et al.* (2005).

Raster layers of distance from wombat fatality to the nearest river or watercourse (m), the nearest blackberry bush (m) and the nearest burrow (m) were generated using the Euclidian distance function in ArcGIS Spatial Analyst. A raster layer of slope (degrees) was derived from a 20 m resolution Digital Elevation Model (DEM). Hillshade was used as an alternative to aspect because aspect is a circular variable and does not behave well in correlative studies (Beers et al. 1966). Hillshade, generated using the Raster Surface toolbox in ArcGIS, was used to provide a proxy for relative radiation load.

An NDVI image at 15 m resolution (acquired 26 Dec 2000) was used as an index of greenness within the study area. NDVI values were created by the Australian Bureau of Meteorology from visible and near-infrared reflectance measurements ($NDVI = (NIR - VIS) / (NIR + VIS)$), where NIR is the near infrared light reflected by the vegetation and VIS the visible light reflected by the vegetation (Pettorelli et al. 2006). Negative NDVI values correspond to an absence of vegetation, while higher values are associated with greater density and greenness of the plant canopy (Justice et al. 1985). The NDVI values were then converted into a habitat complexity index (NDVI-SD) by taking the standard deviation of values within a 200 m radius. Focal statistics within ArcGIS was used to resample the 15 m advanced spaceborne thermal emission and reflection radiometer (ASTER) cell sizes to conform to the 25 m used for the remainder of the data. In the NDVI-SD index higher values represent mixed forest and grassland while lower values represent pure forest and grassland.

To model burrow clusters in the landscape, clusters of occupied and abandoned wombat burrows were analysed using the Getis-Ord G_i^* spatial clustering statistic (Getis and Ord 1992; Ord and Getis 1995). The G_i^* statistic can detect spatial clusters despite negative tests for global spatial autocorrelation (Swenson and Howard 2005). It measures the degree of spatial clustering of a sample based on how different it is from the mean of the data set. The statistic is a Z-score with a mean of zero and a standard deviation of 1. In our case, a positive G_i^* value represents a cluster of occupied burrows, while a negative G_i^* value represents a cluster of abandoned burrows. The extent to which a G_i^* value is greater or less than the mean represents the strength of the spatial clustering in the sample, with values greater in magnitude than ± 2 approximately at the 95% significance level. The G_i^* statistic was calculated following Laffan (2006), calculations are based on Euclidean distance using circular radii from 125 m to 12,500 m at 125 m increments and aggregated into a single layer using the radius with the greatest magnitude. The Z-score represents the statistical significance of clustering for a specified distance.

Fatality model

A binary logistic regression model was constructed using wombat fatality presences and randomly generated absences. Generalized Additive Models (GAMs) were constructed for each possible combination of predictors in R (R Development Core Team 2005). All predictor variables were checked for collinearity before use. Predictor variables were normalized by transformation in order to stabilize variances. The logarithmic transformation was applied to the distance to blackberry, river and burrow variables, while the square-root transformation was applied to the forest, slope and hillshade variables. The relationship between each predictor and the dependent variable was assessed to choose the appropriate degrees of freedom for each predictor based on

realistic ecological relationships. Plausibility of response shapes was used to discern the relationship between variables. Relationships were either left linear or splined with 2, 3, or 4 degrees of freedom.

Model Selection

Eight variables were considered for inclusion in the fatality model, for a total of 256 candidate models. This is a "model selection" problem, which we addressed by finding the model that best predicted new observations using a cross-validation approach known as the bootstrap .632 rule. This has been shown to be appropriate for model selection when the underlying parameter distributions are unknown (Hastie et al. 2001), or when robustness of underlying model assumptions is desired. A penalty-based approach such as AIC does not share such properties. Bootstrapping was used because it has been shown to improve cross-validation, particularly when using the .632 rule (Efron 1983; Efron and Tibshirani 1997).

To evaluate performance in predicting new observations, two loss functions were employed: misclassification error rate and deviance. Misclassification error rate is a natural and readily interpreted measure of predictive performance, whereas deviance is a measure of predictive success that has theoretical rather than pragmatic origins. In particular, cross-validation approaches using the deviance function have been shown to estimate the same quantity as AIC (Efron 2004), although using a data-driven approach rather than a parametric, large sample argument.

Use of the misclassification error rate requires a threshold value to classify the predicted probability as presence or absence. Rather than choosing an arbitrary threshold, a Receiver Operating Characteristic (ROC) curve was used to find the threshold that best discriminates between the sensitivity (probability that a wombat fatality is correctly predicted) and 1 minus specificity (a false positive prediction)

(Ferrier et al. 2002). For the deviance loss function, the deviance per observation was calculated rather than the total deviance, so that it was comparable across re-samples in which the validation datasets had different sizes.

Following Ramp *et al.* (2005), the final model was selected by comparing all models subsets for the eight predictors and employing the one standard error rule (Hastie et al. 2001) to select the best model set. That is, the final model was the most parsimonious model within 1 SE of the model with best predictive performance. Using this approach ensures a model with good predictive performance that is small, hence readily interpretable. Final model selection was based on comparing the best models (within both loss function groups) that contained the fewest number of predictor variables. Due to reviewer concerns, model selection was repeated using Akaike Information Criterion (AIC), which resulted in similar results in terms of model rankings to use of the bootstrap .632 rule as applied to the deviance criterion.

Hierarchical Partitioning was used to lend additional support to the model selection process (Mac Nally 2000; Brambilla et al. 2006). A goodness of fit measure for the entire hierarchy of models using all combinations of predictor variables was calculated using maximum likelihood. The contribution of each predictor to variability in the full model was identified and compared to results from the bootstrapping process.

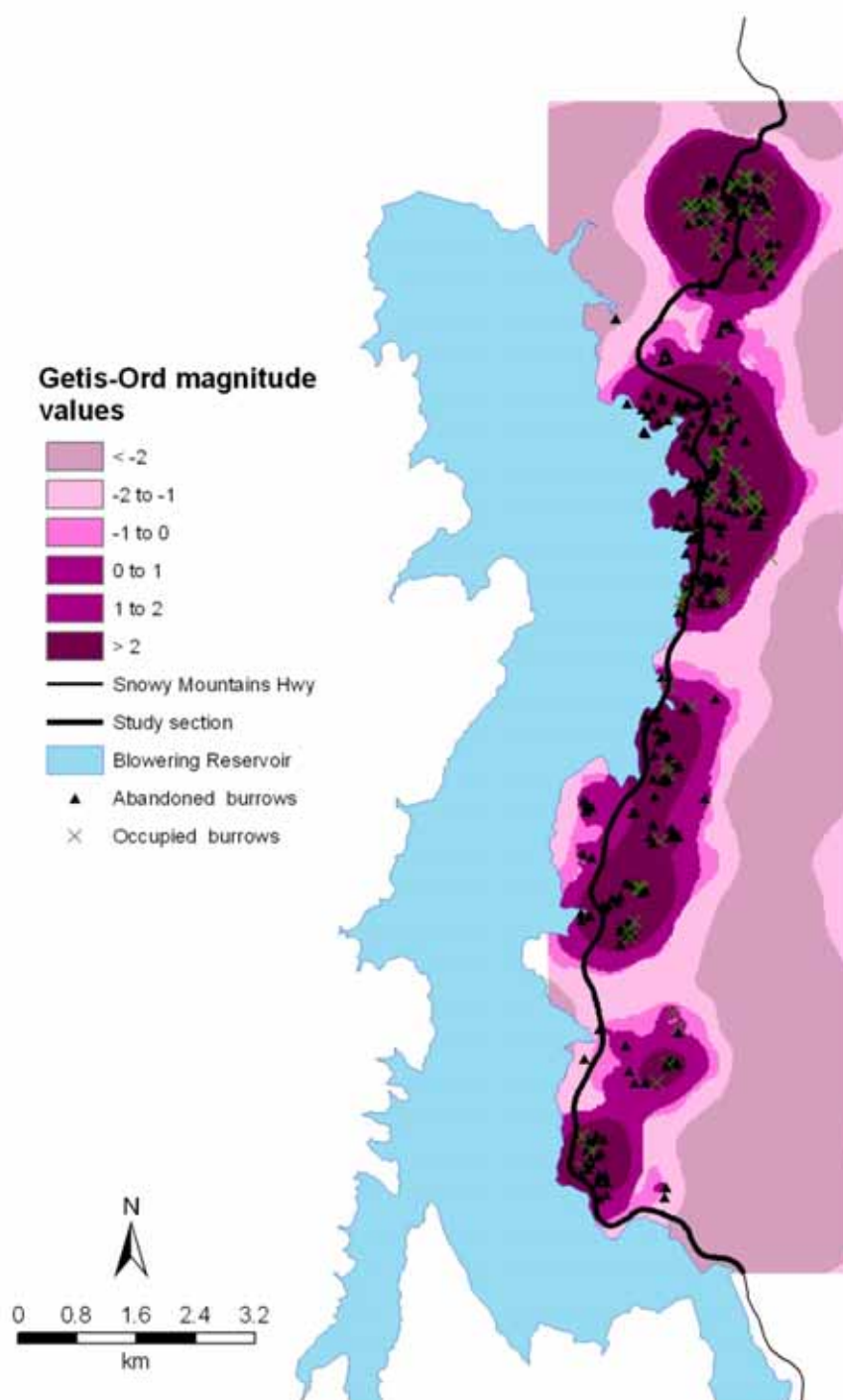


Figure 2. The G_i^* values grouped into magnitude classes, values range between <-2 and >2. Occupied and abandoned burrows are overlayed. Also displayed are the Blowering Reservoir and the Snowy Mountains Highway.

RESULTS

A total of 81 occupied and 297 abandoned burrows were identified in the 30 km² of the study area. Burrows were not evenly distributed throughout the landscape and were clearly clumped into occupied and abandoned clusters (Fig.2). A total of 209 wombat fatalities were recorded over the 40 km length of highway between 1998 and 2005 (Fig. 3). For the 15 km road length used in this study, 104 were recorded between March 2002 and December 2005. The number of fatalities varied among years, with a mean number of 23.2 ± 5.18 per year between the period of 1998 and 2005 for the 40 km stretch of highway. For the 15 km length used in the analysis, a mean number of 27.3 ± 7.12 per year between 2002 and 2005 were recorded (or 0.005 wombat kills per day per km). Fatalities were not evenly distributed along the highway, and were clearly clumped (Ramp et al. 2005).

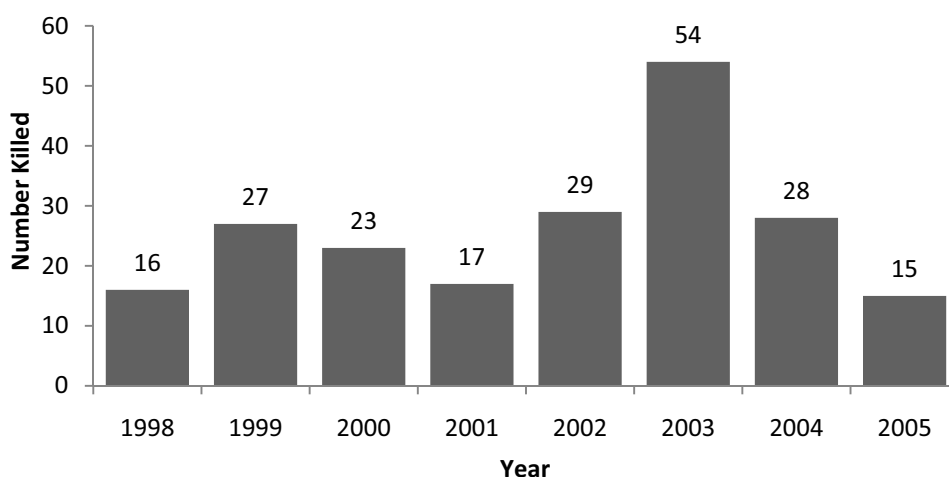


Figure 3. Number of common wombats killed along a 40 km length of the Snowy Mountains Highway between Tumut and Talbingo (1998-2005).

Fatality model

The misclassification error rate and deviance loss functions identified 50 and 202 models respectively within 1SE of the best model (Table 1). Discrimination among predictors using the deviance loss function was relatively poor compared to misclassification error. NDVI-SD and the G_i^* statistic were selected in 100% of models in the best model set using misclassification error. There was good agreement on the final model among the three methods of model selection, selecting NDVI-SD, distance to blackberries, the proportion of forest cover, distance to the nearest burrow and the G_i^* statistic (Table 2).

The final model explained 61.9% of the deviance (Table 3), [area under a curve (AUC) 0.887], Misclassification Error 0.1856. NDVI-SD explained 45% of the variation in the model and was positively correlated with fatality probability, tapering off at higher NDVI-SD values (Fig. 4). The probability of a fatality was higher closer to blackberry bushes, explaining 29% of the variation in the model. The G_i^* statistic, representing occupied and abandoned burrow clusters, explained 18% of the model variation and was negatively correlated with the probability of a fatality. Distance to the nearest burrow and the proportion of forest were included in the final model but explained less model variation. The probability of a fatality decreased with increasing burrow distance, while generally decreasing as forest cover increased until cover was greater than 80%.

Table 1.

Model results for road fatality probability. Table presents the number of models within 1SE of the best model and the proportion of models containing the variable within 1SE of the best model for each criterion.

Model	Loss Function	Total # Models	bl	f	s	riv	h	n	bu	g	Median no. of variables
Predicting fatalities	Misclass. error Rate	50	0.62	0.60	0.56	0.48	0.50	1.0	0.56	1.0	6
	Deviance	202	0.56	0.51	0.51	0.52	0.50	0.63	0.56	0.58	6

Symbols for predictor variables occurring in model set are distance to blackberry (bl), percent forest cover (f), slope (s), distance to river (riv), hillshade (h), normalised difference vegetation index-SD (n), distance to burrow (bu) and G_i^* statistic (g).

Table 2.

Variable coefficients and Z-scores for the predicting wombat fatality model.

Model	Variable	d.f.	Coefficient	Independent contribution	Chi-Squared	P
Predicting Fatalities	Intercept		-3.072			
	Blackberry	2	-0.114	29.0374	7.7253	0.005
	Burrow	1	-0.519	5.7326	0.0098	0.018
	NDVI-SD	3	57.077	45.1481	15.9365	< 0.001
	G_i^* statistic	1	-1.009	18.7980	8.9496	0.003
	Forest	3	-0.533	1.2836	10.0467	0.007

The independent contribution of each variable was determined through hierarchical partitioning is presented as a percentage of the total explained variance.

Table 3.

Comparison of the deviance explained by our final model and Ramp *et al.* (2005) using the complete data set with degrees of freedom (d.f.) along with the area under the curve (AUC).

Model	Final Model	Null	Residual	% Deviance explained	AUC
Predicting fatalities Current model	f + bu + g + n + bl	286.1 (df=206)	108.9 (df=194)	61.9	0.887
Predicting fatalities Ramp et al. 2005	S + SIN + SOI + T + W + E	777.2 (df=2135)	691.9 (df=2129)	11.0	0.778

Symbols for predictor variables occurring in model set are distance to blackberry bush (bl), percent forest cover (f), distance to burrow (bu), normalised difference vegetation index-SD (n) and G_i^* statistic (g). Symbols for predictor variables for Ramp et al. 2005 are slope (S), sinuosity (SIN), southern oscillation index (SOI), distance to nearest town (T), distance to water (W), and elevation (E).

DISCUSSION

Incorporating common wombat habitat use considerably improved the predictive capacity of road fatality modelling. Despite the exclusion of variables describing road characteristics and temporal variability, our model explained 61.9% of the deviance. In comparison, the model presented by Ramp *et al.* (2005) only explained 11% of the deviance. Our model benefited from two additional years of fatality point data. Ramp *et al.* (2005) had considered variables based on species ecology (such as species home range) when generating possible predictors, however, their selection was not founded on proven relationships between the species of interest and habitat use.

The variables included in the final model were all indicative of habitat use by wombats. Wombats preferentially forage in habitats with a mixed forest canopy cover and with abundant and high quality grass (Evans et al. 2006). The positive relationship with NDVI-SD suggests that wombats have a higher probability of being killed when foraging in their preferred habitats. Similarly, the probability of a fatality decreased with increasing distance from blackberry bushes. Despite being an invasive plant species,

common wombats have adapted to the abundance of this thorny shrub, using it for shelter as their burrows are often located directly beneath the dense bushes. As is typical for invasive weeds, blackberries often occur in abundance along roadsides. The implication of this finding for managers is clear: reducing the density of this weed along roadsides will likely reduce the likelihood of wombat road fatalities. Consideration, however, should be given to the potential effect that this loss of habitat may have on population persistence, despite the likely reduction in mortality due to collisions with vehicles.

Both variables included to specifically represent habitat use were present in the final model. Distance to the nearest burrow was used to reflect environments where wombat density is likely to be higher. The probability of a fatality decreased as distance from burrows increased, vindicating the use of this measure of habitat use. Also included was the G_i^* statistic. More than just an indication of burrow density, this statistic provided information on clusters of occupied or abandoned burrows in the landscape. Fatality probability was highest in areas within close proximity to abandoned clusters, while the probability of a fatality was lower where burrows clusters were occupied. Road fatalities are by far the highest source of mortality in the region for common wombats. Hence, areas with high fatality rates may deplete the local population resulting in a greater proportion of abandoned burrows. Vacated burrows are likely repopulated by migrating animals from source populations over time (E. Roger, S.W. Laffan & D. Ramp, unpubl. data). Evidence for this theory can also be found in the large variation in annual numbers of wombats killed on the road (Fig. 3), and is likely a reflection of changes in wombat density in the area, rather than changes in traffic volume or speed. An alternative for explaining why fatality probability was highest in proximity to abandoned burrow clusters is that wombats are killed travelling

to areas with abandoned burrow clusters to forage as the territory is unoccupied. It remains to be tested whether the location of abandoned and occupied burrow clusters in the landscape changes and over what temporal scale.

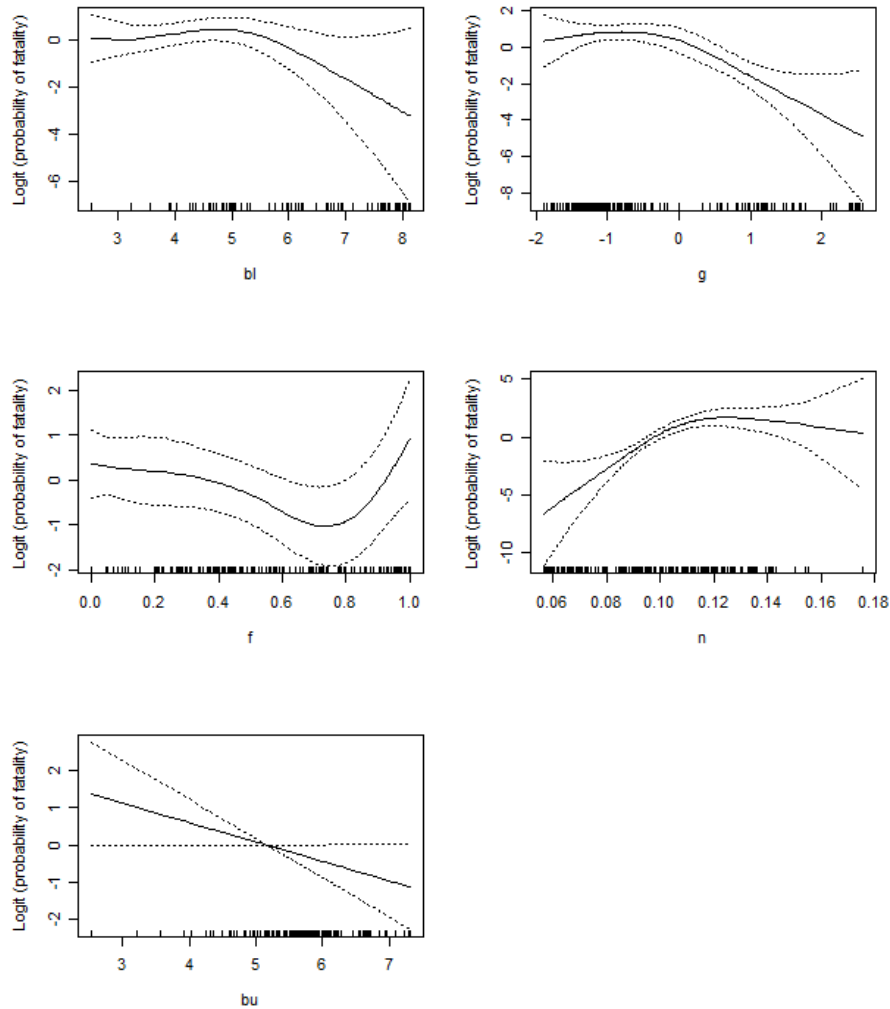


Figure 4. Partial plots of the relationship between the probability of a fatality and the predictor variables included in the final model. The x-axis represents the range of values for each environmental variable [(f) percent forest cover, (bl) distance to blackberry, (bu) distance to burrow, (g) G_i^* statistic and, (n) normalised difference vegetation index-SD]. Probabilities on the y-axis are plotted in transformed ‘logit’ space, so that they can be interpreted in the same way as linear regressions. Dashed lines represent 95% confidence intervals around the fitted response shape.

Implications for fatality modelling

Seldom do studies explicitly and *a priori* assert the relevance of predictors (Austin 2002). The current trend in predictive fatality modelling is to take an exploratory or data

mining approach to the selection of predictor variables, with most predictors describing the road and road environment. Often predictors are not carefully selected and their inclusion can lead to arbitrary fitting of predictor-dependent variable relationships. The number of possible predictor variables used in predictive modelling papers range from ten in Ramp *et al.* (2005) and Clevenger, Chruszcz & Gunson (2003) to as many as 28 in Malo, Suárez & Díez (2004). Instead, fatality models can be greatly improved by reducing the amount of possible predictors and utilizing knowledge on species use of habitat. These data are often difficult to come by but the improvement on their inclusion suggests greater emphasis should be placed on their attainment. Austin (2007) noted that species responses depended on the nature of environmental predictors and associated ecological processes and that use of existing knowledge to choose potential predictor variables is paramount. Likewise, as occupancy patterns of many species within landscapes vary according to the composition and configuration of land cover (Swihart *et al.* 2006), the extent of species habitat use should be reflective of the landscape extent of the fatalities being modelled. Caution should be taken before extrapolating values across broader landscapes for these reasons.

A number of studies have used a variety of predictor variables to develop predictive fatality models (Finder *et al.* 1999; Clevenger *et al.* 2003; Nielsen *et al.* 2003; Malo *et al.* 2004; Saeki and Macdonald 2004; Jaeger *et al.* 2005; Ramp *et al.* 2005; Seiler 2005; Jaarsma *et al.* 2006). Many have highlighted the importance of considering multiple spatial scales and landscape level as well as road attributes in the analyses (Lode 2000; Clevenger *et al.* 2003; Malo *et al.* 2004; Saeki and Macdonald 2004; Taylor and Goldingay 2004), but few have stressed the importance of incorporating species patterns of habitat use as an important predictor.

Evidence for the importance of animal density and movement patterns influencing proximity to roads exists for a wide range of species (Kramer-Schadt et al. 2004; McDonald and St Clair 2004; Alexander et al. 2005; Clevenger and Waltho 2005; Barnum et al. 2007). In modelling the effect of road traffic on amphibian species, Carr & Fahrig (2001) incorporated pond variables into their models of traffic density. The relationship between stream length and frog dispersal was thought to be a major factor in understanding frog road-related mortality. Seiler (2005), along with measures of landscape and road and traffic data, incorporated a measure of moose density/abundance (although this variable was not spatially-explicit) in the modelling process. This information was based on hunting records, but its inclusion was only used to explore whether controlling moose density could be used as a measure of reducing moose fatalities. Seiler (2005) noted that better knowledge of moose abundance and the occurrence of preferred forage may have improved the predictive power of the models. Both Jaeger *et al.* (2005) and Jaarsma, van Langevelde & Botma (2006) considered species-specific characteristics, but only in reference to crossing behaviour or characteristics that may make species more susceptible to collisions with vehicles. Use of species specific habitat use in fatality models has to date received minimal attention.

As a large, wide-ranging herbivore, the common wombat as a study species has wide applicability for highlighting the importance of incorporating habitat use in fatality models. Despite common wombats being territorial in nature, such high site fidelity is not necessary for species-specific measures of habitat use to be important in fatality models. Other indirect methods of habitat use can be used to model target species (e.g. nests, tree hollows, and tracks) that coupled with habitat use variables can improve the performance of fatality models.

The demand for solutions to decrease animal-vehicle collisions is driving the development of predictive fatality models. Improved predictive modelling can be achieved by incorporating variables that describe species distributions in the landscape and careful *a priori* consideration of which predictor variables should be modelled. Ideally, selection of predictors should be based on knowledge of the species being modelled and that are correlated with species distributions. If mitigation of animal-vehicle collisions is to be successful, we suggest that monitoring of species occurrence and movement within the landscape is vital for the development of accurate, reliable and robust models of fatality hotspots. Failure to do so reduces the ability to understand the role of habitat characteristics in determining species distributions and the susceptibility of fauna to collisions with vehicles.

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Chapter 4

Road impacts a tipping point for wildlife populations in threatened landscapes

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Key words: common wombats; habitat use; landscape connectivity; pva; RAMAS GIS; road-kill.

Abstract

The conservation of wildlife populations living adjacent to roads is gaining international recognition as a worldwide concern. Populations living in road-impacted environments are influenced by spatial parameters including the amount and arrangement of suitable habitat. Similarly, heterogeneity in threatening processes can act at a variety of spatial scales and be crucial in affecting population persistence. Common wombats (*Vombatus ursinus*) are considered both widespread and abundant throughout their eastern Australian continental distribution. They nevertheless face many threats, primarily human induced. As well as impacts from disease and predation by introduced species, high roadside fatality rates on many rural roads are frequently reported. We parameterized a model for common wombat population viability analysis within a 750 km² area of the north-western corner of Kosciuszko National Park in New South Wales, Australia and tested its sensitivity to changes in the values of basic parameters. We then assessed the relative efficiency of various mitigation measures by examining the combined impact from roads, disease and predation on wombat subpopulation persistence in the area. We constructed a stage-structured and spatially-explicit model incorporating estimates of survival and fecundity parameters for each of the identified subpopulations using RAMAS GIS. Estimates of current threatening processes suggest mitigating road-kill is the most effective management solution. Results highlight the importance of recognizing the interplay between various threats and how their combination has the capacity to drive local depletion events.

Introduction

Human impacts pervade most ecosystems, while the range of potential and documented impacts are extensive and often vary across species, populations and through space (Johnson et al. 2005). The effect of roads and traffic on habitat and wildlife is far-reaching, affecting both the biotic and abiotic environment. Worldwide, estimates suggest that up to 20% of land in developed countries is affected by roads (Forman 2000). Roads can alter the quality of habitat surrounding a roadway, impede wildlife movement, are directly involved in the loss of habitat, and result in high mortality of individuals living within their boundaries (Forman and Alexander 1998). The loss of individuals to road mortality can affect the structure, growth, and persistence of roadside populations (Fahrig 2007; Fahrig and Rytwinski 2009). How these individuals are replaced has not been addressed, and it remains as a pertinent ecological possibility that road-based fatalities may be influencing dynamics of subpopulations far from the road.

Recent reviews have highlighted the need to stop thinking about the effects of roads linearly and think in terms of landscape (Spellerberg 1998; Forman et al. 2003). Disappointingly, few attempts have been made to associate the impacts of roads with landscape level responses (Roedenbeck et al. 2007). Habitat modification as a result of road construction can transform landscapes into discrete habitat patches (Ovaskainen and Hanski 2003). Species that evolve in patchy habitat and have high movement probabilities, readily move through many cover types, including high risk matrix habitat (Fahrig 2007). These species are predicted to be highly susceptible to decreased immigration, due to increasing patch isolation, and increased probability of mortality during movement in the matrix (Fahrig 2007). Spatial patterning in landscape structure and threats is therefore important in determining the capacity of an area to sustain viable

populations. While this importance is often clear for already listed threatened species, the contribution of local populations to species persistence is often missed for common species until the species is in decline.

Species are often considered common if they have extensive ranges and are abundant. Often few data exist on these species as they are typically not prioritized in conservation efforts (Gaston and Fuller 2008). Information on variation in population densities and range extent is generally of better quality for species with restricted ranges or endangered status (Gaston and Fuller 2007), thereby reducing the capacity of conservation agencies to detect declines in widespread species. In addition geopolitical boundaries often affect the comprehensiveness of data, as species status can vary between states and countries which share migratory species. Common species have crucial roles in maintaining ecosystem function and structure (Smith and Knapp 2003), where even small declines in abundance of common species can result in significant absolute losses of individuals and biomass (Gaston and Fuller 2008). In the absence of monitoring, depletions of common species frequently go unnoticed.

In Australia, concern has been raised over the potential decline of the common wombat (*Vombatus ursinus*) (Triggs 1988). Common wombats are often considered abundant throughout their extensive range (Buchan and Goldney 1998), covering much of the temperate region of eastern Australia. They are adaptable, utilizing a variety of habitats, although there is evidence that their distribution has declined at the extremes of their range, particularly in western Victoria, southern Queensland, and northern South Australia (McIlroy 1995; Buchan and Goldney 1998). This range reduction is largely anecdotal, as there are few data describing population distributions or how different threatening processes are contributing to this decline.

Fragmentation resulting from habitat loss is without doubt a major contributor to decline of many native species. Use of edge habitat, in particular agricultural areas, has promoted the thought that common wombats are one of the few intermediate sized species to be somewhat resilient to fragmentation (Borchard et al. 2008). However, because they sometimes cause damage to fencing, farmers typically consider them as pests and have adopted several potentially harmful management techniques (Borchard and Collins 2001). Three other threatening processes are likely to have contributed to their range reduction: predation, disease, and road-kill. Common wombats have few native predators, with the dingo (*Canis lupis*) and Tasmanian devil (*Sarcophilus harrisii*) being exceptions (Triggs 1988). On mainland Australia juvenile mortality has been attributed to both the introduced red fox (*Vulpes vulpes*) and wild dogs (May and Norton 1996). Extended periods of drought exacerbate disease outbreaks and can cause wombats to be more susceptible to predation (Triggs 1988). The most prevalent disease affecting common wombats is sarcoptic mange, caused by a parasitic mite (*Sarcoptes scabiei*) that affects the skin (Martin et al. 1998). Mange is widespread and usually fatal; a main vector of transference is the red fox (Skerratt 2001). The impact of roads on wombat populations is poorly understood, with very little data on numbers killed. Road-killed individuals have been reported to account for at least half of the total localized population in areas where such data are available (Roger and Ramp 2009). Although information on each of these threats exists, their impact has only been examined separately, not in conjunction.

Spatial analysis of the pattern of the impact of various threats in relation to variation in habitat suitability is necessary in order to develop an understanding of the persistence of common wombats at landscape extents. To address this we parameterized a demographic model on the basis of our own field data and published findings.

Through a sensitivity analysis, we assessed which parameters most strongly affected common wombat population trajectories. Then we applied the model to a system of 7 habitat patches (i.e., subpopulations) where a spatially-explicit population viability analysis was used to evaluate the efficacy of three management strategies. Our aims were 1) to explore the impact of various threats on wombat populations; 2) to examine the benefits of different management strategies in mitigating threats to population persistence. The role of management in mitigating the impacts of different threats across the landscape is crucial to the development of appropriate and holistic conservation strategies for species like the common wombat.

Methods

Study area

The study was conducted in a 750 km² area near the township of Tumut (35°19'S, 148°14'E), incorporating the northwestern boundary of Kosciuszko National Park (35°29'S, 148°33'E) in southern New South Wales, Australia (Fig. 1). It is a patchy landscape extensively modified by humans, with a matrix of native forest, private farmland, state forest, and reclaimed conservation land. Because individuals remain connected through matrix habitat we use the term subpopulation to define individuals occupying distinct habitat patches within the greater network of populations. Vegetation includes almost equal parts of cleared land, shrubland consisting of blackberry thickets (*Rubus fruticosus*), patches of bracken fern (*Pteridium esculentum*) and briar bushes (*Rosa rubiginosa*), and both moist and dry forest. The Snowy Mountains Highway (speed limit 100 km h⁻¹) runs parallel to the Blowering Reservoir and fragments an expansive grassy foreshore from the western boundary of Kosciuszko National Park. Common wombats utilize the foreshore, the open pasture of adjacent agricultural areas, and forested areas. They share the area with other native and introduced fauna;

including kangaroos (*Macropus giganteus*), swamp wallabies (*Wallabia bicolor*), emus (*Dromaius novaehollandiae*), feral pigs (*Sus scrofa*) and European rabbits (*Oryctolagus cuniculus*) (Lindenmayer et al. 1999; Roger et al. 2007). Feral animals and sarcoptic mange are both prevalent in this area (E. Roger, unpublished data).

Study species

Common wombats are slow breeders, producing on average one young every two years (Triggs 1988). They have home ranges that vary between 5 and 25 hectares, dependent on habitat quality and patch structure (Buchan and Goldney 1998; Banks et al. 2002a; Banks et al. 2002b; Skerratt et al. 2004a). As burrow dwelling animals, wombats emerge from their burrow at dusk and re-enter at dawn. They generally have at least four major burrows, distinguishable from minor burrows by their larger than 2100 cm² opening size (McIlroy 1973; Triggs 1988). They are edge specialists, preferring landscapes with a mix of open and closed forest close to watercourses or drainage lines. This preference to modified landscapes brings considerable cost as they are frequently killed on roads in proximity to areas that have been cleared for stock grazing (Roger and Ramp 2009).

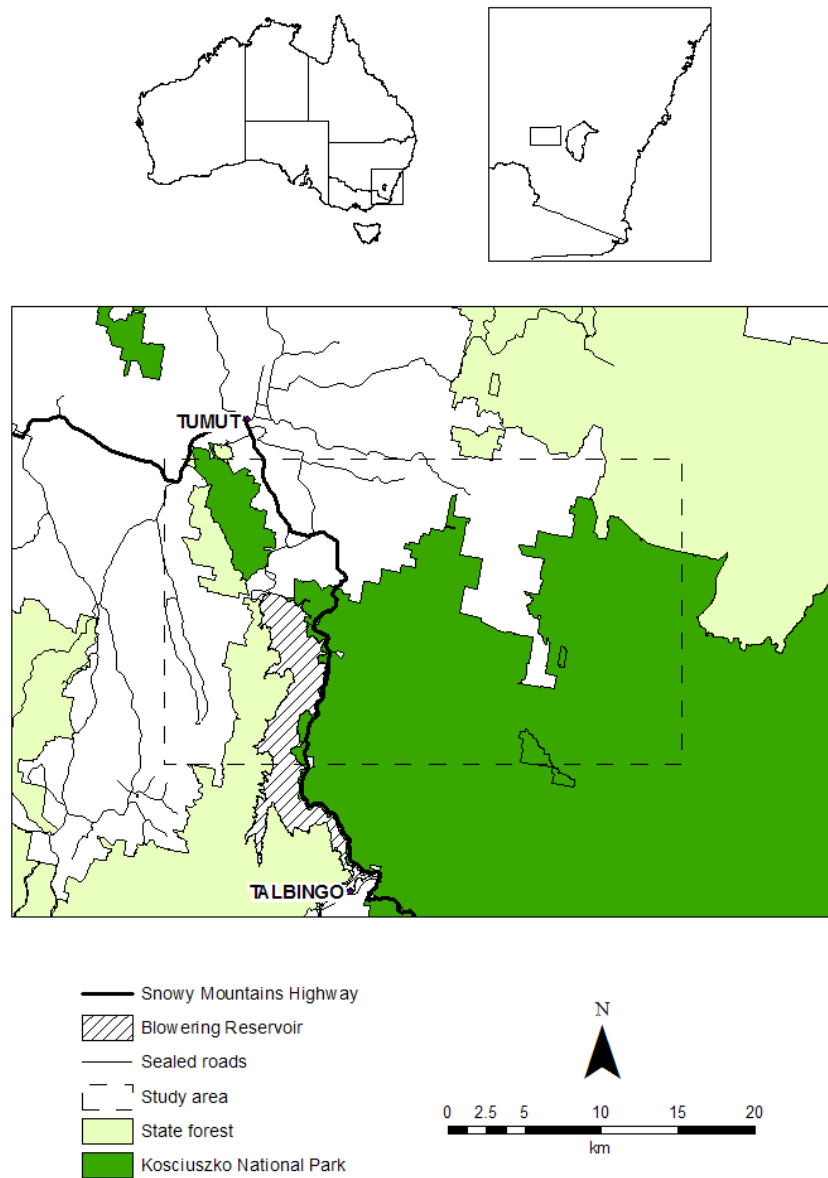


Figure 1. The study area is bound in the west by the State Forest (light green), with the Snowy Mountains Highway running along the eastern side of the Blowering Reservoir (hatched). The western extreme of the site is bound by the Goobarragandra Region which is the north-eastern boundary of Kosciuszko National Park (dark green). Cleared areas are represented by white coloring.

Data collection

Habitat use was determined by recording the location of common wombat burrows in the study area (Roger et al. 2007). Variations of wombat density have been shown to be correlated with the placement of the burrow within a landscape (Downes et al. 1997), primarily because wombats construct burrows in relation to physiographic features of the landscape. Burrow surveys were conducted in 2006 by systematically surveying a sub sampled area of the landscape on foot, following Rishworth *et al.* (1995). The sub sampled landscape was comprised of ten survey blocks randomly stratified across the study area. Transects within each survey block spaced lengthwise 50 meters apart and running east-west were traversed by two observers. Each transect ran for an average distance of 1000 m. Approximately 100 transects per observer were traversed in total, covering a surveyed area of 10 km². Burrow locations were recorded using a global positioning system (GPS) device. A raster layer of burrow location data was then created in ArcGIS 9.2 (ESRI 2007). A total of 320 burrows were recorded.

Roadside fatality rates

Fatality rates of roadside populations were determined from five years of fatality data recorded between March 2002 and April 2007 along a 15 km segment of the Snowy Mountains Highway. Fatalities were recorded using a hand-held GPS device (Garmin II Plus) following (Ramp et al. 2005). The road was travelled twice daily five days per week. The annual mean number of wombats killed on the highway (26.7 ± 13.79 killed per year, mean \pm standard deviation) is 40 % of the projected total roadside population (approximately 40 to 60 individuals) (Roger and Ramp 2009). Annual patterns of the number of wombats killed appear to be cyclic and this is reflected in patterns of

occupancy of burrows. Clusters of occupied and abandoned burrows varied temporally, reflecting temporal patterning in road-kill hotspot locations (Roger and Ramp 2009).

Habitat suitability model

Explanatory variables selected for inclusion in the habitat suitability model were the same variables included in a previously published model conducted in the same sampling region (Roger et al. 2007). Predictor variables were provided by the New South Wales Department of Environment and Climate Change (DECC) in the form of digital raster maps with a resolution of 100 m (acquired July, 2007). Predictor variables sampled in ArcGIS 9.2 (ESRI 2007) at each of the 320 burrow locations included: percent forest cover, distance to rivers, foliage projective cover (FPC) and a burrow clustering (kernel density analysis) measure (Silverman 1986). Percent forest cover was derived from LANDSAT data and used to calculate the proportion of forest cover surrounding each burrow, created by using the Euclidean distance function within ArcGIS. Foliage projective cover (FPC) was calculated as the percentage of ground area covered by the vertical projection of photosynthetic tissue, generated via a regression of reflectance values and ground values (Lu et al. 2003). FPC was used as a surrogate for NDVI-SD used in Roger et al. (2007) due to a lack of NDVI coverage availability. Distance to rivers was calculated by using the Euclidean distance function within ArcGIS and is the distance from burrow to the closest water source.

Presence only Generalized Additive Models (GAMs), within the software package R (R Development Core Team 2005) were constructed for each possible combination of predictors based on the sampled kernel density values (the response variable). To validate the models we ran a bootstrapping procedure using the .632 estimator rule, which is suitable when distributions are unknown (Hastie et al. 2001),

and can outperform cross-validation (Efron 1983; Efron and Tibshirani 1997). This approach provides a predictive performance estimate of a model without the expense of collecting a completely new model testing set (Wintle et al. 2005a). Once the final model (which included all three predictive variables) was selected, kernel values were predicted across the entire study area at a resolution of 100 m (to better reflect the habitat scale at which wombats operate). Subsequently, the predicted raster was then imported in RAMAS GIS (Akçakaya and Raphael 1998; Akçakaya 2000; Akçakaya et al. 2004) to derive a subpopulation map for further patch network analysis (Akçakaya and Atwood 1997).

We linked the habitat suitability map to the common wombat stage matrix (see below) using a habitat suitability threshold and a measure of average home range (neighborhood distance) (Akçakaya and Atwood 1997). The threshold for habitat suitability was defined by the minimum habitat suitability value below which wombat habitat is not considered suitable for reproduction and survival (0.32): determined using the Jenks' Natural Breaks method within ArcGIS (ESRI 2007). The Jenks' natural breaks classification scheme determines the best arrangement of values into classes by iteratively comparing sums of the squared difference between observed values within each class and class means (Brewer and Pickle 2002). Neighborhood distance was parameterized such that any two suitable points within 320 m of each other were considered part of the same habitat patch, where 320 m is the diameter of the mean reported home range for wombats (McIlroy 1973; Buchan and Goldney 1998; Skerratt et al. 2004a).

Model for Demographic Simulations

We used RAMAS GIS to analyze the viability and structure of the subpopulations. This interface allowed us to build stage-structured spatially explicit models with patch-specific model demographic parameters and dispersal rates. We built discrete-time models on the basis of a stage matrix with environmental stochasticity, density dependence, and effective dispersal rates among local subpopulations. We ran 10,000 replicates for each 100-year simulation which allowed us to compute the risk of decline: the probability of decline by a given amount from the initial population size (Stevens and Baguette 2008). Seven common wombat subpopulations (patches) were identified as occupying the study landscape.

Stage-matrix parameters

Dynamics within each patch were modeled using a stage-matrix based on the survival and reproductive parameters of pouch young (aged 0), juveniles (aged 1), and one adult class (2+) (Table 1). Wombats are a polygamous species and the absence of sexual dimorphism is thought to reflect little variation in reproductive success between sexes (Banks et al. 2002a). We modeled both males and females separately in the stage-matrix. This was done because studies have demonstrated a higher proportion of adult females within a population; this, combined with a higher ratio of juvenile males, is thought to reflect reduced juvenile male survival rates (Skerratt et al. 2004a).

The age of first reproduction was set at two years of age (McIlroy 1973; Banks et al. 2002a; Skerratt et al. 2004a), with a 0.45/0.55 female to male sex ratio at birth (Skerratt et al. 2004a). We specified that 84 % of female adult wombats breed once every two years (Skerratt et al. 2004a) with a maximum survival age of ten years (McIlroy 1973; Triggs 1988). We defined the mean wombat litter size as 0.5 pouch

young per year; twins have been reported but are extremely rare (Triggs 1988). Age specific survival rates were based on estimates calculated by Banks et al. (2002a; 2002b) and Skerratt et al. (2004a) (Table 1). All populations had the same demographic rates (we assumed equal levels of threatening processes throughout populations) with the exception of the roadside populations which had a reduction in survival of 40 % in accordance with number of individuals killed on the road per population estimate (Roger and Ramp 2009).

Table 1. Stage matrix for the common wombat specifying annual reproductive and survival input parameters which are multiplied by the relative survival and fecundity values specified in each population's dialog box.

Adult				Adult			
	Pouch	Juvenile	2+		Pouch	Juvenile	2+ years
	Young		years		Young		
<i>Female</i>				<i>Male</i>			
Fecundity	0.0	0.18 ^a	0.18 ^a	Fecundity	0.0	0.22 ^b	0.22 ^b
Survival	0.8	0.0	0.0	Survival	0.80	0.0	0.0
Survival	0.0	0.90	0.0	Survival	0.0	0.85	0.0
Survival	0.0	0.0	0.97	Survival	0.0	0.0	0.97

^a Number of female offspring produced per adult female.

^b Number of male offspring produced per adult female.

Fecundity was calculated as 1.0 (litter size)*0.84 (percentage of females that reproduce)*0.5 (females reproduce once every two years)*0.97 (annual female survival rate) =0.4074.

Table 2. Current (2009) best estimate values of parameters used in population modeling for common wombats in study area, southern NSW, Australia.

Parameter	Value	Reference
Type of mating system	Polygamous	(McIlroy 1973)
Age of first reproduction (females)	Two	(McIlroy 1973; Banks et al. 2002b; Skerratt et al. 2004a)
Age of first reproduction (males)	Two	(McIlroy 1973; Banks et al. 2002b; Skerratt et al. 2004a)
Age after which adults do not reproduce	Ten	(McIlroy 1973; Triggs 1988)
Sex ratio at birth F:M	0.45/0.55	(Skerratt et al. 2004a)
Fertility	0.5	(Skerratt et al. 2004a)
Maximum litter size/ year	1.0	(Triggs 1988)
% females breeding annually	84 %	(Skerratt et al. 2004a)
Breeding	Polyoestrous	(Triggs 1988)
Parentage analysis	1.8 females/ male	(Skerratt et al. 2004a)
% Adult females dispersing	80 %	(McIlroy 1973; Banks et al. 2002a; Banks et al. 2002b; Skerratt et al. 2004a)
% Adult males dispersing	20 %	(McIlroy 1973; Banks et al. 2002a; Banks et al. 2002b; Skerratt et al. 2004a)

Limitations to exponential growth

As common wombats are territorial in nature, aside from breeding individuals and females rearing young (Triggs 1988), we specified that all vital rates in the model would be affected by density dependence under a ceiling type model. Each subpopulation was assigned a carrying capacity (K). Under this model the population was allowed to grow exponentially until it reached K , remaining there until the population declined because of mortality, environmental stochasticity or emigration (Haines et al. 2006; Stevens and Baguette 2008). If abundances increased above carrying capacity (corresponded to a stable distribution of life stages with 0.3 wombats per hectare of habitat (McIlroy 1973), then it was decreased to the ceiling.

Dispersal

Dispersal was modeled as the proportion of individuals moving from one patch to another (Akçakaya 2000). Dispersal rates among patches were based on a dispersal-distance function fitted to the data on the reported total dispersal distance. Results of the RAMAS Spatial Data program calculated distances between habitat patches, which we specified to be the shortest distance from patch edge to patch edge. We used the RAMAS Metapopulation program to calculate a dispersal-matrix which defined dispersal rates based on distance between habitat patches, with a maximum dispersal distance of 10 km. In addition we specified stage-specific dispersal within RAMAS GIS stating that 80 % of adult females would disperse annually while just 20 % of adult males would (Banks et al. 2002b). Wombats are one of the few mammal species where dispersal is female biased (Banks et al. 2002b; Skerratt et al. 2004a), although the extent of this bias is currently not clear as conflicting findings exist (Banks et al. 2002a). All models assumed density dependent dispersal predisposition and dispersal ability. As dispersal mortality has not been documented in common wombats no additional mortality was set for dispersing adults.

Sensitivity Analysis

In common wombats, there are two main causes of variation in survival: 1) biotic causes (diseases, competition, predation) and 2) anthropogenic causes (road-kill, culling). We conducted sensitivity analyses to examine how the key threatening process of road-kill impacts on subpopulation persistence, uncoupled from variations in survival parameters within the stage matrix. Variations in survival were modeled as the number of common wombats that would normally survive annually in the absence of road-kill. Variations in

the percentage of individuals killed annually on roads were then applied to those individuals.

We performed a sensitivity analysis on seven model parameters to assess the degree to which perturbations in each affected population viability. These were fecundity, juvenile survival, adult survival, initial abundance (N), carrying capacity (K), and dispersal rate.

We tested sensitivity of the model by varying fecundity between 0.4 and 0.6 pouch young per female per year. We varied male and female survival of adults and juveniles by $\pm 10\%$. Those range of values corresponded to demographic values reported for common wombat populations (Banks et al. 2002a; Banks et al. 2002b; Skerratt et al. 2004a). We ran a series of simulations in which we varied N and K between 0.12 and 1.9 wombats per hectare of habitat in the stable distribution of life stages which corresponds to the range of reported common wombat densities (Evans 2008). To test for sensitivity to dispersal rate, we varied dispersal rates by $\pm 10\%$. To identify which assumptions significantly changed model results, we used the Comparison of Results program Kolmogorov-Smirnov test statistic (Akçakaya 2000), which is the built-in comparison of sensitivity results within RAMAS GIS.

Applications

Seven common wombat subpopulations were identified as occupying the study landscape (Fig. 2). We assessed the impact of three simulated conservation actions and their combinations, totaling seven scenarios. A control scenario was used to represent current fecundity, dispersal, and survival rates and assumed that no recovery strategies would be implemented within the next 100 years. A road-kill scenario was used to simulate the effect of a 20 % reduction in road-kill on subpopulation trajectory (an

increase of half of the total estimate of individuals killed). A disease scenario was used to model the population effects of increased survivorship and fecundity by assuming treatment would increase fecundity and survivorship by half (11 %) of the proportion of individuals affected by mange (22 %) within the population. A predation scenario was used to simulate a 20 % release from predation of juveniles as 20 % is the current target for the reduction of feral predators in the region by the DECC (Jo Caldwell, pers. comm.).

We compared the four scenarios using the Kolmogorov-Smirnov test statistic D , which measured the maximum vertical distance between risk curves of two or more different model scenarios (Akçakaya 2000). We compared the probability of a 50 % risk of decline when $p < 0.001$ (which is the default measure of statistical significance in the RAMAS program). Based on these tests we ranked the effectiveness of each scenario and the effectiveness of possible recovery strategies.

Finally, we tested for the effect of landscape context. We simulated the trajectory of all seven of the subpopulations, with varying exchanges of percentages of dispersing individuals, and compared the length of extinction for each local subpopulation.

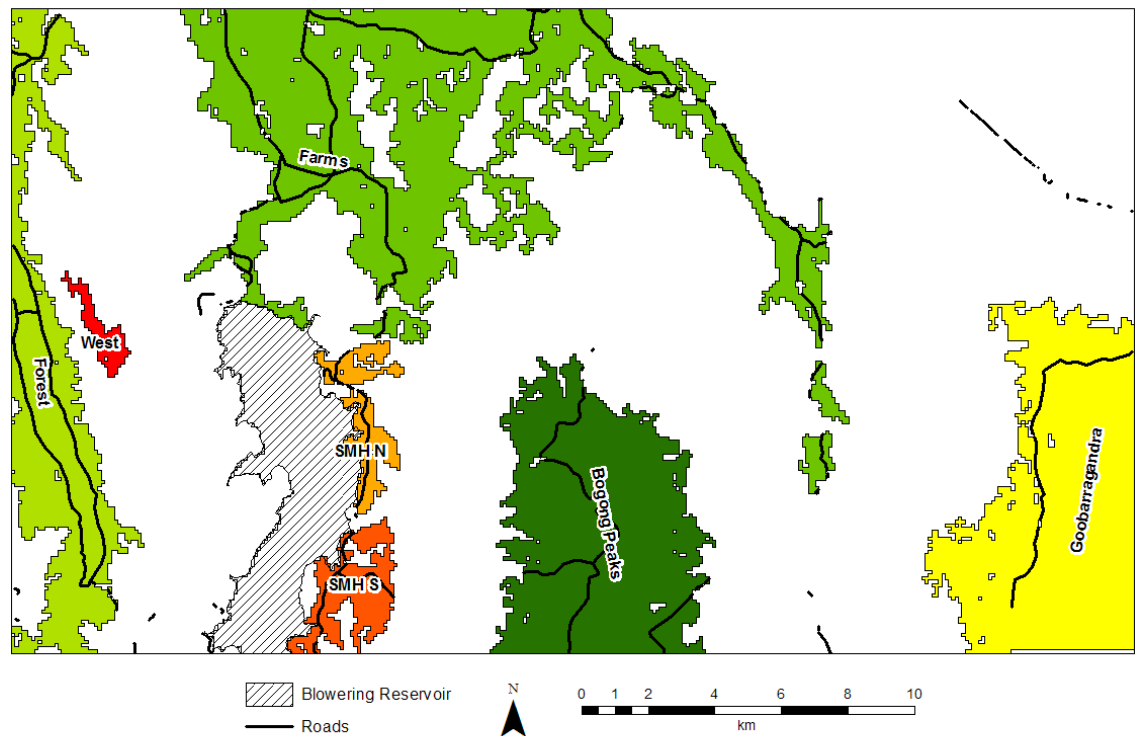


Figure 2. Seven habitat patches (subpopulations) were identified across the study area: Bogong Peaks, Farms, State Forest (Forest), Goobarragandra, Snowy Mountains Highway North (SMH N), Snowy Mountains Highway South (SMH S) and Blowering West (West). The Blowering Reservoir and major roads are also indicated.

Results

Habitat suitability model

The habitat suitability model included all three predictor variables: percent forest cover, foliage projective cover and distance to rivers. The final model explained 55 % of the deviance indicating the model had good explanatory power (AUC 0.770) (Table 3). The mapping of suitability indicated that much of the area had moderate to good suitability with the exception of heavily forested areas (Fig. 3).

Table 3. Deviance explained by the final model along with degrees of freedom (d.f.) with the AUC value.

Final model	Null	Residual	% deviance explained	AUC
forest + fpc + rivers	1584060 (d.f.=227)	718065 (d.f.=210)	55	0.770

Symbols for predictor variables occurring in model set are percent forest cover (forest), foliage projection cover (fpc) and distance to rivers (rivers).

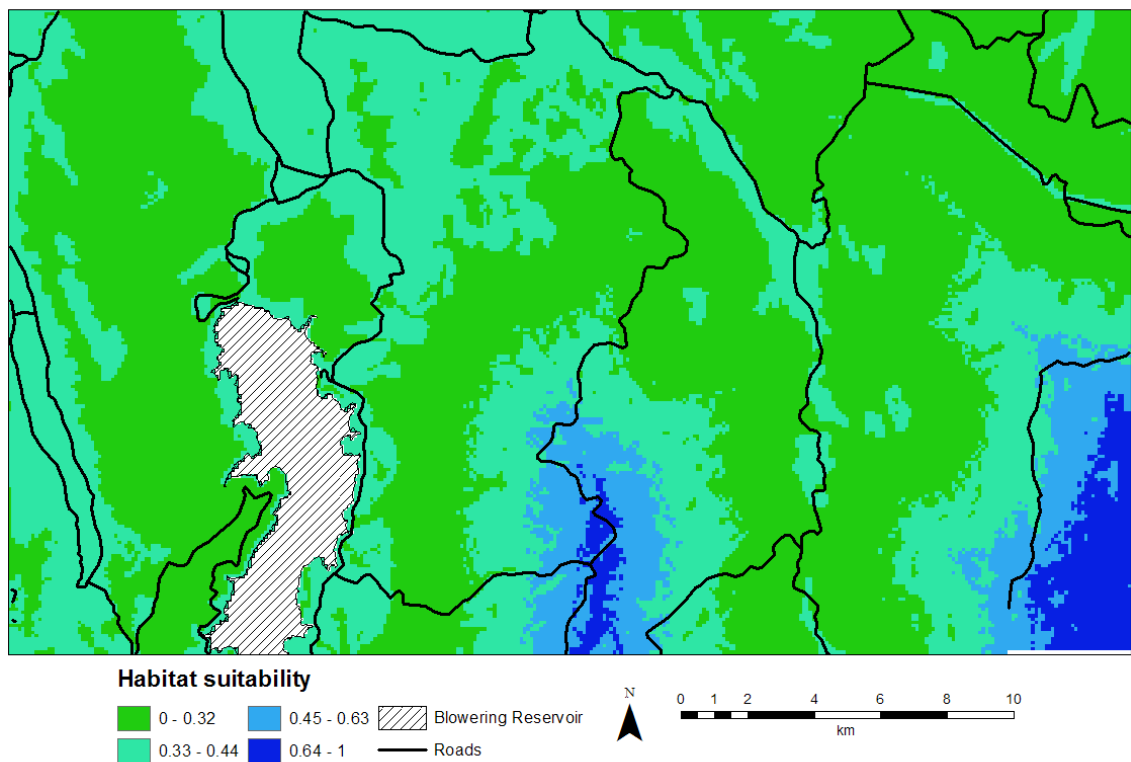


Figure 3. Habitat suitability values across the study area.

Sensitivity analysis

Populations with high levels of road fatalities (40 %) had high probability of a 50 % risk of decline, whatever the value of the other parameters in the model (Table 4). The reverse was true for populations with 10 % annual road fatalities which always had low probabilities of a 50 % risk of decline. Populations with intermediate road fatalities were more sensitive to variation in demographic parameters: changes in juvenile

survival and fecundity and to a lesser extent adult survival affected the future of these populations (Table 4).

The demographic model was nearly insensitive to (N) and (K) when populations sustained large annual amounts of road-kill. Populations with 40 % annual road fatality always presented high probability of risk of decline even for the largest (N) and (K) values (Table 3). The model was not overly sensitive to varying dispersal by ± 10 %; much larger increases in dispersal would likely be needed to sustain populations with moderate to large numbers of annual fatalities (Table 4) and (Fig. 4).

Table 4. Sensitivity analysis for the common wombat population viability analysis

Parameter	Value	Probability of 50 % decline from the initial population size		
		10 % road mortality	25 % road mortality	40 % road mortality
Null models		<0.01	<0.01	0.62
Fecundity	0.4	<0.01	0.09	0.44
	0.6	<0.01	<0.01	0.39
Juvenile survival	-10 %	0.16	0.44	0.85
	+10 %	<0.01	<0.01	0.24
Adult survival	-10 %	0.07	0.38	0.81
	+10 %	<0.01	0.27	0.18
N	0.12	<0.01	0.02	0.42
	0.23	<0.01	0.01	0.27
	0.5	<0.01	<0.01	0.10
	1.9	<0.01	<0.01	0.05
K	0.12	<0.01	0.02	0.20
	0.23	<0.01	0.01	0.09
	0.5	<0.01	<0.01	0.01
	1.9	<0.01	<0.01	<0.01
Dispersal rate	-10 %	<0.01	0.20	0.68
	+10 %	<0.01	0.09	0.20

Null models correspond to populations where fecundity = 0.5 pouch young/female, male juvenile survival = 0.85, female juvenile survival = 0.90, female adult survival = 0.97, male adult survival = 0.97, initial abundance (N) = 1200, and carrying capacity K = 1400 in the stable distribution of life stages.

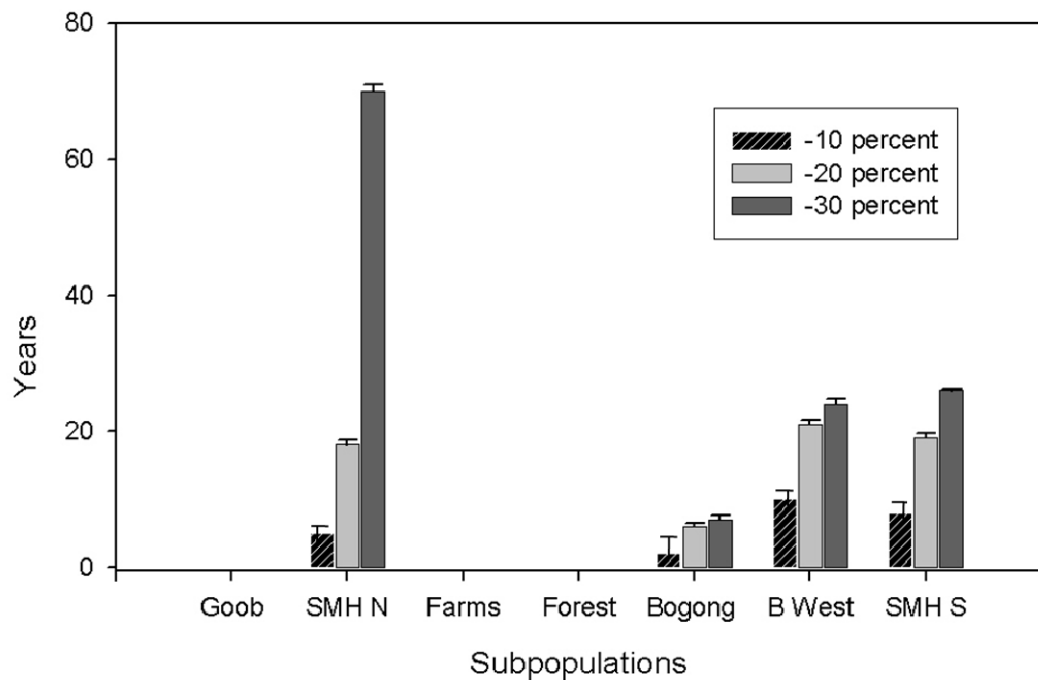


Figure 4. Summary of the maximum number of consecutive years a subpopulation remains unoccupied under three different dispersal scenarios (10 %, 20 % and 30 % reduction). Subpopulations are Goobarragandra (Goob), Snowy Mountains Highway North (SMH N), Farms, State Forest (Forest), Bogong Peaks, Blowering West (B. West) and Snowy Mountains Highway South (SMH S) over the simulated period of 100 years.

Applications

In the absence of conservation effort, the control scenario had the highest probability of a 50 % risk of decline (Table 5). All three additional management actions significantly enhanced the viability of the subpopulations, although their effects were not similar. As isolated recovery strategies, the road mitigation scenario was predicted to be the most effective in reducing the risk of decline. The combination of two or more conservation actions had additive effects (Table 5).

The connectivity of the subpopulations affected their persistence (Fig.4). The risk of decline for roadside and other subpopulations significantly increased when dispersal was reduced (Fig. 4).

Table 5. Results of eight habitat-based PVA scenarios during a 100 year period

Scenario	Np	N	Risk of decline (50 %)		R
			<i>P</i>	CI	
Control	3	613	0.93	(0.84-1.0)	1
Predation	5	620	0.89	(0.80-0.97)	2
Disease	6	782	0.02	(0-0.11)	3
Road	7	873	0.01	(0-0.09)	4
Predation + Disease	7	952	0.001	(0-0.09)	5
Predation + Road	7	1015	0.001	(0-0.09)	6
Road+ Disease	7	1025	0.001	(0-0.09)	7
Predation + Disease + Road	7	1027	0.001	(0-0.09)	7

Np, mean number of occupied patches; *N*, final population size; *p*, probability of decline as a function of 50 % decline from the initial population size; CI, 95 % confidence intervals; R, rank of recovery strategies from least to most effective based on the Kolmogorov-Smirnov test statistic of the quasi-extinction risk curve with significance $p < 0.001$.

Discussion

Population viability analysis (PVA) is an established tool used to identify threats faced by a species and evaluate the likelihood it will persist for a given time into the future (Chisholm and Wintle 2007). It is commonly used to assess threats faced by species as it enables the projection of population trajectories to evaluate sources of risk and potential mitigation strategies. Its advantages lie in the evaluation of alternative population and habitat management strategies (Larson et al. 2004; Kohmann et al.

2005), and highlighting ones that are most likely to provide valuable results. Our analysis revealed two important results for common wombat conservation. Firstly, road fatalities can be a decisive parameter in determining demographic trajectories of common wombats. Decreased survivorship in roadside subpopulations can result in reduced persistence of species within a patch network. Secondly, the connectivity of landscapes is an important parameter for population viability. A significant influence of connectivity on local subpopulations points to important source-sink dynamics, where dispersers contribute markedly to local dynamics (Jaquiery et al. 2008).

Management scenarios

The combination of high road-kill rates with impacts from mange and predation significantly reduced subpopulations. Anecdotal observations of decline in wombat numbers in the area complements this finding and provides justification for the implementation of conservation strategies targeted towards these threatening processes. Reducing the frequency of wombat fatalities on roads most decreased the probability of decline in the area. Importantly, evidence garnered on population level effects of species at local extents will raise concerns about the persistence of species in road environments throughout their distribution and help integrate wildlife needs into road design and planning (Jaarsma et al. 2006; Bissonette and Adair 2008; Bond and Jones 2008; Mata et al. 2008; Glista et al. 2009). Mitigation measures that would significantly reduce the amount of fatalities could involve the construction of wildlife fencing. The placement of wildlife crossing structures, along with additional mitigation measures, has also been shown to significantly reduce wildlife vehicle collisions for other animals (Bissonette and Adair 2008). Revegetation of cleared areas in proximity to the road would also

reduce the number of individuals living in proximity to the highway and hence the number of individuals killed (Roger and Ramp 2009).

Strategies aimed at reducing mange were ranked second amongst recovery scenarios. Mange is prevalent throughout the study area and can affect up to 22 % of wombats within a single population (Skerratt 2001). Although mange is often fatal for the infected individual, the benefits of wide-scale treatment targeting a 50 % improvement in infection rates was not as effective as reducing road fatalities in maintaining population persistence (Table 5). The feasibility of reaching a 50 % decline in infection is also doubtful as mange in wild animals is difficult to manage and animals often require repeated treatment (Skerratt et al. 1999; Hartley and English 2005). At present, treating mange on a landscape or population scale is a costly management option. Some alternatives in development however are promising, such as long-acting antibiotic treatment, or applicator devices fixed over burrow entrances that deliver small treatment doses. These measures would greatly facilitate control of sarcoptic mange in wombat populations by reducing the number of times that wombats would need to be caught for treatment (Skerratt 2001).

Strategies aimed at minimizing predation by introduced foxes and wild dogs were predicted to have the least impact on persistence (Table 5). Radio-tracking and mark-recapture studies have indicated wild dog densities between 1 to 6 individuals per km² in Kosciuszko National Park (Corbett 1995). Within the Park, the Department of Environment and Climate Change currently employs up to six dog trappers and two permanent staff dedicated to controlling wild dogs/dingoes, at an annual cost of \$33,938 (2006-2007) (English and Chapple 2002). The current management target is to maintain a wild dog abundance rating on bi-weekly monitored sand plots of less than 5 % (English and Chapple 2002). To match the projections of the road mitigation scenario,

the predation scenario would need to increase juvenile survival by an additional 30 %. It is doubtful whether this is an achievable target for management.

Through modeling we have shown that management strategies aimed at increasing populations via translocation would also prove ineffective in preventing common wombat decline. Increasing initial abundance (N) did not significantly modify projections in the sensitivity analysis (Table 4). Survivorship, particularly in roadside subpopulations, was too low as any increase in abundance was quickly offset by the high fatality rates attributed to the road

Landscape connectivity

Dispersal greatly affected local subpopulation persistence and highlighted the importance of immigration and connectivity in the area in maintaining current population structure. The risk of decline for roadside subpopulations was significantly higher when dispersal was reduced (Fig. 4). Given that roadside subpopulations appear persistent, albeit cyclic, these subpopulations must be supported by unsuspecting wombats migrating from source areas, drawn by high grazing quality and uninhabited territory. Loss of individuals to road-kill impacts the stability of these subpopulations, supporting the notion that patch networks of connected subpopulations mask the effects of localized extinction.

Limitations

The benefits of the PVA approach applied here to common wombats is its ability to contrast management strategies (Brook et al. 2000; Coulson et al. 2001). We provide a summary of the contributions of various parameters to extinction risk and rank the effects of various mitigation scenarios. Our analyses have three notable weaknesses.

First, we had to rely on published data from other populations for some demographic parameters. Second, by projecting populations over a time period of 100 years, we ignored changes in habitat suitability over time (we assumed a stable K). Hence, our estimates of extinction probabilities are not absolute forecasts. Thirdly, the bounds of our study area were arbitrary. We acknowledge that additional populations and subpopulations exist outside the periphery and ‘feed’ individuals into additional patch networks. Nevertheless, limitations aside, our analysis highlights key features that must be taken into account in landscape scale planning and management.

Conclusion

Historic and recent examples highlight that common species are not immune to becoming threatened or extinct (Farrow 1995; Rodewald et al. 2005; Bank et al. 2006; Gaston and Fuller 2008). Common species can readily succumb to population pressures (Gaston and Fuller 2007, 2008), yet legislation and management have been particularly slow in recognizing both their ecological importance and the precariousness of common species status. With much management focus principally concerned with threatened species there is lack of quantifiable information detailing current common species’ distribution and status. Furthermore, we suggest there is a tendency of equating native common widespread species with feral animals; viewing both as typically overabundant (common), widespread, and destructive. Given the importance of common species (Jetz and Rahbek 2002; Lennon et al. 2004), it has become all the more crucial not only to identify systems in which common species no longer perform key ecological functions (Gaston and Fuller 2008) but to monitor and mitigate factors that affect persistence.

The spatial configuration and connectivity of habitat patches in heterogeneous landscapes is often overlooked (Minor and Urban 2007). Dispersal among patches is a

key process in the survival of local subpopulations, while the existence of several or many populations is critical for species that inhabit patches in shifting landscape mosaics (Rohlf 1991). Loss of individuals can therefore affect the long term persistence of the larger population, particularly if an area is acting as an attractive sink (Delibes et al. 2001). The integration of spatially explicit population models with threats operating within the same domain allows management to determine the capacity of an area to sustain viable populations, while the potential effects of no management and alternative management strategies can also be examined (Dunning et al. 1995; Turner et al. 1995). Finally, It would be remiss to presume that threats act independently of each other and it is crucial to recognize the interplay between various threats when evaluating the long-term threat to species persistence.

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Chapter 5

Rethinking the impact of roads on common species persistence

Erin Roger, Daniel Ramp, Gilad Bino, and Shawn W. Laffan

In review Landscape Ecology

Key words: GAMs; habitat modelling, reserves; road-kill; spatial analysis; threatening processes

Abstract

Road development is strongly correlated with economic growth and natural resource degradation. To offset development, conservation reserves are charged with the task of preserving biota in a manner that facilitates resilience to global threatening processes. Yet reserves are not impermeable and many threatening processes breach their borders. Roads penetrate conservation areas and many high profile reserves contain surprisingly high densities of roads, an often overlooked threat. How important this infiltration is for populations will vary among species. Large numbers of common species are frequently killed on roads within reserves. However, largely due to perceptions of abundance, many common species are omitted from reserve management and mitigation plans. As a consequence, knowledge of the impact of roads on common species persistence over broad spatial scales is severely lacking, limiting our ability to quantify the degree of threat faced by species in road environments and hence also limiting the utility of reserves. Here we provide a landscape scale habitat analysis for a common species, the common wombat. We found that despite the broad distribution of the species (211,100 km²), 80 % of highly suitable habitat falls within the reserve network. However, areas of suitable habitat were found to be correlated with higher probabilities of wombat fatalities. Results suggest that reserves themselves are potential population sinks for road impacted species and that the level of protection offered by the reserve system cannot be assumed. Increased effort should be expended in evaluating how reserves confer resilience to species from the impacts of roads.

Introduction

Roads are strongly correlated with both economic growth and natural resource degradation, while their effects on biota can extend outwards hundreds of metres due to the road-effect zone (Forman and Alexander 1998; Wilkie et al. 2000; Bissonette and Adair 2008). The global expansion of road networks means there is a pressing need to assess the conservation implications of the impact of roads on biodiversity. To date, most research on roads has focussed on localised impacts over small spatial areas (Clevenger and Waltho 2000; Carr and Fahrig 2001; Ramp et al. 2005; Klöcker et al. 2006; Roger and Ramp 2009), but assessment over broad extents is also critical because the impact of roads can vary depending on the scale of investigation (Forman et al. 2003). Research suggests that road impacts can operate on a continuum that includes biogeographic, landscape, and patch level effects (Trombulak and Frissell 2000). This is important because some species may appear to be persisting in road impacted environments on smaller spatial extents (typically common species) but could be suffering large scale range reductions as a result. The concern is that dependencies between the population dynamics of local populations can lead to reductions in their abundances and ultimately lead to declines in overall species persistence (Gaston and Fuller 2008). Both landscape and smaller spatial scale extents need to be considered in order to assess the regional conservation significance of local management areas.

The importance of scale for impacts of roads has implications for biodiversity conservation efforts, for which the primary mechanism is the setting aside of reserves (Regan et al. 2008). Due to the variety and severity of threats facing wildlife, reserves are charged with the task of preserving biota in a manner that facilitates resilience to global threatening processes (McDonnell et al. 2002). Reserves are at the forefront of many regional and global conservation strategies, yet they are not impermeable and

many threatening processes breach their borders (Deguise and Kerr 2006). Because of this it has become crucial to quantify how effective reserves are at enhancing resilience to threatening processes (Pressey et al. 2000; Crofts 2004; Wilson et al. 2007; Alvaro Soutullo et al. 2008). Roads are an often overlooked threat that penetrate many protected areas, and many high profile reserves have surprisingly high densities of roads within them (e.g. Ramp and Ben-Ami 2006). Roads are a serious obstacle to maintaining ecological connectivity within reserves and wildlife populations in reserve areas are vulnerable to road impacts (Ramp and Ben-Ami 2006; Ament et al. 2008). Most reserves are structured to fulfil the dual roles of protecting resource values as well as providing for visitor enjoyment, but these roles are often difficult to balance as visitation can impact natural systems (Ament et al. 2008). Large numbers of common species are frequently killed on roads within reserves (Clevenger et al. 2003; Ramp et al. 2005) however, due to perceived abundances, many common species are often omitted from reserve management and mitigation plans.

Conservation investment routinely targets already threatened species and the areas where they are still found (McKinney and Lockwood 1999; Warren et al. 2001; Devictor et al. 2007), however anthropogenic threats also impact common species (Gaston and Fuller 2008). Common species are those species that are both abundant and widespread (Gaston and Fuller 2007). The response of common species to land use change remains largely unexplored, despite the fact that vulnerability to different risks is largely determined by a species' own ecology rather than their conservation status (Owens and Bennett 2000; Blumstein et al. 2005). Overexploitation has led to species extinction, such as the once common passenger pigeon (*Ectopistes migratorius*) (Farrow 1995), and there is growing evidence that large numbers of presently common species are undergoing considerable declines (Gaston and Fuller 2007, 2008). Given the

functional role many common species have in facilitating ecosystem processes (Gaston 2008; Gaston and Fuller 2008), maintaining viable and functional populations of common species is a vital component of biodiversity conservation efforts (Lennon et al. 2004; Lyons et al. 2005; Pearman and Weber 2007). As a consequence it is necessary to assess if reserve networks are able to support and sustain populations of common species. This is best achieved over a range of spatial scales because studies within a single reserve are often too small to capture the true risk to common taxa.

Here we investigate how roads affect the persistence of common species over large spatial scales and evaluate how effective reserves are at enhancing resilience. We quantify the percentage of core habitat that exists within the reserve network and assess if fatality rates are correlated with habitat suitability and road category. We then combine the two assessments to determine how much resilience is conferred by the reserve network. To achieve this, we develop a habitat suitability model for the common wombat (*Vombatus ursinus*); a typical example of a common species that is impacted by roads at small scales, but for which the risk over large scales has never previously been examined.

Methods

Study species

The common wombat is a common species which is thought to be both widespread and abundant throughout south-eastern Australia (McIlroy 1995). Little informative data describing population distributions across their range is currently available (Roger et al. 2007), although their distribution appears to have contracted southwards since European settlement (McIlroy 1995; Buchan and Goldney 1998). Common wombats are generalists that utilise a wide range of environments, largely because of their low energy requirements, and hence low food and water requirements (Evans 2008). Common

wombats are distributed within isolated pockets in southern Queensland (QLD) and South Australia (SA), but the majority of their range occurs throughout eastern New South Wales (NSW), Victoria (VIC), Tasmania (TAS), and the Australian Capital Territory (ACT) (Fig. 1).

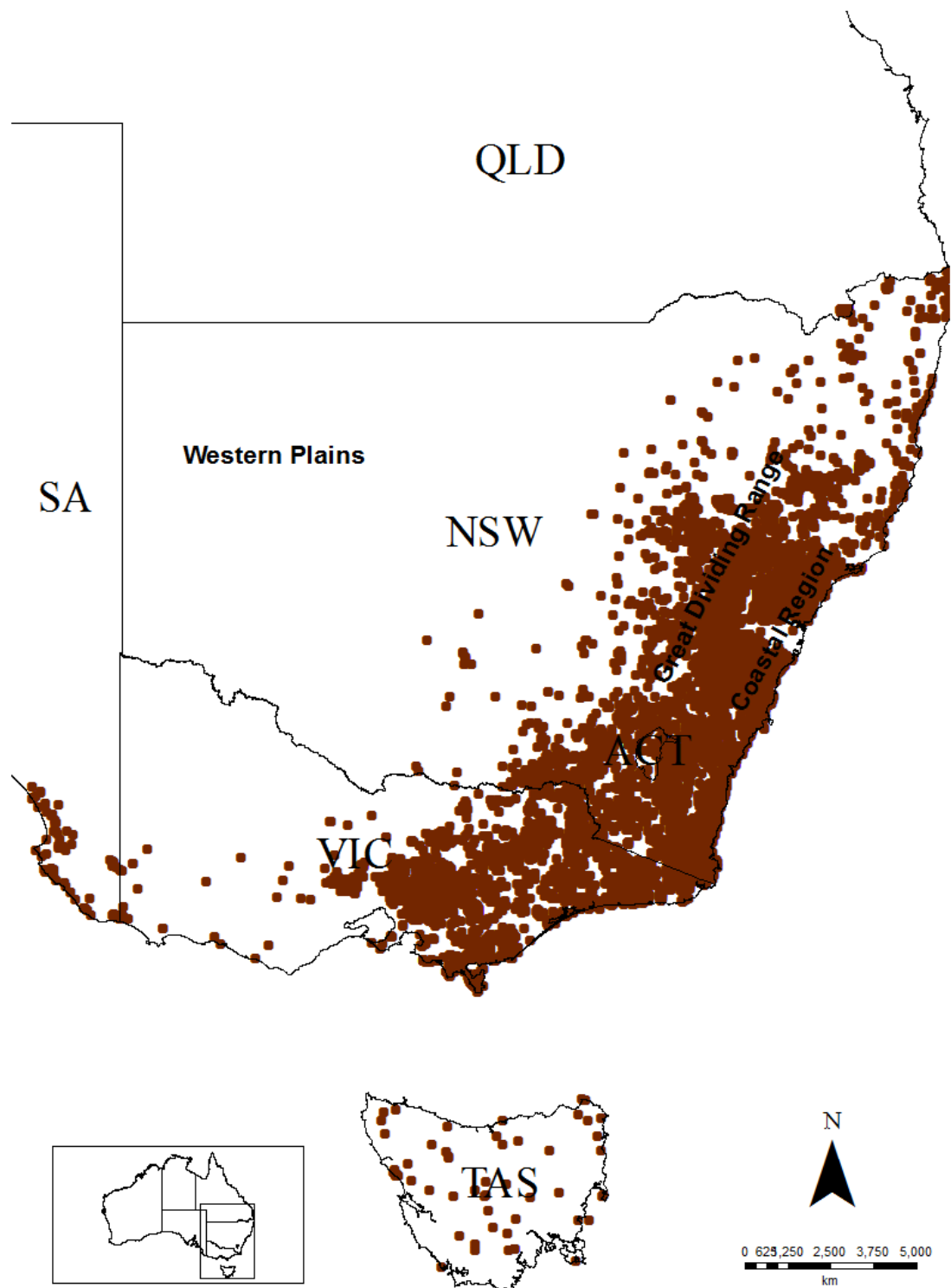


Figure 1. Sighting locations of common wombats across their range throughout south-eastern Australia.

Landscape modification since European settlement has unquestionably altered the abundance and range of many native species, including common wombats, although comprehensive evidence is lacking. Unlike many native species they can benefit from the clearing of native bushland which increases food resources (Evans 2008). Their broad niche suggests they are a relatively robust and adaptable species, reflected by their use of agricultural and other modified landscapes (Roger et al. 2007; Roger and Ramp 2009). This adaptation to modified landscapes brings considerable cost as they are frequently killed on roads in proximity to areas that have been cleared for stock grazing (Roger and Ramp 2009), and they are often the targets of culling by farmers on account of damage common wombats often do to fences (Borchard and Collins 2001). There are very few data detailing the frequency of wombat vehicle collisions and the number of associated fatalities across their range. At a local level, the evidence suggests road environments can act as attractive sinks, drawing animals from surrounding habitat to unoccupied quality grazing land, replacing individuals lost to collisions and thereby rapidly increasing the likelihood of further losses (Roger and Ramp 2009).

Study area

Here we present a landscape scale evaluation of common wombat habitat for the state of NSW and the ACT, an area that encompasses approximately half of the species' total distribution (Fig. 1). NSW is Australia's most populous state and is located on the east coast of the continent with an area of 810,000 km². The ACT is an enclave within NSW with a total land area of 2,400 km². The study area can be physically divided into three sections; a thin easterly coastal region, a mountainous region (the Great Dividing Range) running north-south, and the Western Plains covering almost two thirds of the state (Geoscience Australia Australian 2009). There are 752 reserves that are greater than 10 km² within the ACT and NSW, including 447 forestry reserves, 280 nature

conservation reserves, 24 water supply reserves, and one indigenous reserve with a total area of 86,164 km². Areas of established agricultural activity comprise by far the largest land area of the state (630,000 km²), with built-up areas comprising (2,903 km²) (Australian Bureau of Statistics Australian 2005). NSW has 184,118 km of roads that are grouped into five categories: freeways, highways, major roads, minor roads and tracks. The highest density of roads is in the east with only one interstate freeway running from central NSW into the state of Victoria. All road categories except freeways are found within reserves.

Habitat Suitability Modelling

The distribution of common wombats was derived from data provided by the NSW Department of Environment and Climate Change (acquired October 2008). Opportunistic sighting locations contained within the NSW Wildlife Atlas were used as presence points. These sighting locations are obtained by contributions from DECC staff, the Australian Museum staff, naturalists, environmental consultants, and land management officers. Species sighting data has been routinely used in species habitat modelling (Woolf et al. 2002; Hatten et al. 2005; Zarnetske et al. 2007) and were the best data available over a landscape scale extent from which to model the spatial distribution of probabilities of suitable habitat. The models estimate the probability of a wombat sighting which we also refer to as habitat suitability. To minimise any spatial errors associated with the data we discarded observations recorded prior to 1990 or that had a spatial uncertainty greater than 500 m.

We avoided the often criticised use of randomly selected pseudo-absence points (Zarnetske et al. 2007) by generating wombat absences from non wombat opportunistic sightings within the Atlas database. Although these locations are still pseudo-absences, their selection has advantages over randomly selected points because they have been

derived from the same dataset as the presence data, enabling the negation of sampling bias associated with frequently visited areas (such as survey plots in proximity to roads). To reduce false negatives we excluded absence points within the average home range distance of a presence point (circular sampling area with a diameter of 320 m) (Ramp et al. 2005). A total of 1,594 presence and 14,696 absence data points were used.

Environmental variables

We collated large scale environmental and climatic variables for the study area using small scale studies on common wombats to guide variable selection (Skerratt et al. 2004a; Roger et al. 2007; Evans 2008). The initial set of variables covered aspects of terrain, vegetation, and climate (Appendix A). A Digital Elevation Model (DEM) was obtained from the Shuttle Radar Topography Mission (SRTM) with a spatial resolution of 3 arc seconds (approximately 90 m) (Farr et al. 2007). Slope and aspect were derived from the DEM using ArcGIS 9.2 (ESRI 2007). Topographic wetness (an estimate of the accumulation of overland water flow across catchments), slope steepness (Moore et al. 1991), and roughness (Allmaras et al. 1966) indices were generated to describe the surface properties of the DEM. Data for Fraction of Photosynthetic Active Radiation (fPAR; a measure of canopy absorption) developed by Donohue et al. (2008), was downloaded from CSIRO Land and Water. Three indices of fPAR were used: (1) persistent fPAR (fper), which approximately represents non-deciduous perennial vegetation, (2) recurrent fPAR (frec), which approximates deciduous, annual, and ephemeral vegetation, and (3) the total fPAR (ftot = fper + frec). All available monthly measurements were obtained for each of the three indices, between 1996 and 2005. For each year the average and variance were calculated and the overall ten year average was calculated, providing six variables in total. An additional vegetation type raster layer (woody/non-woody) was obtained from DECC's 2008 NSW Interim Native Vegetation

Extent Dataset (DECC 2008). The presence of woody vegetation within a cell was scored as 1, with all other cells receiving a 0. Climatic variables across the study area were obtained using the correlative modelling tool BIOCLIM 5.1 (Nix 1986). Twenty seven climatic parameters were interpolated from recorded climatic data and elevation (Nix 1986; Houlder et al. 2000) (Appendix A).

Model development

We employed Generalised Additive Models (GAMs) within the R statistical environment (Version 2.8.0) (R Development Core Team 2005), using the ‘gam’ package (Version 1.0). We ran univariate logistic GAMs for the binary response of presence points for each of the 39 predictor variables. In order to avoid choosing collinear predictors in the final model we grouped the 39 variables into six categories. We selected the best variable from each group using the pseudo- R^2 (calculated as the 1-Deviance/Null Deviance). We constructed GAMs for each of the 64 possible combinations of the top six variables. To validate the models we ran a bootstrapping procedure using the .632 estimator rule, which is suitable when distributions are unknown (Hastie et al. 2001), and can outperform cross-validation (Efron 1983; Efron and Tibshirani 1997). This approach provides a predictive performance estimate of a model without the expense of collecting a completely new model testing set (Wintle et al. 2005a).

We evaluated model performance by calculating the area under the receiver operating curve (AUC), which can be used to evaluate the extent to which a model successfully estimates positive and negative observations and then ranks the observations accordingly (Hirzel et al. 2006). A best model was selected by identifying all models with an AUC within one standard error from the model with the highest AUC value. The one standard error rule is often used to find a more parsimonious

model than the top model selected in the model selection process (Hastie et al. 2001). Selection of the best model was made using a trade off between the models within one standard error that had the fewest numbers of predictor variables and the largest AUC value. Model selection was repeated using Akaike's Information Criterion (AIC), which was used as a cross-check on the model selection process (Table 1). Using the best model, we predicted wombat probability values across the entire study area at a resolution of 90 m.

Table 1.

Model results for wombat sighting probability. Table presents the number of models within one standard error (1SE) of the best model and the number of models containing the variable within 1SE of the best model for AUC. Findings from AIC model selection are also presented.

Model	Model Selection	Total # Models	Elev	fpar	mtcq	pwq	miwq	vtype
Sighting probability	AUC	7	7	7	6	5	5	7
	AIC	7	7	7	6	5	4	7

Symbols for predictor variables occurring in model set are elevation (elev), average total Fraction of Photosynthetic Active Radiation (fpar), mean temperature of the coldest quarter (mtcq), precipitation of the warmest quarter (pwq), mean moisture index of warmest quarter (miwq), and vegetation type (vtype).

Distribution and representation in reserves

We calculated the total distribution (km²) of the common wombat across the study area using ArcGIS. To exclude areas where common wombats are known not to occur, such as the Western Plains of NSW (McIlroy 1995), we removed probability values less than 0.07, determined using the Jenks' Natural Breaks method within ArcGIS (ESRI 2007). The Jenks' natural breaks classification scheme determines the best arrangement of values into classes by iteratively comparing sums of the squared difference between observed values within each class and class means (Brewer and Pickle 2002). We were then able to assess the representation of wombats within reserves by summing the

predicted suitability values within each reserve. To account for reserve area, we divided suitability values by total reserve area to derive the average suitability per unit area.

To identify areas of the most suitable habitat for wombats, also termed core habitats (Shen et al. 2008), we derived a ROC plot (receiver operating characteristic) by plotting all sensitivity values on the y axis against their equivalent 1-specificity values to obtain the optimal threshold that minimized misclassification errors (0.6) (Fielding and Bell 1997; Manel et al. 2001; McPherson et al. 2004). We classified cells greater than 0.6 as 1 and all other values as 0. To evaluate areas of the most suitable habitat contained within the reserve network we then used ArcGIS to calculate the percentage of core habitat that was contained within reserve boundaries.

Road impacts

We made use of two additional data sources to quantify the impact of roads on wombats. We obtained a NSW road layer from DECC (Appendix A). The road layer contained 2,632 segments of road throughout NSW, where a segment is a section of road from one intersection of road to another. The road layer was divided into four categories: freeways, highways, major roads, and minor roads (excluding unsealed roads). Our second data source was TADS (Traffic Accident Database System of NSW) which is a computer system that stores and produces statistics on road traffic accidents in NSW (Appendix A). Data are gathered and included in TADS only when road crashes are reported to NSW Police (Ramp and Roger 2008). There were 150 wombat related accidents recorded in the TADS database for the ten year period between 1996 and 2005. The TADS database was the best available data set that had the spatial extent required for the analysis. Data are not available that detail the number of wombats killed annually on roads in NSW and we recognise that the TADS database provides a gross underestimate.

In order to derive a measure of wombat road fatalities per kilometre of road within NSW we sampled all wombat fatality records contained in the TADS database using ArcGIS. Road segments without any recorded collisions were assigned zero. In order to account for variability in road use, the ratio between wombat related vehicle collisions and all other wildlife related vehicle collisions was then calculated and standardized by length of road segment. Finally, the average wombat fatality probability per 1 km of road per 10 years was generated for each category of road.

To assess the relationship between habitat suitability and the probability of a wombat fatality, we overlaid the suitability map with the road layer within ArcGIS. Suitability values were then averaged per road segment, weighted by the length of the segment using Hawth's Analysis Tools add-on for ArcGIS (Beyer 2004). Average suitability probabilities were stratified into four categories: low (<0.25), medium (<0.5), high (<0.75), and optimal (<1) which allowed us to calculate the probability of a wombat fatality in relation to categories of suitable habitat. We then examined the probability of a wombat fatality when taking both suitability category and road category into account. As a final measure of road impacts, we determined the percentage of the 'road effect zone' (Forman and Alexander 1998) within all reserves in the study area by constructing a 1 km buffer around each road using ArcGIS and dividing by total reserve area. A 1 km buffer was chosen based on previous research which has documented changes in wombat burrow occupancy up to 1 km from a road (Roger et al. 2007).

Results

Suitability model

There was good agreement on the final model among the two methods of model selection. Both the .632 and AIC methods selected elevation, average total fPar, mean temperature of the coldest quarter, precipitation in warmest quarter, and the vegetation

type layer. Mean moisture index of warmest quarter was excluded from the final model to improve parsimony (Table 1). The two climatic variables included in the final model had the highest independent contribution to the model, although all included variables were strongly significant with the exception of vegetation type (Table 2). The final model explained 20.6 % of the deviance (AUC 0.7926) (Table 1).

Table 2.

Variable coefficients and z scores for the top wombat sighting probability model. The AUC value for the final model was 0.7924.

Model	Variable	Coefficient	Standard Error	Independent Contribution	Z score	P
Sighting probability	Intercept	1.190	0.462		3.937	<0.001
	elev	-0.001	0.000	14.24	-2.575	0.01
	fpar	0.796	0.444	6.27	1.792	0.07
	mtcq	-0.024	0.004	35.44	-6.353	<0.001
	pwq	-0.038	0.003	40.22	-13.618	<0.001
	vtype	0.246	0.111	3.83	2.220	0.026

Symbols for predictor variables occurring in model set are as listed in Table 1.

The independent contribution of each variable was determined through hierarchical partitioning, and is presented as a percentage of the total explained variance. The deviance explained by the final model was 20.6 %. Null deviance was 10,090.1 (df=14,695) and residual deviance was 8313.31(df=14,678).

The factors explaining climatic conditions had the largest independent contributions to the model and suggest that common wombats are negatively associated with warmer temperatures (Fig. 2). The inclusion of precipitation in summer reflects the latitudinal constraint of the distribution of wombats and accounts for their absence in northern NSW. The negative relationship with mean temperature in winter represents the longitudinal restriction of wombat distribution and accounts for their absence from the warmer, arid Western Plains of NSW. Wombat probability was positively associated with both average total fPar and vegetation type (Fig. 2). The inclusion of fPar, a measure of greenness (similar to the normalized vegetation index used in Roger et al. 2007) and vegetation type indicates that although wombats can make use of agricultural

land for grazing, their distribution is still constrained to wooded areas and or cleared areas in proximity to remnant vegetation. Elevation had a weakly negative but significant relationship with wombat probability, indicating that common wombats are not overly constrained by elevation and can be found both at higher elevations and in lower lying temperate regions (Fig. 2).

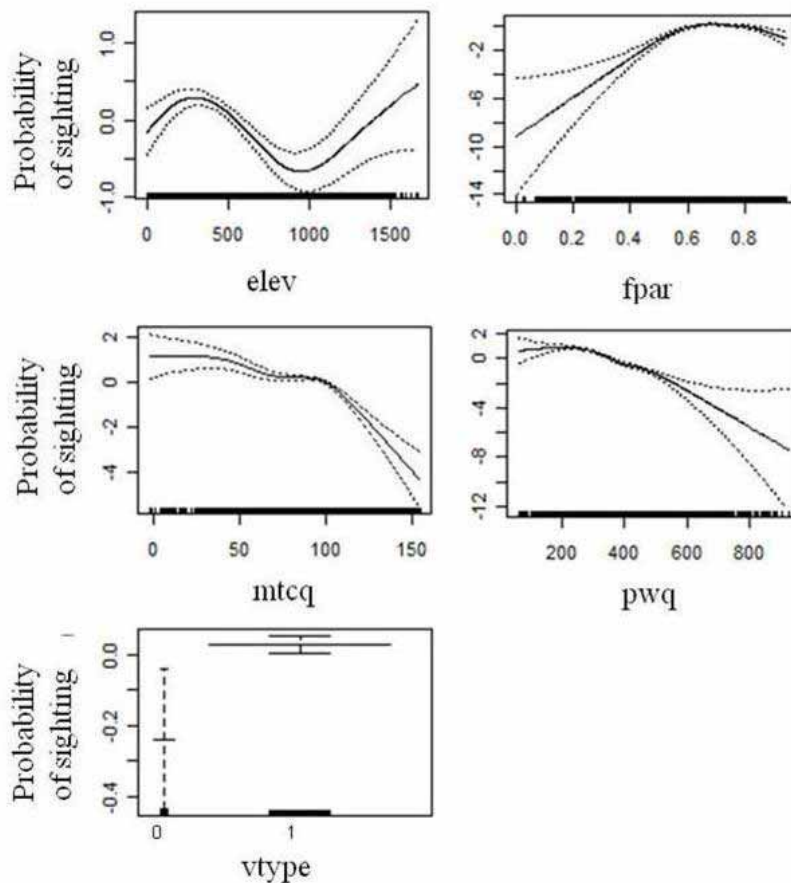


Figure 2. Partial plots of the relationship between the probability of a wombat sighting (y-axis) and the predictor variables included in the final model. The x-axis represents the range of values for each environmental variable, elevation (elev), average total Fraction of Photosynthetic Active Radiation (fpar), mean temperature of the coldest quarter (mtcq), precipitation of the warmest quarter (pwq), and vegetation type (vtype).

There was good concordance with expert opinion on common wombat distribution (Triggs 1988), with suitability values extending throughout NSW and the ACT, except in northern NSW (Fig. 3). Suitability values west of the Great Dividing Range were low, in accordance with previous descriptions of common wombat habitat (Catling and Burt 1995; Buchan and Goldney 1998; Catling et al. 2000; Roger et al. 2007; Borchard et al. 2008). The habitat suitability model identified areas of high habitat suitability to occur mostly within the mountainous regions of the Great Dividing Range and in some coastal temperate regions. Suitability results indicate that common wombat distribution is bound by a large climatic envelope that limits them to mesic and semi arid environments of south-eastern Australia.

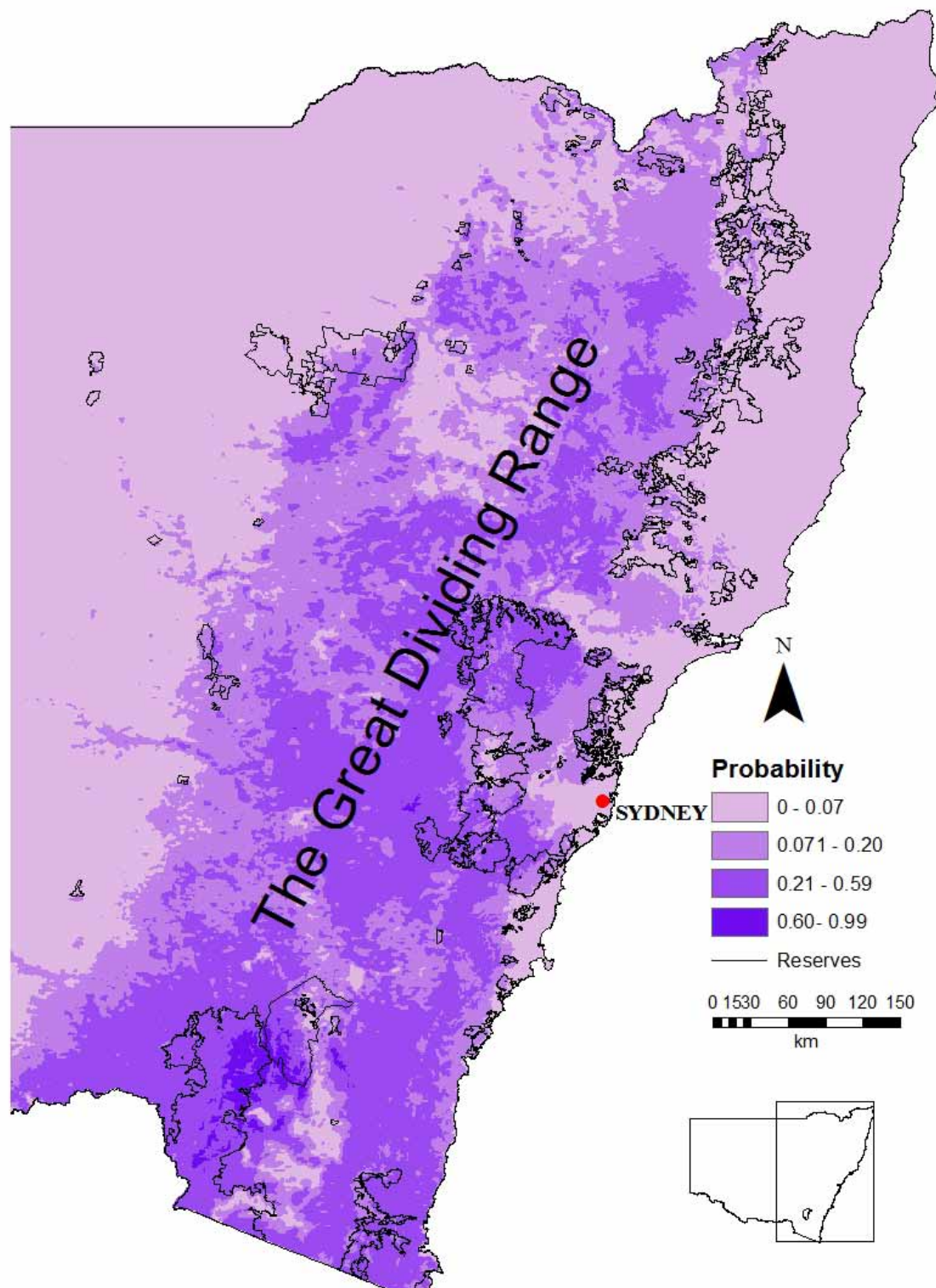


Figure 3. Habitat suitability values (probabilities) across NSW and ACT. Major reserve networks within NSW and the ACT are also shown.

Distribution and representation in reserves

The model predicted common wombats were distributed across 211,107 km² of eastern NSW and the ACT (Fig. 3) with 23.3 % of their distribution contained within reserves. The extent of core habitat was calculated at 2,569 km² using the optimal threshold value of 0.6 (Fig. 3), with 79.6 % of core habitat located within reserves (Fig. 3). Of the 162 reserves predicted to have common wombats, the top ten reserves by weighted sum were all located in southern NSW, concentrated around Kosciuszko National Park (Table 3). Seven of these ten reserves were included within core habitat areas.

Table 3.

Top ten reserves within NSW and the ACT with the highest representation of wombats by weighted sum and by percent representation. Corresponding percentages of road effect zone and road category are also given.

Name		Sum of probabilities	Reserve area (km ²)	Weighted sum	Representation in reserves (%)	Road effect zone (%)	Road categories within reserves
Vulcan Forest	State	27,903	198	0.53	0.21	4.28	3
Namadgi National Park		151,063	1,054	0.52	1.13	4.41	4
Tallaganda National Park		23,887	167	0.45	0.16	2.68	4
Tinderry Reserve	Nature	21,338	149	0.44	0.14	*	*
Kosciuszko National Park		994,597	6902	0.43	6.19	7.51	2, 3, 4
Maragle Forest	State	22,633	157	0.40	0.13	7.63	4
Tallaganda Forest	State	37,016	258	0.38	0.20	2.63	4
Sunny Corner State Forest		29,547	212	0.38	0.16	3.29	2, 4
Brindabella National Park		25,999	182	0.36	0.13	*	*
Woomargama National Park		33,750	231	0.34	0.17	5.24	4

Sum of probabilities is the sum of habitat suitability values within each reserve. Weighted sum is the suitability values divided by total reserve area to derive the average suitability per unit area. The four categories of roads: 1) freeways, 2) highways, 3) major roads, and 4) minor roads. * denotes unsealed roads only.

Road impacts

High and optimal suitability groups were correlated with increasing probabilities of wombat fatalities (Fig. 4), with the probability of a fatality increasing with predicted suitability values. The probability of a wombat fatality was also related to road category within suitability groupings (Fig. 5). Within the optimal suitability grouping, both major

and minor roads were correlated with a higher probability of a wombat fatality despite freeways being absent from areas of high and optimal suitability (Fig. 5). The majority of the top ten reserves for wombat representation had category 4 (minor) roads; however Kosciuszko National Park had three of the four road categories included within its boundary (Table 3). The percentage of road effect zone within the top ten reserves for wombat representation ranged from 0 to 7.63 % (Table 3).

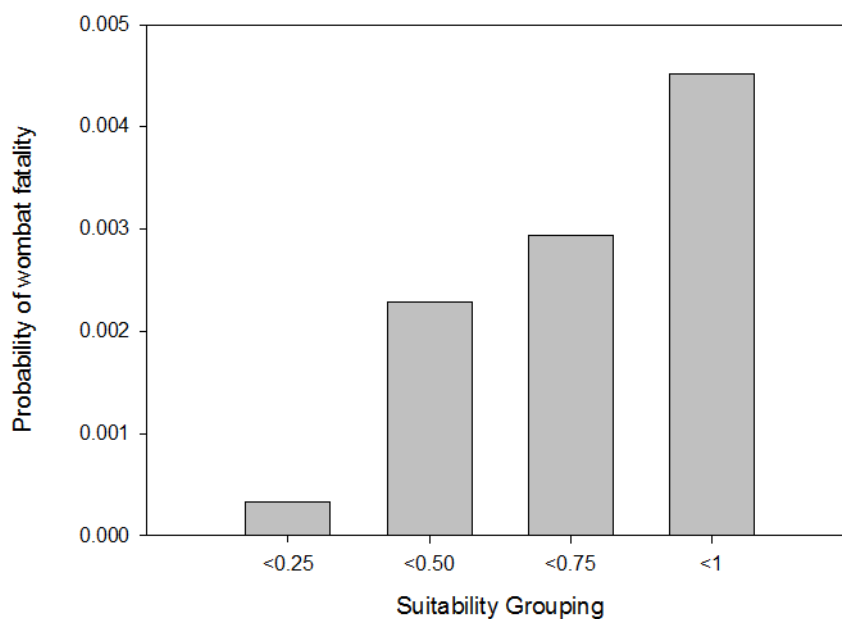


Figure 4. Probability of a wombat fatality plotted against stratified suitability groupings 1) low (<0.25), 2) medium (<0.5), high (<0.75) and optimal (<1).

Discussion

The wide distribution (211,107) km² of common wombats across a range of elevations throughout eastern NSW is in agreement with previous studies describing common wombat range extent (Catling and Burt 1995; Buchan and Goldney 1998; Catling et al. 2000; Roger et al. 2007; Borchard et al. 2008). Contrary to the ecological/biological mechanisms that have been proposed as good predictors of wombat distribution at local scales of analysis (Catling et al. 2000, 2002; Roger et al. 2007), regulation of broad

scale wombat distribution seems largely dependent upon climatic controls. The inclusion of two climatic variables in the model suggests that the trait most closely associated with common wombat distribution is the extent of the environmental conditions under which they occur. Given that common wombat distribution has contracted southwards since European settlement (McIlroy 1995), it would be interesting to explore if this southern contraction is as a result of changing climatic conditions, human changes in land-use, introduced threats, or a combination of all three. Common wombats were also influenced by vegetation variables. fPar and vegetation type reflect wombat preference for good foraging habitat near cover (Evans 2008). This is supported by McIlroy (1973) and Buchan and Goldney (1998) who considered forest cover important for protection from predators and extreme weather. Such conditions are typical of many road environments within Australia's reserve systems which can offer cleared land for grazing in proximity to wooded habitat (Roger et al. 2007).

In this study we assessed the relative abundance of common wombats within reserves across the study area as well as the percentage of core habitat contained within the reserve network. We showed that almost one quarter (23.6 %) of common wombat distribution lies within reserves, while the percentage of core habitat conserved within the reserve network increases to 79.6 %. Core habitat analysis results suggest that it is the differences in habitat suitability that may explain varying distributions of common wombats within reserves and outside reserve areas. Our results also suggest that reserves constitute important spatial refuges for common wombats and at first (given their predicted abundance within them) this seems to bode well for the continued persistence of the species. Similar findings were found in Devictor et al. (2007) who demonstrated that reserves, despite being designed to protect threatened species, also included high densities of common species.

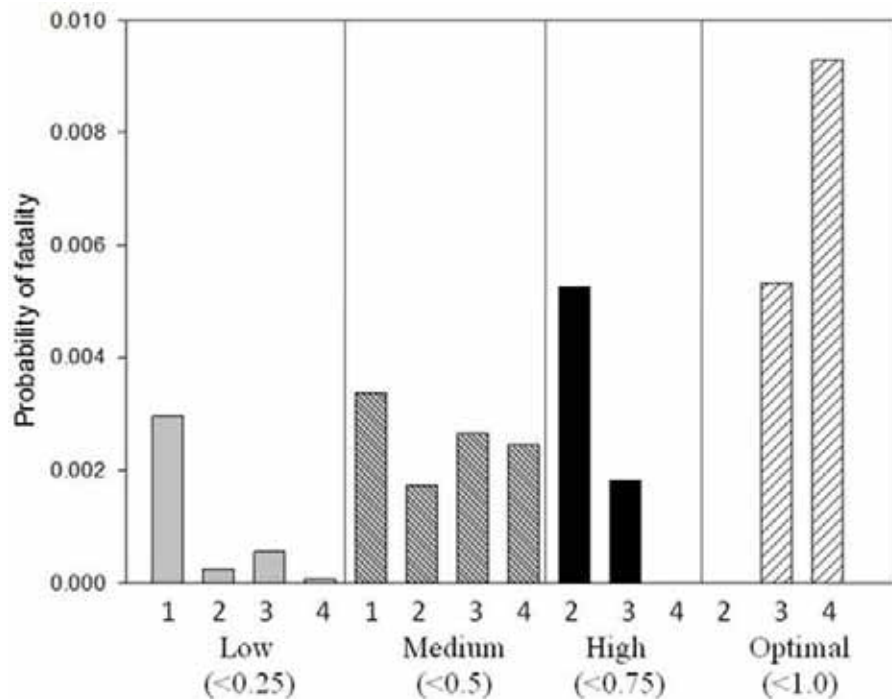


Figure 5. Probability of a wombat fatality plotted against road category and suitability groupings. The four road categories are: 1) freeways, 2) highways 3) major roads, and 4) minor roads. Freeways were absent from high and optimal suitability grouping areas.

Interestingly, we also showed that the probability of a wombat road fatality is correlated with areas of highly suitable habitat (Fig. 4). This finding makes sense given that suitable habitat is correlated with higher densities of species, and this can result in increased road fatality rates (Forman and Alexander 1998). A common assumption of reserve networks is that they act as sources for species within a broader landscape context, particularly if they constitute substantial components of the remaining or better quality habitat (Gaston et al. 2008). Our findings suggest otherwise and have important implications for the management of roads within reserves. They demonstrate that it is vitally important to quantify what the consequences are when species are lost within reserves and in particular within core habitat areas. Although not a direct link to road impacts in isolation, the numbers and rates of extinctions within reserves have been shown to be positively correlated with human density (Gaston et al. 2008). When

species are lost within reserves it is likely that the reserves themselves become population sinks and become dependent on a flow of individuals from outside in order to sustain them (Hansen and Rotella 2002).

The road effect zone is the area over which significant ecological effects extend outward from a road and typically over hundreds of meters (Forman and Alexander 1998). Considering the density of roads plus the road effect zone permits us to estimate the proportion of the land that is ecologically affected by roads within reserves. The top ten reserves identified as important for common wombat representation had varying percentages of road effect zone, with three of the four categories of roads occurring within the top ten reserve group (Table 3). The relationship between road category and suitability grouping allowed us to demonstrate that the probability of a wombat fatality within highly suitable habitat remains high despite road category (Fig. 5). This is important for management who may not have considered major and minor roads as significant locales of wombat fatalities. Kosciuszko National Park was among the top ten reserves for percentage of wombat representation (Table 3) and also constituted a large portion of core wombat habitat. In addition, Kosciuszko National Park has amongst the highest percentage of the road effect zone (Table 3). The combination of these factors is reflected in research which has documented frequent wombat road fatalities within the National Park (Ramp et al. 2005; Roger et al. 2007; Roger and Ramp 2009). We suggest that due to the predicted density of wombats within many reserves, wombats may appear to be persisting. However, localised road impacts will likely result in gradual small scale reductions in population size (Roger et al. 2007) and this may result in large scale range reductions over time. This effect is likely heightened in areas of highly suitable habitat, areas that should be acting as population sources.

In a review of the ecological effects of roads, Forman and Alexander (1998) considered road fatalities unlikely to affect persistence of common species because birth rate often exceeds the road fatality rate for many species. As a result species level conservation in road impacted environments tends to remain focused on those species that are highly threatened with regional extinction in the near future (Forman et al. 2003). However, a number of studies have documented population level depletions of common species as a result of road impacts at local scales (Jones 2000; Ramp and Ben-Ami 2006; Fahrig and Rytwinski 2009). An immediate concern for conservation managers is that road fatalities in core habitat areas could affect persistence of even common species in road impacted environments. The key issues for wildlife populations are how individual based habitat selection decisions change with distance from the road and the implications of these decisions, coupled with fatalities, on the viability of roadside populations.

Judgements about extinction risk are driving conservation priority and legislation (Gaston and Fuller 2008). Species at the greatest risk of being lost are typically the key targets of conservation, but there is growing evidence that many common species are undergoing decline (Gaston and Fuller 2007). There is a pressing need to quantify how different forms of land use are impacting on biodiversity and how ultimately common species will persist as processes that underpin their decline intensify. How the threat of roads within reserves is impacting species persistence should be of vital interest to conservation practitioners. An immediate concern is that core habitat areas could themselves be population sinks and effort should be expended in evaluating how reserves confer species resilience from the impacts of roads. Caution should also be taken when extrapolating perceptions of commonality based on optimal core habitat areas across common species broad ranges.

Acknowledgements

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Chapter 6

Conclusion

The approach taken in this doctoral research has provided insights into how information on species habitat use can be used to identify aspects that make them susceptible to the impacts of roads independently and in conjunction with other forms of disturbance. This thesis asserts for the need to focus conservation attention to species considered abundant and widespread. I have quantitatively shown that common wombats, as an example of a common species, can be susceptible to local threats, and that when examined holistically, these threats can result in increases in extinction risk at larger scale extents.

Key findings from this thesis

Chapter 2 demonstrated that habitat suitability models are a useful tool in evaluating species habitat use at local scales. Modelling results revealed several habitat variables that are good predictors of common wombat habitat use. Results suggest that common wombats are ‘edge specialists’, preferring a mix of open and closed forest in proximity to good grazing land. Population estimates suggest the area once supported much higher numbers of wombats but that limiting factors such as road mortality and disease have reduced wombat populations in proximity to roads.

Chapter 3 incorporated measures of common wombat habitat use and environmental variables into a predictive model of wombat road mortality. The predictive model had high discriminatory power and highlighted the importance of incorporating variables that describe habitat use by fauna for improved predictive modelling of animal-vehicle collisions. The results suggest that monitoring of species occurrence and movement within the landscape is vital for reliable and robust predictive

models and important for understanding the role of habitat in determining species distributions and susceptibility to animal-vehicle collisions.

Chapter 4 described a population viability analysis that analysed potential limiting factors of common wombat populations. The results suggest that roads in combination with other limiting factors such as disease and predation have the capacity to deplete subpopulations of common wombats. The study showed that roads can impact the survival of common species at locally and that this may have broader implications for species persistence at larger scale extents, particularly if roads act as attractive sinks for species.

Chapter 5 provided the first landscape level predictive model of common wombat distribution across parts of their range. Species distribution data allowed for further analysis on core habitat and quantification of representation in reserves. Results indicate that that 80 % of optimal common wombat habitat is within reserves, highlighting the importance reserves play in their continued persistence. Habitat suitability was also correlated with fatality rates while results suggest that reserves themselves can be potential population sinks for road impacted species and that the level of protection offered by the reserve system cannot be assumed.

Summary of emergent themes

Little is known of the toll of road fatalities on animal populations and how these impacts vary with the extent of the investigation. Part of the reason for this is the perception that impacts are localised and that animals killed are typically considered common. Local scale studies are beneficial in demonstrating localised road impacts, where the immediate threat to rare species becomes particularly apparent. At such scales it is important to recognise the interplay between various threats and how their combination has the capacity to drive local extinction rates. Evidence garnered on

population level effects of species at local scales raises concerns about the persistence of species in road environments throughout their distribution.

By broadening the scope of study, research can begin to quantify landscape extent impacts of roads on populations and how patterns of habitat use and selection change with road-based fatality rates. It is vital that we develop an understanding of the motivations behind animal presence and movement to fully comprehend how roads interact with susceptible species in a dynamic and heterogeneous landscape (Fahrig 2007). Broad scale studies also have the capacity to evaluate roads in context with other threats in two dimensions, moving away from the treatment of roads as linear features.

Linking to management

Important recommendations for management that can improve mitigation and planning techniques emerged from this research. Management of species populations should begin with the identification of where and when to take action. Action may revolve around a decision threshold where factors such as property damage, injury to humans and the species impacted are considered. Identification and modelling of road mortality hotspots is an important component of the action process (Ramp et al. 2005; Roger and Ramp 2009). Planning efforts also need to include mitigation that targets the appropriate scale (Roedenbeck et al. 2007); this is largely dependent on the species being impacted. Local scale mitigation may be appropriate for threatened species but common species mitigation is likely more complex. As a starting point, mitigation of hotspots within identified core habitat areas may be an important first step in addressing such a large scale problem.

Driver awareness near animal hotspots and information on animal avoidance is vitally important. Public education programs that discuss animal vehicle collisions as a major threat to susceptible wildlife species (Fahrig and Rytwinski 2009) as well as the

associated risk of human injury (Ramp and Roger 2008; Rowden et al. 2008) are additional management tools. An important part of the education process is the recognition of the disparity between the number of reported animal vehicle crashes and the number of actual animals killed on the road. However, awareness and stated willingness does not always result in changed driver behaviour. Because of this, integrating wildlife needs into road design and planning is likely the best tool for mitigating animal vehicle collisions for future road construction projects (Jaarsma et al. 2006; Bissonette and Adair 2008; Bond and Jones 2008; Mata et al. 2008; Glista et al. 2009). The establishment of nature corridors that aid in the dispersal and movement of wildlife is a well established approach for addressing and alleviating road impacts (Forman et al. 2003). However, due to the density of roads within them, reserves should not automatically be viewed as areas that can provide this connectivity. The next step for reserve managers should be quantifying how effective reserves are at maintaining wildlife persistence as well providing connectivity between reserve systems. The applicability (given Australia's unique fauna) of overseas mitigation approaches is also an important management consideration under Australian conditions.

Lessons learned from this research

This thesis was limited by time and resources. Ideally measures of species habitat use could have been improved by using radio or gps collars. Collars can provide an informative measure of habitat use in addition to information on home range size and dispersal events. Our capture efforts were unsuccessful in the area as the low number of occupied burrows meant the capture effort soon became beyond the resources of the study. We overcame this issue by using wombat burrow location data as a measure of habitat use. Although not as informative as movement data, burrow location information provided a measure of where wombats had actively decided to construct burrows. We

were able to demonstrate that use of burrows is a viable alternative for measures of habitat use.

Replication in space is also an issue. The majority of the research focussed on a single road. The decision was made to investigate one road section in depth rather than several perfunctorily. The Snowy Mountains Highway was selected due to existing fatality data for this stretch of road. This highway is one of the few roads in Australia for which good fatality data now exists for wombats, and this limited the conclusions and predictions we were able to draw from our results. The scarcity of wombat fatality data highlights the need for government, road authorities, and wildlife carer groups to establish far more accessible and comprehensive databases on animal fatalities; meanwhile the lack of data is limiting our ability to properly quantify the impacts of roads for many species within Australia.

This thesis was also limited by the amount of species data available for common wombats. Despite their commonality, very little information exists, including information on distribution, life expectancy, and dispersal. The population viability analysis in particular would have benefited from population specific demographic, dispersal, and survival information. We tried to overcome this by performing sensitivity analyses around all model parameters.

Future research directions

The approach taken in this study, focusing on selected issues of road impacts on the common wombat within the broader topic of road ecology, provides a platform from which further research questions can be posed.

Most obviously, a quantitative evaluation of the role of common wombats in ecosystem functioning is needed. One approach would be to test their role in creating, modifying and maintaining habitat. Species that perform this function are known as

ecosystem engineers (*sensu* Jones et al. 1997). Ecosystem engineers are predicted to have positive effects on species richness at the landscape scale by providing a mixture of modified and unmodified patches (Jones et al. 1997). As burrow dwelling animals that turnover large quantities of soil, common wombats likely play an important role in maintaining ecosystem functioning particularly by impacting soil nutrition. Evidence of their role as ecosystem engineers would help place common wombats firmly within the conservation agenda.

Equally of interest is the importance of rethinking the value of all common species as valuable assets for conservation and ecosystem function. Legislation allows for conservationists to work to maintain minimum viable populations of threatened species, and while this may prevent species extinction (Redford et al. 2003), reductions in population sizes of common species will go unnoticed. Unless we monitor the impact of threats on common species abundance and distribution, managers will only ever be able to be reactive to declines, rather than proactively preventing them. Studies that consider changes in abundance and density of common species at varying spatial scales are crucial. In order to quantify risk, it is important to obtain measures of how definitions of commonality change depending on the spatial scale being modelled.

With our current level of ecological knowledge it is not yet possible to predict how roads impact on biodiversity. Seldom discussed is the impact of roads on local populations when considered in conjunction with other threats (e.g., Haines et al. 2006). Further research is required that examines the interplay between various threats and how their combination has the capacity to impact on species persistence.

Increasingly, genetic information is seen as a key component in conservation management plans and can provide a deeper level of understanding of the biology of the species in question (Appendix B). Genetic information can also provide practical

information as to how to manage species effectively and aide in demonstrating ecological theories (such as the source-sink theory) that are difficult to document in field-based and modelling-based research (Appendix B). Applying genetic information in conjunction with spatial analysis is an important avenue of future research.

Finally, the combination of susceptibility to roads and the distribution and abundance of species across the landscape poses some interesting questions. Given the substantial evidence for the impacts of roads on wildlife (Forman et al. 2003), certain morphological, biological and ecological traits may confer either susceptibility or suitability to road impacted environments. By contrasting species whose population level road impacts have been studied, it can be shown that susceptibility interacts strongly with abundance to determine the magnitude of road effects (Table 1). If species are highly susceptible to the impacts of roads then both rare and abundant species are potentially at great threat especially if their reproductive rates or recruitment rates are low. Variations in susceptibility or suitability of species to roads may mean that the road environment can act as a selecting agent for species, leading to decline and extinction in species with traits that confer susceptibility. The significance of the interplay between susceptibility, abundance and range size on species vulnerability in road environments remains unexplored particularly on large scales.

Table 1. Contrasting susceptibility and abundance to determine local scale road impacts. Large scale impacts remain to be quantified for many species.

Example Species	Reference	Susceptibility	Abundance	Local scale road impacts
Desert tortoise (<i>Gopherus agassizii</i>)	Boarman & Sazaki (2006)	High (morphological)	Rare	Negative
Turkey vulture (<i>Cathartes aura</i>)	Coleman & Fraser (1989)	Low (flight response)	Common	Positive - due to abundance of roadside prey
Small mammal communities	Bissonette & Rosa (2009)	Low (biological)	Locally Common	Neutral
White tailed deer (<i>Odocoileus virginianus</i>)	Carbaugh et al. (1975)	High (foraging behaviour and flight response) Low (high reproductive rate)	Common	Neutral
Grizzly bear (<i>Ursus arctos horribilis</i>)	Roever et al.(2008) Mace et al. (1999)	High (habitat use also evidence of road avoidance)	Common	Negative
American toad (<i>Bufo Americanus</i>)	Eigenbrod et al. (2008)	High (habitat use)	Locally Common	Negative
Swamp wallaby (<i>Wallabia bicolor</i>)	Ramp & Ben-Ami (2006)	High (foraging behaviour and flight response)	Common	Negative

Information for the table was obtained by conducting a literature search on reported road impacts on species of varying abundances.

Appendix A. All variables, layers and databases used in analyses along with their resolution and source.

Abbreviated name	Variable	Resolution	Source
Elev	Elevation	90 m	SRTM
nsw_slope	Slope	90 m	SRTM derivative
nsw_aspect	Aspect	90 m	SRTM derivative
roughness	Surface Roughness	90 m	SRTM derivative
Wetness	Wetness Index	90 m	SRTM derivative
Fpar	Mean Yearly Persistent fPAR	1 km	CSIRO Land and Water
per_avgvar	Mean Yearly Variance of Persistent fPAR	1 km	CSIRO Land and Water
rec_avg	Mean Yearly Recurrent fPAR	1 km	CSIRO Land and Water
rec_avgvar	Mean Yearly Variance of Recurrent fPAR	1 km	CSIRO Land and Water
total_avg	Mean Yearly Total fPAR	1 km	CSIRO Land and Water
total_avgvar	Mean Yearly Variance of Total fPAR	1 km	CSIRO Land and Water
Amt	Annual Mean Temperature	90 m	AnuClim
Mdr	Mean Diurnal Range (Mean(period max-min))	90 m	AnuClim
I	Isothermality 2/7	90 m	AnuClim
Ts	Temperature Seasonality (C of V)	90 m	AnuClim
Mtwp	Max Temperature of Warmest Period	90 m	AnuClim
Mtcp	Min Temperature of Coldest Period	90 m	AnuClim
Tar	Temperature Annual Range (5-6)	90 m	AnuClim
Mtwq	Mean Temperature of Wettest Quarter	90 m	AnuClim
Mtdq	Mean Temperature of Driest Quarter	90 m	AnuClim
Mtwq	Mean Temperature of Warmest Quarter	90 m	AnuClim
Mtcq	Mean Temperature of Coldest Quarter	90 m	AnuClim
Ap	Annual Precipitation	90 m	AnuClim
Pwp	Precipitation of Wettest Period	90 m	AnuClim
Pdp	Precipitation of Driest Period	90 m	AnuClim
Ps	Precipitation Seasonality(C of V)	90 m	AnuClim
Psq	Precipitation of Wettest Quarter	90 m	AnuClim
Pdq	Precipitation of Driest Quarter	90 m	AnuClim
Pwq	Precipitation of Warmest Quarter	90 m	AnuClim
Pcq	Precipitation of Coldest Quarter	90 m	AnuClim
Ammi	Annual Mean Moisture Index (M.I.)	90 m	AnuClim
Hpmi	Highest Period Moisture Index	90 m	AnuClim
Lpmi	Lowest Period Moisture Index	90 m	AnuClim

Mis	Moisture Index Seasonality (C of V)	90 m	AnuClim
Mihq	Mean Moisture Index of High Quarter	90 m	AnuClim
Milq	Mean Moisture Index of Low Quarter	90 m	AnuClim
Miwq	Mean Moisture Index of Warm Quarter	90 m	AnuClim
Micq	Mean Moisture Index of Cold Quarter	90 m	AnuClim
Vtype	Woody\NonWoody Vegetation	20 m	DECC
Road	Road Layer of New South Wales		DECC
Reserve	Reserve Layer of New South Wales		DECC
TADS	Traffic and Accident Database System of New South Wales		Roads and Traffic Authority of NSW

All variables used were for the extent of NSW. The three layers provided by DECC were for Australia and clipped to the NSW extent.

Appendix B.

The work included in this appendix uses genetic and spatial information in an attempt to quantify if roads act as attractive sinks for common wombats. This work represents future research, and was included in order to demonstrate the potential for the integration of genetics and spatial analyses in order to evaluate landscape level impacts of roads. The presented work represents preliminary analysis only, due to a proportion of the genetic samples which failed to amplify at most loci, indicating poor tissue quality. As a consequence the genetic laboratory component will likely be repeated with additional DNA testing as additional results are necessary in order to proceed with further analysis. The work is in preparation for submission to *Molecular Ecology*.

Introduction

Animals must often assess the suitability of habitats indirectly, uncoupling the attractiveness of a habitat from its actual suitability. As a consequence, lower quality or less suitable habitat may appear more attractive than habitats that are, in reality, more suitable (Robertson and Hutto 2006). This situation is hypothesised to occur when species are unable to accurately perceive a process that renders the habitat poor and results in increased mortality. Habitats of this type have been described as attractive sinks and arise when animals lack cues associated with reduced fitness and consequently select habitat inappropriately (Delibes et al. 2001). Thus, an attractive sink is simply a sink habitat that is preferred rather than avoided (Pulliam 1988). One source of mortality that many species may not perceive is from roads, yet few published research has explored this likelihood, despite existing as a robust ecological theory for many decades (Delibes et al. 2001; Bunnefeld et al. 2006; Roever et al. 2008; Falcucci et al. 2009).

Increasingly, genetic information is seen as a key component in conservation management and can provide a deeper level of understanding of the biology of the species in question (Hazlitt et al. 2006; Howeth et al. 2008). In this study we used microsatellite markers to investigate genetic diversity and population genetic structure. We examined the population genetic structure among the sampled areas using genetic differentiation. Future analysis are planned in order to quantify relatedness between individuals, which will give us an understanding if roads can act as attractive sinks, effectively drawing animals from areas of high fitness to areas of severely reduced fitness/mortality.

Methods

Study species

Genetic diversity and population genetic structure was investigated in the common wombat (*Vombatus ursinus*) using microsatellite genetic data collected. The common wombat is both widespread and abundant across south-eastern Australia. Their broad niche suggests they are a relatively robust and adaptable species, reflected by their use of agricultural and other modified landscapes (Roger et al. 2007; Roger and Ramp 2009). This adaptation to modified landscapes brings considerable cost as they are frequently killed on roads in proximity to areas that have been cleared for stock grazing (Roger and Ramp 2009).

Study site and sample collection

Forty three common wombats were sampled in two regions within New South Wales (NSW), Australia (Fig. 1). Tissue and hair samples were collected over a 300 km² area near Tumut NSW in proximity and within Kosciuszko National Park (Fig. 2). Kosciuszko National Park (KNP) is the largest National Park in NSW and covers

approximately 6980 km² and is nationally recognized as a UNESCO Biosphere reserve (Scherrer and Pickering 2005). The National Park is located in the south-eastern corner of the Australian mainland. Samples were collected from 23 individuals from animals killed on roads and also hair samples from live individuals. Individuals from KNP were grouped into three sub-populations based on the relative distance from the centroid of the population to the edge (Fig. 2). Twenty tissue and hair samples were collected from the Jenolan Caves region over an area of 100 km² and were grouped into one population (Population 4). The Jenolan Caves region is contained within The Greater Blue Mountains World Heritage Area (GBMWhA) which is the largest integrated system of protected areas in New South Wales. The GBMWhA lies 60-180 km inland of Australia's largest city (Sydney, population 4.2 million), and covers just over 1.03 million hectares (Fig. 1). Individuals sampled were all killed on roads within the surrounding region. All individuals were input into ArcGIS (ESRI 2007) and a distance matrix for all populations was derived using the point distance tool and exported into a text file for use in genetic analyses.

Where possible gender and age class, weight and morphometric measures were recorded for each individual sampled. A gps coordinate was also taken for each individual. Tissue or hair or both were collected from all animals and stored in 80 % ethanol before total cellular DNA was extracted using Gentra PureGene DNA isolation Kit. Extraction was as per the manufacturer's instructions with the exception that 20 ul of DTT was added to the hair extractions at the cell lysis step.

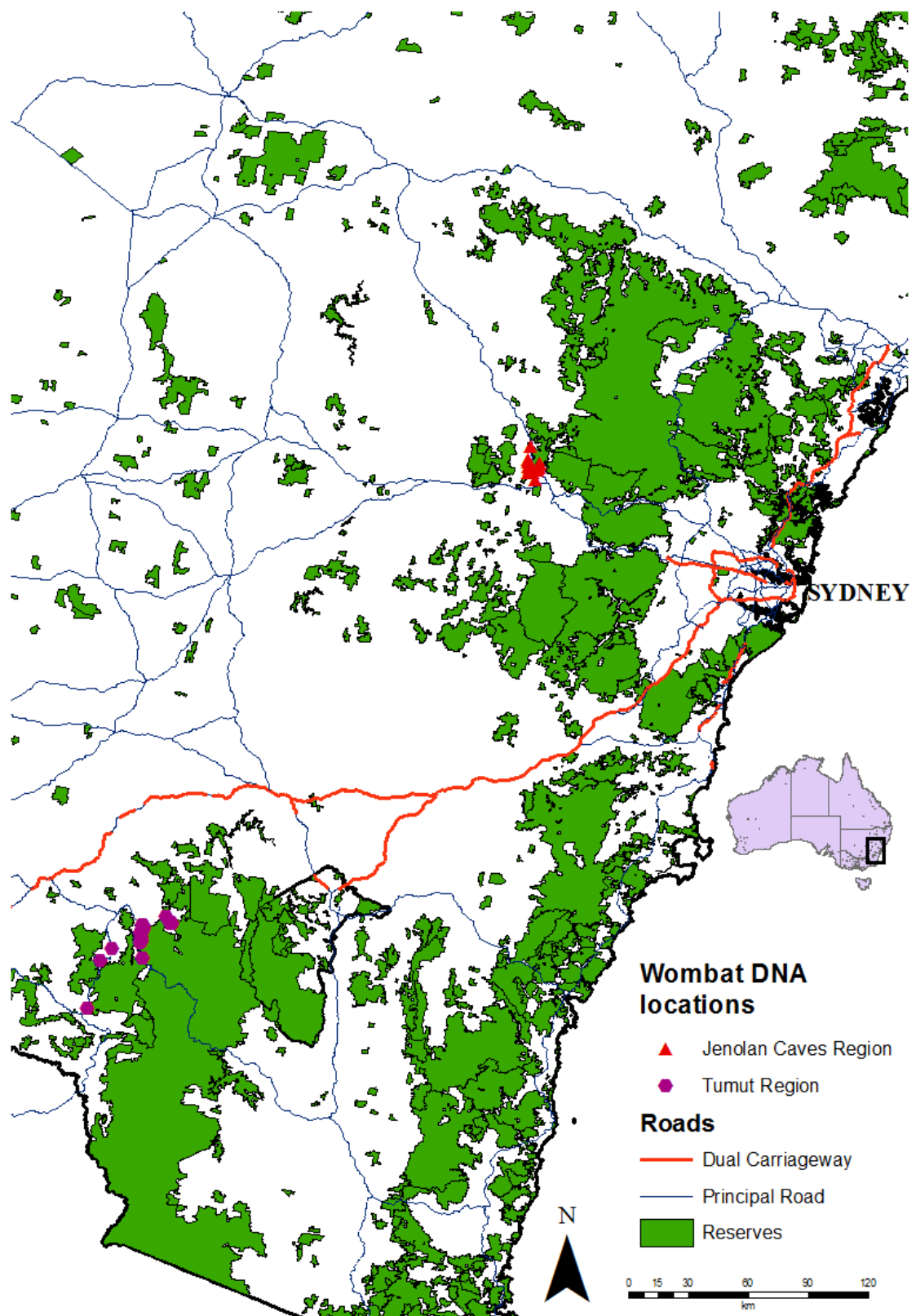


Figure 1. The two study regions located in New South Wales, Australia.

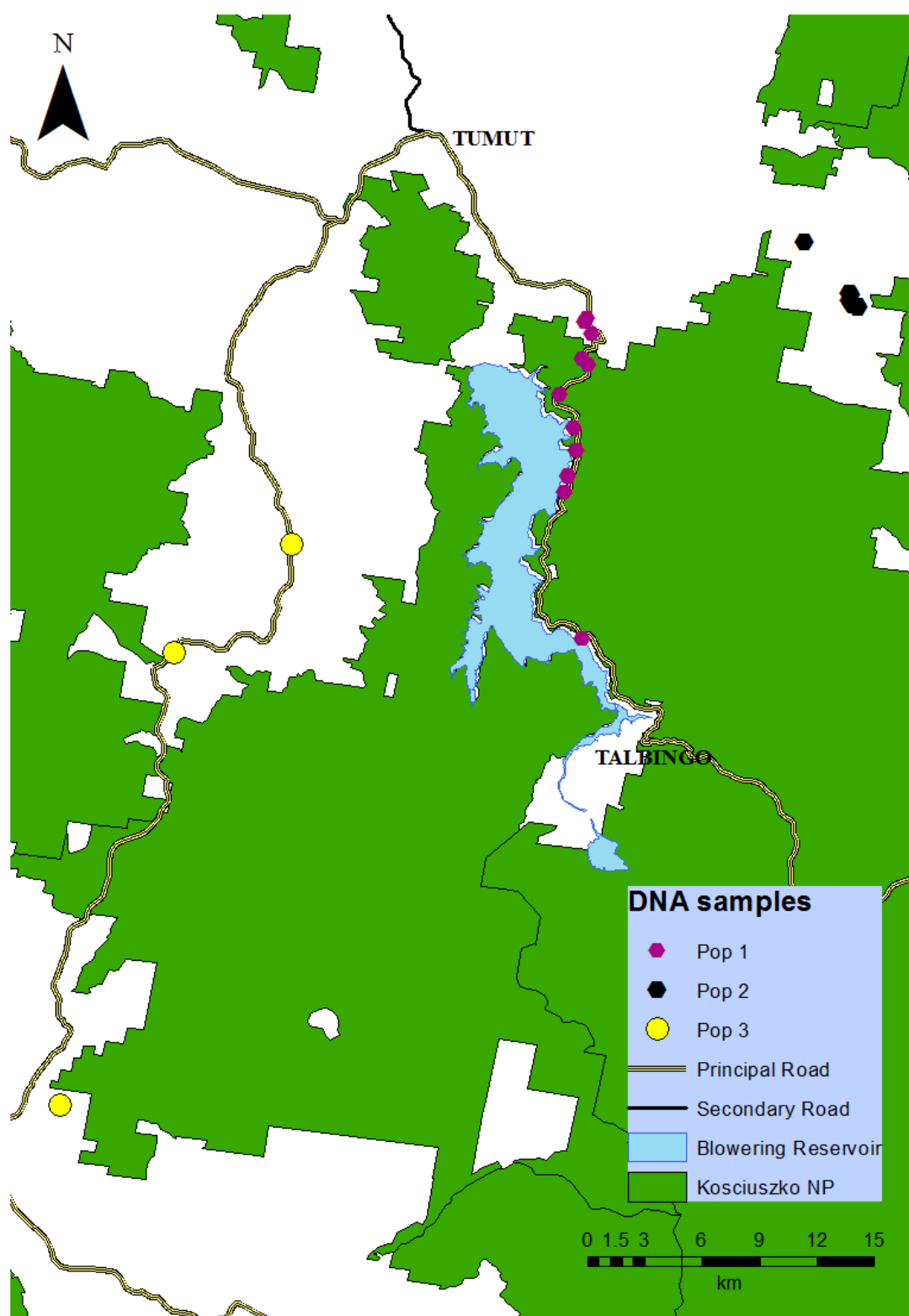


Figure 2. Tissue and hair samples were taken from common wombats in proximity to two Principal roads in the region (Pop 1) and (Pop 3) as well as additional samples taken a mean distance of 10 km from any major road (Pop 2).

Genetic analyses

Each sample was screened with five polymorphic microsatellite loci using fluorescently labelled primer pairs (Table 1). Each locus was amplified in 10ul reactions containing approximately 50-100ng of template DNA, 0.2 units of Hotmaster *Taq* DNA Polymerase (5 Prime, Germany), 1x buffer with 2.5mM Mg^{2+} , 0.2uM of each primer, 0.2mM of each dNTP and 0.1mg/mL of BSA. The thermocycler profile for each locus used a touchdown protocol with an initial denaturing step of 94°C for 2mins; then 8 cycles of 94°C for 30s, T_{a1} - T_{a2} for 30s (annealing temp decreased by 1°C per cycle) (Table 1), and 70°C for 45s; then 30 cycles of 94°C for 30s, T_{a2} for 30s, and 70°C for 45s; and then a final annealing step of 70°C for 10mins. The PCR products were then pooled into 2 multiplex solutions and a 1 in 5 dilution was used as template for separation on an ABI 3730 (Applied Biosystems, USA) automated sequencer using the LIZ 500 (-250) size standard by the Australian Genome Research Facility Ltd (Adelaide, Australia). Alleles were scored using Genemapper v.4 software (Applied Biosystems, USA) with manual editing.

Table 1. Microsatellite loci, source and annealing temperatures (Ta) used to infer genetic structure in the common wombat populations.

Locus	Primers	Ta (X₁-X₂)
L12	(Beheregaray et al. 2000)	62-55
Lk26	(Beheregaray et al. 2000)	65-58 and 55-47
Lla68	(Beheregaray et al. 2000)	55-47
Lla54CA	(Beheregaray et al. 2000)	62-50 and 62-55
Lkr109	(Beheregaray et al. 2000)	62-55
Lla16CA	(Beheregaray et al. 2000)	55-47
Lk34	(Beheregaray et al. 2000)	55-47
Lk27	(Beheregaray et al. 2000)	55-47
Lla71CA	(Beheregaray et al. 2000)	55-47
Lk09	(Beheregaray et al. 2000)	55-47
Lkr107	(Beheregaray et al. 2000)	62-55
Lla67CA	(Beheregaray et al. 2000)	55-47

We estimated genetic diversity for each population (P) by calculating the number of alleles per locus, allelic richness, the expected (He) and observed (Ho) heterozygosities (Table 2). Locus independence and Hardy–Weinberg equilibrium probability tests were conducted using the Markov chain method (10,000 iterations) implemented in GENEPOP v4.0.10. Pairwise F_{ST} (Weir and Cockerham 1984) was calculated for each population pair and a mantel test was used to check for significant isolation by geographic distance using Arelquin v3.11 (Excoffier and Heckel 2006).

Statistical significance levels were corrected for multiple comparisons using sequential Bonferroni adjustments (Rice 1989).

Population structure was detected using the assignment method implemented in the program STRUCTURE v2.3.1. This method employs a Bayesian clustering approach using multilocus genotypes to infer population structure and assign individuals to populations. The method does not require *a priori* classification of source populations for each individual thus removing the bias of any arbitrary assumptions of population boundaries. Individuals are assigned probabilistically to populations or jointly to two or more populations if their genotypes indicate that they are admixed, with the assumptions that within samples, the loci are independent and at Hardy-Weinberg equilibrium. Only loci that met these assumptions were included in the assignment test. We used the method outlined in Evanno et al. (2005) to infer the number of clusters of individuals in our sample. This method uses ΔK , and ad hoc quantity related to the second order rate of change of the log probability of data with respect to the number of groups, to predict the real number of population clusters. We used an admixture model with independent allele frequencies and a burn-in period of 100,000 steps followed by 1,000,000 MCMC replicates. The summary statistics alpha (α), P(D) and likelihood, which describe the rate of convergence of the Markov chain, were checked to ensure that burn-in and run lengths were adequate (Pritchard et al. 2000). Batch runs were conducted with 20 iterations each testing K=1 to K=5. The estimated proportion of ancestry values are the posterior mean values of q_i , the proportion of each individual's (i) genotype that is derived from each cluster. We report the means for the individual admixture proportions q_i and their 95 % probability intervals for the inferred number of clusters.

Table 2. The genetic diversity for each population (P) along with the number of alleles per locus, allelic richness, the expected (He) and observed (Ho) heterozygosities .

Locus	Total No. alleles	P1 No. alleles	N=10 AR	Ho	He	P2 No. alleles	N=8 AR	Ho	He	P3 No. alleles	N=5 AR	Ho	He	P4 No. alleles	N=19 AR	Ho	He
Lk09	6	5	1.76	0.40	0.76	1	1.00			1	1.00			4	1.66	0.38	0.66
Lla67CA	10	5	1.74	0.67	0.74	3	1.65	0.43	0.65	3	1.46	0.50	0.46	5	1.69	0.26	0.71
Lla16CA	5	4	1.71	0.57	0.71	2	1.50	0.50	0.50	4	1.79	0.50	0.79	3	1.46	0.50	0.46
Lla68CA	6	6	1.65	0.70	0.73	4	1.60	0.63	0.64	4	1.71	0.80	0.71	3	1.35	0.22	0.39
Lla71CA	8	7	1.77	0.80	0.77	4	1.65	0.50	0.65	3	1.71	0.60	0.71	6	1.74	0.63	0.73
Lkr107	8	6	1.85	0.63	0.85	4	1.80	0.67	0.80	2	1.50	0.50	0.50	4	1.68	0.33	0.68
Lkr109	10	8	1.88	1.00	0.88	4	1.76	0.17	0.74	5	1.79	0.75	0.79	7	1.74	0.56	0.72
L12	7	3	1.60	0.33	0.60	2	1.67	0.00	0.67	2	1.67	0.00	0.67	4	1.75	0.25	0.75
Lk34	4	3	1.44	0.40	0.47	4	1.67	0.57	0.67	4	1.82	1.00	0.82	3	1.22	0.25	0.24
Lk26	10	4	1.78	0.40	0.78	3	1.83	0.50	0.83	4	1.87	0.33	0.87	6	1.88	0.80	0.89
Lk27	5	4	1.77	0.50	0.77	1	1.00			4	1.64	0.75	0.64	2	1.53	0.80	0.53
Lla54CA	11	6	1.89	1.00	0.89	7	1.91	0.80	0.91	5	1.86	1.00	0.86	8	1.86	0.63	0.86
mean	7.5	5.08	1.74	0.62	0.75	3.25	1.59	0.48	0.71	3.42	1.65	0.61	0.71	4.58	1.63	0.47	0.63
stdev	2.35	1.56	0.13	0.23	0.12	1.66	0.3	0.24	0.12	1.24	0.24	0.29	0.13	1.83	0.2	0.21	0.19

Results

All loci assorted independently. All loci conformed to Hardy–Weinberg equilibrium except LLA67CA in the Jenolean Caves population (P4). With the exception of population 3 (P3), all population groups exhibited a significant heterozygote deficiency (P1: $P=0.001$; P2: $P=0.001$; P3: $P=0.068$; P4: $P=0.001$). In P1 and P2 this is likely to be a consequence of small sample size and incomplete genotyping however, in P4 the heterozygote deficiency may be a result of a recent population bottleneck as indicated by a low G-W statistic estimated in Arlequin v3.11 ($G-W=0.19$) (Garza and Williamson 2001; Excoffier and Heckel 2006). There was no difference in allelic richness among populations (Kruskal-Wallis chi-squared = 2.5843, $df = 3$, $p\text{-value} = 0.4603$). Pairwise F_{ST} values varied greatly but significant population differentiation was not observed (Table 3). A mantel test did not reveal any significant degree of isolation by distance ($P=0.075$).

Table 3. Pairwise FST estimates.

Population	1	2	3	4
1	-			
2	0.082	1		
3	0.039	0.095	-	
4	0.117	0.156	0.155	-

The modal value of the distribution of ΔK was found to be $K=2$. The assignment test results show that individuals samples from Kosciuszko National Park (P1, P2 and P3) fall into one cluster while individuals sampled near Jenolean Cave fall into the second cluster.

Discussion

Preliminary analysis revealed that our two sampling regions represent distinct populations of common wombats. This was expected due to the large geographic distance between the two regions (approximately 200 km). Interestingly, all wombats sampled within the Kosciuszko region were found to be from one population, even though sampling was over a large (300 km²) geographic distance. This finding provides preliminary support for our source-sink hypothesis. In the future we intend on using assignment tests and structure analysis to identify dispersers within the region to look at the spatial patterns of relatedness between individuals. We also intend on using further indirect and direct genetic methods to examine if genetic differentiation exists between the localised road wombat populations and potential source populations.

The finding that wombats sampled in the Jenolan Caves region have likely undergone a genetic bottleneck is a surprising result, given the seeming connectivity to the Greater Blue Mountains World Heritage Area. It is possible that decreased

heterozygosity is a result of loss of connectivity in the region due to roads. This remains a future area of investigation.

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