Conserving Australia's predator-threatened mammals

Jeremy Liam Ringma

BSc. Zoology/Ecology

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Abstract

Australian mammals are amongst the most threatened in the world. Predation by invasive cats and foxes has driven many species to extinction, and has caused rapid declines and extirpation among others. Many Australian mammals now only persist in a small number of refugial populations of few individuals with a high risk of extinction from demographic population failure and catastrophic events. The persistence of many Australian mammal species now depends on continuous management, and the creation of new populations through translocations into predator controlled areas. Predator exclusion fences have become pivotal for effectively abating the predation threat for remnant populations and translocations. However, translocations are notoriously costly and failure prone, making it particularly important to identify protocols that maximize the likelihood of success. Thorough assessments are therefore required to improve outcomes, but knowledge to make them is often lacking. In this thesis, I address key knowledge gaps associated with translocation and predator management for Australian mammals, with particular regard to conservation fences.

In Chapter 2 I address the issue of uncertainty of the accuracy of habitat models. Reintroductions often rely on models to identify suitable habitat, and such modelling requires occurrence data from a representative sample of a species’ niche. However, the historic distributions of species that have subsequently declined are often poorly sampled. Therefore, we need to know how thoroughly a species’ historic distribution was sampled before habitat suitability models can be trusted. I propose and test a method for determining whether a species’ niche is well sampled pre-decline for Australian marsupials, by comparing accumulation curves of niche volume when data are arranged in forward and reverse chronological order. I found that accumulation curves can be used to test if a species’ niche is poorly sampled, and that poor association between chronologically and randomly arranged data implies an under sampled niche.

A good understanding of how translocated animals use the space within a fence is crucial in making choices about its size. In Chapter 3. I investigate the spatial use of woylies (Bettongia penicillata) a species of acute conservation concern at the Australian Wildlife Conservancy’s Scotia Sanctuary in the arid extreme of their known historic distribution. Using GPS tracking devices, I measured the movements of woylies in two adjacent fenced populations. The higher density population occupied foraging ranges similar in size to those previously reported (37ha) while woylies at lower density had homes ranges 2.5 times greater in size (96 ha). The woylies in the lower density population increased the size of their foraging range by covering more unique ground each evening, and spending more time further away from their nest. While the differences between the two populations are most likely related to density, it remains uncertain whether intraspecific competition or environmental stochasticity is the main driver of population differences. The example of Scotia Sanctuary demonstrates that stochastic variability in spatial requirements needs to be incorporated into translocation feasibility assessments.
In Chapter 4 I set about developing a framework for prioritizing new fenced translocation projects. Instead of the standard representation problem often used in conservation prioritisations, sites were instead prioritised using a population viability approach. This approach is far more appropriate given the inconsistent nature of threat listing for Australian mammals, and the crisis circumstances of Australian mammal populations. The approach also considers the conservation community’s priorities, capacity to act, and limitations of a decentralised network while using a complementarity framework. I demonstrated that under this framework, similar outcomes could be achieved 17 times more efficiently than an ad hoc approach, highlighting the utility of prioritisation frameworks in conservation fencing.

To many, the ultimate conservation goal for Australian mammals is to re-establish fully wild and unfenced populations. To achieve this, predators need to be managed effectively in a broader landscape. In Chapter 5 I investigated whether taking advantage of underlying ecological cycles could allow managers to improve conservation outcomes for a predator-affected mammal through poison baiting programs. Over the long term, implementation can range from consistent, maintained baiting programs to ad hoc, spontaneous pulses. I wanted to test if dynamic baiting schedules which varied in intensity in harmony with the El Niño Southern Oscillation (ENSO) cycle could improve overall cost-effectiveness. I modeled populations of rabbits (*Oryctolagus cuniculus*), foxes (*Vulpes vulpes*) and bilbies (*Macrotis lagotis*) in a semi-arid community across the duration of the ENSO cycle. I found that the system’s intrinsic stochasticity overshadowed the potential benefit of dynamic baiting. While modest savings can be made by avoiding baiting when predator populations are naturally diminished, the majority of conservation benefit comes from the amount of baiting, not the time or sequence of its application.

In sum, my thesis demonstrates that improvements in cost-effectiveness for management of Australian mammals could be made through systematic planning. By treating fenced translocations as a portfolio rather than a set of individual units, we can achieve significant improvements in outcomes, however, more widespread reporting of project costs and outcomes could greatly improve estimates of future recovery projects. Yet from an ecological perspective, the effects of environmental stochasticity particularly in multi-species translocations within fences, reduces our ability to explain project outcomes. While significant improvements to current practices could still be made through systematic planning, in stochastic systems, increased ecological knowledge may not equate to a capacity to improve management effectiveness.
Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature


**Other publications**


**Reports**


**Conference abstracts**


Ringma et al. 2015 Differences in Habitat use Between Two Adjacent Fenced Populations of Woylie (*Bettongia penicillata*). Scotia Symposium. Scotia Sanctuary, Australia.

**Publications included in this thesis**

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Contributions by others to the thesis

Chapter 1

Ringma JL, RA Fuller and AW Goldizen all contributed to editing and writing

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JLR, JOH and RAF designed the study. JLR and JOF prepared data ran the analysis. DOF compiled an occurrence dataset used in the analysis. All authors discussed the results and edited the manuscript.

Chapter 3

Ringma JL, AW Goldizen, RG Dwyer, DA Roshier and RA Fuller. Movement ecology of reintroduced woylies (Bettongia penicillata) in adjacent feral predator-free fenced areas

JLR, AWG and RAF designed the study. JLR and RGD prepared data ran the analysis. All authors discussed the results and edited the manuscript.

Chapter 4


JLR, MB BAW and RAF designed the study. JLR and MB prepared data ran the analysis. All authors designed the study, discussed the results and edited the manuscript.

Chapter 5

Ringma JL, GD Iacona, T Skorda, HP Possingham and M Bode. Can dynamic baiting improve conservation outcomes across highly stochastic environmental cycles?

All authors designed the study, discussed the results and edited the manuscript. JLR, GDI, TS, MB prepared and analysed data and configured the model.

Chapter 6

Ringma JL, RA Fuller and AW Goldizen all contributed to editing and writing
Statement of parts of the thesis submitted to qualify for the award of another degree

None
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Around the world, a growing number of people are being awarded a PhD. Post graduate qualification are now quite common, estimates suggest that as many as 1 in 50 people in OECD countries have been awarded with a PhD. It is perhaps easy to forget then that such a title, while a result of hard work, is also only possible for those of immense privilege. Throughout my PhD, and at crucial points in my life leading up to this time I have been provided with continued support from teachers, friends and family, all incrementally contributing to a point four years ago where I was able to choose a path of continued study, rather than the "easy” alternatives. Most of all I must thank my parents for a spare room for me to return to, keeping the truck running smoothly, and all the cups of tea and coffee. Megan, for staying through until the end and for the beginning of a new adventure.

To this day, I'm not entirely sure why Richard agreed to take me on as a PhD student. I suspect it was less to do about my academic achievements (or lack thereof) and more to do with our mutual enthusiasm for the natural world, and in particular, birds. It has been a long progression from a field naturalist four years ago to a conservation scientist today. Part of that process has included, for better or worse, room to explore different thoughts and ideas, often hugely tangential to the actual course of my primary topic. During my PhD, I have been immensely privileged to be part of an amazing institution. The University of Queensland’s Environmental Decisions Group and funding from the Centre for Excellence in Environmental Decision making has collected some of the best minds and characters in conservation science. The inclusiveness, expertise of my colleagues and mentors, and ability to freely pursue ideas as they arise means that experience I have taken away is far greater than the sum of the chapters in this thesis. I’d like to thank Richard, Mike and Hugh for acting as mentors and everyone who I have worked with, talked to, and bounced ideas off at the centre. It would not have been the same without you.

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**Keywords**

translocation, predator exclusion fence, invasive alien species, spatial optimisation, stochasticity, critical weight range, Australian mammals

**Australian and New Zealand Standard Research Classifications (ANZSRC)**

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**Fields of Research (FoR) Classification**

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<th>Description</th>
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<tr>
<td>AWC</td>
<td>Australian Wildlife Conservancy</td>
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<tr>
<td>BB</td>
<td>Brownian Bridge</td>
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<tr>
<td>BNT</td>
<td>Bridled nailtail wallaby</td>
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<tr>
<td>CAPAD</td>
<td>Collaborative Australian Protected Area Database</td>
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<tr>
<td>CWR</td>
<td>Critical Weight Range</td>
</tr>
<tr>
<td>DCA</td>
<td>Detrended Principal Component Analysis</td>
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<tr>
<td>ENSO</td>
<td>El Niño southern oscillation</td>
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<tr>
<td>EPBC</td>
<td>The Environment Protection and Biodiversity Conservation Act 1999</td>
</tr>
<tr>
<td>GLMM</td>
<td>General Linear Mixed-Model</td>
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<tr>
<td>GPS</td>
<td>Global Positioning System</td>
</tr>
<tr>
<td>IUCN</td>
<td>International Union for Conservation of Nature</td>
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<tr>
<td>KUD</td>
<td>Kernel Utilisation Distributions</td>
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<tr>
<td>LM</td>
<td>Linear Model</td>
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<tr>
<td>NSW</td>
<td>New South Wales</td>
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<tr>
<td>NVIS</td>
<td>National Vegetation Information System</td>
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<tr>
<td>PH</td>
<td>Pech and Hood (1998)</td>
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<tr>
<td>S1</td>
<td>Stage 1</td>
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<td>S2</td>
<td>Stage 2</td>
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<tr>
<td>SDM</td>
<td>Species Distribution model</td>
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<td>TAF</td>
<td>Time Above Floor</td>
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<tr>
<td>TB</td>
<td>Total Bilbies</td>
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<td>VHF</td>
<td>Very High Frequency</td>
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Chapter 1

Introduction
1 Introduction

We are in the midst of an extinction crisis. Biodiversity has been lost at a rate several orders of magnitude higher than background expectation (Barnosky et al. 2011) and many species are at imminent risk of extinction (Schipper et al. 2008, Kuussaari et al. 2009). Anthropogenic influences are the primary cause of this decline (Lande 1998), although not all species have been affected equally. Extinction risk varies taxonomically and geographically (Purvis et al. 2005, Fritz et al. 2009), is correlated with the intensity of extrinsic threats (Cardillo et al. 2004), and is moderated by the intrinsic susceptibility of taxa to those threats (Lockwood et al. 2002). To date habitat clearance, persecution and invasive species are the three anthropogenic threats implicated in the majority of extinctions and declines in species globally (IUCN 2015).

Often overshadowed by more visible threats such as habitat clearance, invasive predators have been implicated in 60% of mammal extinctions (46 species) and 55% of bird extinctions (77 species; IUCN 2014) globally. The impact of invasive predators has been most significant in island ecosystems (Reaser et al. 2007) where European exploration and settlement have led to both deliberate and inadvertent introduction of a variety of mammalian predators, most notably rodents, felids and canids. Mammals have been strongly affected by this crisis (Ceballos and Ehrlich 2002, Baillie et al. 2004), particularly those from Australia (Woinarski et al. 2014).

Australia hosts a suite of unique and highly threatened mammal species. It is the global epicentre of marsupial diversity, with a long history of biogeographic isolation from the rest of the world (Tyndale-Biscoe 2005). In recent geological time, its terrestrial mammal fauna has been shared only with New Guinea - through the periodic opening of land bridges during glacial maxima (Strahan and Van Dyck 2008). It has otherwise been ecologically isolated from the rest of the world for tens of millions of years. The result is an island continent of extreme endemism, and a mammal fauna highly susceptible to anthropogenic threats. In this thesis, I focus on developing tools to promote the recovery of Australian mammals threatened with extinction by invasive predators.

1.1 Mammal extinctions in Australia

The history of anthropogenic mammal extinction in Australia began in the Pleistocene. Shifting climate and hunting pressure from Aboriginal Australians coincided with a depletion of mammal diversity (Johnson 2006). Although the precise role of Aboriginal Australians in this wave of extinctions is debated (Miller et al. 2005, Johnson 2009, Wroe et al. 2013), it is clear that Aboriginal Australians had a profound influence on the ecology of the Australian landscape. European settlement followed, resulting in novel and often, interacting threats. Persecution was responsible for the extinction of the thylacine Thylacinus cynocephalus, and many threatened marsupials were harvested for fur (Short 1998). Extensive clearing for agriculture resulted in the loss of up to 95% of some ecosystem types, with only small and fragmented patches
remaining (Tulloch et al. 2015a). Pastoralists introduced hard-hoofed ungulates that overgrazed and damaged delicate soils and watercourses (Martin and McIntyre 2007). Increased density of water points in arid environments enabled large macropods and feral herbivores to permanently occupy large proportions of the arid interior and persist at higher densities (Fensham and Fairfax 2008). Most recently, the looming threat of climate change may have already claimed its first Australian victim, the Bramble Cay melomys (*Melomys rubicola*) (Woinarski et al. 2015).

Among mammals globally, life history traits associated with vulnerability to extinction tend to correlate with large body size (Cardillo et al. 2005, Cardillo et al. 2006, Davidson et al. 2009). Large mammals in Australia have not been exempt from decline, although many of these declines occurred during the Pleistocene before European settlement (Flannery and Roberts 1999, Burney and Flannery 2005, Brook et al. 2007), probably due to either hunting by Aboriginal Australians or changed fire regimes (Johnson 2006). In contrast, recent declines in Australian mammals have instead tended to occur in smaller mammals, and are generally accepted to have resulted from predation by introduced species (Johnson and Isaac 2009).

Introduced carnivores have been affecting Australia’s native mammals for four millennia. The arrival of dingoes (*Canis lupis dingo*) to mainland Australia around 3500 years ago coincided with the extirpation of thylacines and Tasmanian devils *Sarcophilus harrisii*, which at the time were positioned at the top of the trophic web, from mainland Australia (Johnson and Wroe 2003, Johnson 2006, Letnic et al. 2012). European colonisation at the end of the 18th century resulted in the introduction of yet more species (Abbott 2002, 2008, 2011). Red foxes (*Vulpes vulpes*), cats (*Felis catus*) and rabbits (*Oryctolagus cuniculus*) spread across the Australian continent, leaving in their wake a wave of localised extirpations and, ultimately, the extinctions of numerous species of smaller bodied, native mammals (Marlow 1958, Finlayson 1961). The impact of introduced cats and foxes often preceded the physical presence of European settlement (Short and Calaby 2001, Abbott 2002, 2008, 2011). Many native mammal species lack suitable avoidance strategies for introduced predators due to an intrinsic evolutionary naivety (Blumstein et al. 2002, Carthey and Banks 2012). In consequence, all but two of Australia’s 22 terrestrial mammal extinctions since European settlement can be attributed to non-native invasive predators, and those same predators are implicated in the decline of a further 58 nationally-listed threatened species (Woinarski et al. 2014, Woinarski et al. 2015).

Evidence for the impact of invasive predators on Australian mammals lies in the type of species that have been affected. Australian mammals within a critical weight range (CWR) of 35 – 5500 g are most strongly affected by extinction risk (Burbidge and McKenzie 1989), and this is the preferred prey size of cats and foxes (Paltridge et al. 1997, Paltridge 2002). As well as a large number of extinctions, many species of critical weight range mammals have become extirpated from large portions of their original distributions (McKenzie et al. 2007). While a variety of observations support the link between feral predators and these declines, the CWR hypothesis has been criticised as overly simplistic or inadequate for describing the state of Australia’s mammal crisis (Cardillo and Bromham 2001) and is subject to much debate (Cardillo and
Bromham 2001, Fisher et al. 2003, Chisholm and Taylor 2010). A major review concluded that the CWR paradigm was only applicable to a specific subset of species (Johnson and Isaac 2009). Australia’s most threatened mammals are (i) terrestrial and thus unable to escape from foxes by climbing, (ii) typically of arid or semi-arid distributions where effects of predation are more pronounced, (iii) still extant in northern Australia where foxes are absent or with unaffected sister species there, and (iv) still extant on offshore islands where introduced predators are absent (McKenzie et al. 2007, Burbidge et al. 2008, Johnson and Isaac 2009, Woinarski et al. 2011). Surviving species often remain in the more mesic part of their distribution, as more complex vegetation structure affords higher protection from predators (McKenzie et al. 2007, Johnson and Isaac 2009).

The impact of invasive predators is often synergistic with other threats. Rabbits both provide a food source for cats and foxes, elevating their numbers, and degrade habitat through extensive grazing and fire (Letnic and Dickman 2006, 2010). Alterations to fire regimes have resulted in catastrophic interactions with predation by cats, particularly in northern savannahs. The latter mechanism has been implicated in the decline of many mammal species from the top end (Woinarski et al. 2011). Until recently it was thought that northern mammal species were not in severe decline owing to their lack of spatial overlap with foxes; however, it has been revealed that declines in these species have either occurred recently or were previously poorly recorded.

In arid and semi-arid Australia, extreme predation upon Australia's native mammals is driven by intrinsically stochastic climatic conditions. Rainfall in these landscapes is highly variable, with the predominant, dry El Niño weather systems interrupted by higher rainfall La Niña conditions, producing a boom/bust cycle (Morton et al. 2011). Numbers of introduced predators are inflated by prey availability during productive conditions (Letnic and Dickman 2006). The consequent impacts on native wildlife result from density-dependent predator (Catling 1988) interactions and a shift in predators’ diets to native species after the bust of eruptive prey (Sinclair et al. 1998, Pavey et. al. 2008). The magnitude of native mammal decline is best described by McKenzie et al (2007), who showed that as much as 60% of mammal richness has been lost throughout the Australian interior.

Cats and foxes not only prevent the recovery of extirpated species, but also continue to cause the decline of many more species, rendering the Australian mammal crisis an urgent and vexing conservation problem. Since the 16th century, mammal declines have occurred more rapidly in Australia than on any other continent, with many species being pushed to the brink of extinction or beyond (Baillie et al. 1996). Currently, the IUCN recognises over 40% of Australia's terrestrial mammals as extinct or threatened with extinction. Many of the affected species were once abundant, highly fecund and played crucial roles as ecosystem engineers, by dispersing seeds, increasing seedling recruitment and improving soil quality (James and Eldridge 2007, James et al. 2009, James et al. 2010). The contemporary extirpation and extinction of Australian mammals as a direct result of the predation of foxes and cats is considered by many to be the most
significant mammal conservation crisis in the world (Woinarski et al. 2015). For remaining species, recovery is highly dependent on reintroductions as a management action.

1.2 Reintroductions as a conservation tool

Because of the degree of extirpations experienced to date by Australian mammals, once predator levels are brought under control, conservation managers have increasingly looked to reintroduction as a management tool (Short 2009). The term "reintroduction" refers to the movement by people of individuals to a former part of the species’ distribution where it is now absent. Reintroductions are a subcategory of translocations, which can broadly be defined as the movement and release of an organism into new habitat for conservation purposes by anthropogenic means (IUCN 1987). Other forms of translocation also include introductions, which are the movement of individuals of a species to an area outside of the species’ former range, and re-stocking/supplementation, referring to the movement of individuals to an area with that already has an existing population of that species (IUCN 1987, 1998). While all three forms of translocations have been used for conservation purposes, reintroductions are most frequently adopted (Fischer and Lindenmayer 2000).

The extent of local extirpations and range reductions experienced by many threatened species makes reintroductions a powerful tool for species’ recovery with the potential to be applied to a multitude of species (Seddon et al. 2007). At least 489 animal species had been reintroduced globally by the early 2000s, with an emphasis on mammals and birds (Seddon et al. 2005). Reintroductions have the potential to increase the total population size of a species, and help to spread risk spatially by establishing additional populations that protect against stochastic events (McCallum et al. 1995). In extreme examples, successful reintroductions as part of integrative management plans have resulted in the downgrading and delisting of previously threatened species such as: the wolf (Canis lupis), peregrine falcon (Falco peregrinus) and Aleutian cackling goose (Branta hutchinsii leucopareia) in the USA (Pagel et al. 1996, Noecker 1998, Mini et al. 2011).


The developing field of reintroduction biology consists largely of retrospective studies focused on single species (Seddon et al. 2007). Recent reviews have summarised these publications in an attempt to identify common causes of successes and failures (Clayton et al. 2014, Fischer and Lindenmayer 2000, Seddon et al. 2005, Seddon et al. 2007, Armstrong and Seddon 2008, Short 2009, Sheean et al. 2012, Armstrong et al. 2015). Costs of reintroductions are seldom reported, but often run into the millions of dollars (Miller et al. 1999, Fischer and Lindenmayer 2000). Reintroductions are notoriously failure prone, with more projects failing than succeeding (Fischer and Lindenmayer 2000, Sheean et al. 2012). The success of reintroductions of species sensitive to predation is typically lower still (Short 2009, Finlayson et al. 2010, Moseby et al.)
Progress in understanding why many reintroductions fail is perhaps most hindered by a lack of monitoring and reporting of both successful and failed reintroduction attempts, and the current lack of a universally applicable definition of success (Short 2009, Shean et al. 2012). Current definitions are often based on the persistence of a population for a defined time period, while more rigorous definitions incorporate population growth rates and survival of progeny (Short 2009). At present, best practice reintroductions set time-based milestones to determine success (Hayward 2012). Reintroduction has been used widely and with increasing frequency as a conservation tool (Soorae 2008, Soorae 2011), yet understanding why many reintroductions fail remains an important research priority (Armstrong and Seddon 2008). Nonetheless, several predictors of reintroduction success have been identified.

1.3 Achieving a successful reintroduction

There are several important elements to a successful reintroduction program. The first and most crucial is the removal of the agent or agents of decline, or to at least the achievement of sufficient control to allow persistence of the reintroduced species (Caughley and Gunn 1996). When predation is the agent of decline, complete elimination is often necessary, since simply reducing predator density has frequently turned out to be inadequate, with reintroduced species being acutely vulnerable even to low predator densities (McCallum et al. 1995, Moseby et al. 2011, Walsh et al. 2012). Second, the number of animals in an initial release must be high enough to found a viable population (Leberg 1993, Hanski et al. 1996), with an additional population buffer large enough to account for losses from stochastic events (McCallum et al. 1995). Ideal release sizes vary among species (Griffith et al. 1989), and when calculating ideal release sizes, modelling of population trends incorporating fecundity of the species and the influence of stochasticity is now common practice in a priori feasibility studies (Southgate and Possingham 1995, Lurz et al. 2003, Seddon et al. 2007). Third, inbreeding depression, caused by low genetic diversity in release populations, can result in low body condition and fecundity, particularly when released populations are under stress (Miller 1994, Pray et al. 1994, Eldridge et al. 1999, Marshall and Spalton 2000, Armbruster and Reed 2005). A genetically diverse release population is therefore an important consideration for a successful reintroduction outcome. The final critical factor for reintroduction success is for the release to occur in suitable habitat (Delroy et al. 1986, Seddon et al. 2007, Shean et al. 2012). A priori habitat assessment through predictive distribution modelling has increasingly been adopted in an attempt to correctly identify suitable habitat (Murray et al. 2008, Bateman et al. 2011, Murray et al. 2011). Identifying appropriate habitat can be difficult, as refugial populations may be occupying places where the agent of their decline is least effective rather than areas of highest habitat suitability (Caughley and Gunn 1996, Hayward et al. 2005, Cromsigt et al. 2012, Kuemmerle et al. 2012).

Several other issues have been identified as important to reintroduction success in particular cases. The health status of released animals can influence an outcome, and ongoing health monitoring post-release can lead to the early detection of any problems (IUCN 1987, Mathews et al. 2006). The origin of release stock has been found to influence survival, fecundity and overall reintroduction outcome (Griffith et al. 1990,
Pople et al. 2001), with animals sourced from wild populations tending to perform better than captive animals. For example, predators released from captive populations are more prone to starvation than wild stock (Jule et al. 2008), while in prey species, captive animals may be more naive to predation (Griffin et al. 2000). Understanding the ecology of the species and ensuring that release animals are acclimated to their new environment is integral to developing an effective strategy for improved survival and reproductive fitness of reintroduced populations (Komers and Curman 2000, Sigg et al. 2005). Finally, conservation managers must overcome the unique socio-political issues associated with the location and jurisdiction of the reintroduction site (Clark and Westrum 1989). Reintroduction success is most likely when all of these factors are accounted for, but success is still not guaranteed. Real world limitations mean that it is not always possible to control all of the factors influencing reintroduction success. It is also possible that other factors critical to the outcome of a particular reintroduction remain unidentified.

1.3.1 Assessment of habitat suitability for reintroductions

Reintroduction failures in Australian CWR species are routinely attributed to insufficient feral predator control (Short 2009). However, based on our poor understanding of habitat preferences of long extirpated species, it seems at least plausible that many such efforts may actually have taken place in suboptimal or unsuitable habitat (Delroy et al. 1986). A critical step in planning a reintroduction is to identify suitable locations for the project. This process may be as simple as using the area defined as habitat in distribution maps from guide books such as Strahan & Van Dyck (2008), locating remnant habitat near historic records, or identifying components of critical habitat (IUCN 2013). This style of distribution map identifies any area that falls within an approximate polygon map based on scattered historical records as potential habitat. When a species has been extirpated for an extended period of time, this may be the best habitat information available. However, for a reintroduction manager this is problematic if it is assumed that our knowledge of the species’ former range is accurate that all areas within its range are equally likely to have been occupied, and that the habitat characteristics of an area have not changed since the species was extirpated. Decisions based on this level of information are most problematic if managers have a predefined area where they wish to make a reintroduction rather than designing a reintroduction with particular species in mind. Further, the places where a species survives today are likely to be defined simply by the absence of the threatening process that caused the extirpation elsewhere (Cromsigt et al. 2012, Kuemmerle et al. 2012), rather than representing the most suitable habitat (Caughley 1994).

Inferences about habitat suitability based on refugial populations are potentially erroneous and could ultimately result in reintroduction failure (Short et al. 1992, Fischer and Lindenmayer 2000, Finlayson et al. 2010, Moseby et al. 2011). Without a better understanding of a species’ habitat requirements, conservation managers are unable to make informed decisions on questions regarding habitat suitability when developing reintroduction plans. Historical records provide a better understanding of habitat requirements over a broad range than extrapolating from refugial populations, and a clear understanding of optimal habitat based on robust modelling of former distributions may be crucial for achieving a higher reintroduction success rate. In
Chapter 2, I develop a method to assess the adequacy of historic datasets for habitat suitability modelling and in Chapter 3, I describe the movement ecology of the frequently translocated woylie in a semi-arid reintroduction site.

1.3.2 Controlling predators

The leading cause of translocation failure is failure to control the agent of decline (IUCN 1998, Short 2009), i.e. the threatening process that originally resulted in the species’ extirpation in the first place. In the case of Australian mammals, translocations are typically unsuccessful unless invasive predators are eradicated or very thoroughly controlled. Predator eradication is expensive in the short term but has conservation benefits and cost efficiencies that extend into the long term. When populations are not spatially constrained eradication is logistically infeasible and thus on the Australian mainland, management of predators is an ongoing enterprise.

One of the most frequently used predator control methods is baiting using 1080 poisoning, either to relieve predation pressure on remnant populations of native mammals or to create safe sites for reintroductions (Short 2009, Dickman 2012). As a form of lethal control, baiting is typically more efficient in terms of cost and effectiveness when compared to alternatives such as trapping and shooting (Short et al. 1997, Rout et al. 2014). Baiting programs range in scale from mass aerial programs to targeted stations at permanent, fixed locations (Bailey 1996, Marks et al. 2002, 2003). Given the difficulty of achieving a viable population with the typically small number of individuals used in translocations (Leberg 1993, Southgate and Possingham 1995, Hanski et al. 1996, Short 2009), predators must be controlled to a much lower density than would be tolerated by an established population. Actions must therefore be of a sufficient intensity to achieve their conservation goal, further increasing project costs. Moreover, baiting programs can be effective against dingoes and foxes, but are often ineffective for the removal of cats. Baiting programs are often implemented at an intensity or scale that is too low to be of benefit to the wildlife they are intended to protect (Gentle et al. 2007, Walsh et al. 2012). For many Australian species, alternative, cost-effective methods for predator control must be found. In Chapter 5, I investigate this topic by investigating whether dynamic scheduling of baiting can improve conservation outcomes.

1.3.3 Conservation and predator exclusion fencing

Conservation fencing has been applied worldwide to abate a variety of threats (Hayward and Kerley 2009), and it is increasing in popularity. Reintroductions of extirpated mammal populations within predator-proof fences has increased in popularity as a response to the mammal extinction crisis in Australia and the difficulty of achieving complete predator control across open landscapes through baiting programs (De Tores and Marlow 2012, Dickman 2012, Hayward and Somers 2012). In Australia, fenced reintroduction sites range in size from several dozen to several thousand hectares. Their construction is expensive, ranging between AUS$6,000 to $30,000/km (Coman and McCutchan 1994, Dickman 2012) in materials and requiring ongoing maintenance at around $1,000/km per annum (Pickard 2007). These prices are justified for highly
sensitive species as fencing may represent the only viable method of threat abatement for reintroduced populations.

Well maintained, systematically tested, and well-designed fences represent the most effective form of long-term predator control (Moseby and Read 2006), providing that ongoing maintenance is thorough and complete predator eradication is achieved after the construction of the fence (Short and Turner 2000, Williams and Manthey 2012). It is not surprising then that reintroduction success of CWR mammals is found to be higher when predator exclusion fences are used as the main form of threat abatement instead of baiting programs (Short 2009). Conceptually, the reintroduction of multiple species of threatened mammals at the same location allows conservation agencies to maximise the return on their capital investment in threat abatement. Fourteen of the 18 fences (78%) identified by Dickman (2012) provide refuge for multiple reintroduced species. However, in a multi-species reintroduction, the ecology of the released species must be considered to ensure long-term persistence of viable populations. The relative expense of both reintroductions and predator eradication programs makes failure a financially costly exercise. Finite stock of release animals (Moir et al. 2012) also makes maximising the chance of success of each reintroduction attempt critical to the continued persistence for many species. In Chapter 4, I create a systematic method for assigning new fences for maximum conservation benefit.

1.4 Research problems addressed in this thesis

Australian mammals are in crisis, and their recent decline due to invasive predators is one of the most urgent conservation issues anywhere in the world (Short and Smith 1994, Woinarski et al. 2015). My project will provide information to help recover this important national asset. Given the long list of threatening processes that affect Australian mammals, management objectives and priorities depend strongly on timeframe of actions. Ultimate goals for Australian mammal conservation might be to achieve security of each individual species, restoration of community structure, and to recover ecosystem function over a reasonable proportion of each species’ historical range. With few exceptions, these are largely unachievable with current technologies, especially when considering limited conservation budgets, and without incorporating large degrees of uncertainty and risk. Remediating the effects of feral predators by securing and creating stable, viable populations must be our priority goal, while considering that technologies might become sufficiently developed for widespread implementation in the future. The focus of this thesis is therefore to address primary short-term goals in a manner that accommodates long-term objectives for mammal conservation, through cost effective, strategic implementation of current management practices. In this thesis, I aim to address a number of applied problems related to the Australian mammal crisis, through both the development of new theoretical conservation tools, and collection of new information about the ecology of Australian mammals.
With many species extirpated from much of their former range and now persisting only in small areas, reintroductions are fast becoming the only viable conservation tool (Griffith et al. 1989). Many translocation attempts end in failure (Finlayson et al. 2010, Sheean et al. 2012), highlighting an urgent need to understand the causes of success and failure so that translocation outcomes can be improved. Recognition that habitat suitability is crucial to translocation outcome (Delroy et al. 1986) has galvanised efforts to assess habitat quality prior to translocation attempts taking place. However, many threatened species subject to translocation as a management strategy have been extirpated from large proportions of their former distribution since the late 1800s. Predictive models such as Maxent (Phillips and Dudík 2008) are increasingly being used to identify and assess suitability of potential sites for translocation beyond a species’ current remnant distribution. Extirpation bias occurs when an agent of decline constricts a threatened species distribution to its contemporary range. In such cases, historical data on species distributions are critical to avoid mischaracterising a species’ niche. Yet, historic records are themselves sparse and often biased with respect to the formerly occupied environmental niche (Cromsigt et al. 2012, Kuemmerle et al. 2012), ultimately resulting in misleading suitability models. With over a century elapsed between extirpation and proposed translocation programs, how does one ascertain the quality of historic occurrence datasets? In Chapter 2, I develop and propose a method to answer this question. By building accumulation curves on chronologically arranged data, one can determine how much the observed accumulation of environmental niche data varies from random expectation, and therefore, whether a historic dataset might be trusted for predictive purposes.

My second analytical chapter investigates how the movement ecology of woylies (Bettongia penicillata) differs between two fenced populations of high and low density. Both populations were released in near identical habitat, but otherwise released in very different conditions, both in terms of the climatic conditions at the time of release and the mammal community assemblages in the two areas. For fenced translocation programs to be efficient, we need to be able to confidently translocate multiple species into the same area. Understanding what ecological factors might affect the expected return on a program is therefore vital for prioritisation of new fence programs. Chapter 3 contributes to this knowledge through new ecological observations of differences in movement behaviour between two populations of the same species.

Building on my first two chapters, in Chapter 4 I tackle choosing the location of new predator exclusion fences. These fences have become increasingly popular as a management tool as they provide a mechanism for the total predator control that is often needed for the persistence of many species. However, the Australian fence network lacks a single overarching governance structure, and is therefore potentially subject to some of the same inefficiencies seen in the expanding protected area network before the development of systematic methods. I develop a tool that managers can use to identify highly beneficial potential fencing projects using population viability and complementarity frameworks (Brown et al. 2015). The method estimates the probability that a species will become extinct based on existing population and demographic
characteristics of the species (Lande 1993), and then identifies the expected reduction of extinction risk when a new fence is built at a given location.

When for logistical reasons eradication is not feasible, managers are restricted to continuous control as a management action with long-term conservation goals. Efficiencies or improvements in effectiveness could occur by better understanding of how long-term cycles may influence this system. However, Australian ecosystems are highly stochastic, reducing the predictability of conservation outcomes from management action. The El Niño southern oscillation (ENSO) cycle is a stochastic, long-term weather pattern that drives ecological fluctuations throughout the globe, including boom-bust phenomena in Australian mammals (Letnic and Dickman 2006, 2010). In these highly stochastic, ENSO-driven systems, conservation outcomes might be improved through dynamic allocation of resources. In my final analytical chapter (Chapter 5), I create a model that investigates the effect of dynamic baiting schedules on simulated populations of threatened bilbies, to identify whether potential for efficiency exists from dynamic allocation of management effort over the long term.
Chapter 2

Measuring environmental niche in declining species
2 Measuring environmental niche in declining species

2.1 Abstract
Understanding the distributions of species, and learning what constitutes suitable habitat are fundamental to making good conservation decisions. Researchers often use environmental niche models to estimate the distribution of suitable habitat, in which occurrence data are matched with environmental data to predict suitability or occupancy beyond the geographic space or time period in which the data were collected. However, such models often assume that available species occurrence data represent the full range of environmental conditions in which a species occurs. This is problematic for conservation applications, as it is likely that occurrence data for species that have declined geographically under-represent the species’ formerly occupied niche. For such species, models may identify only a small subset of the former distribution as suitable habitat and thus overestimate the suitability of the contemporary distribution, leading to suboptimal conservation decisions, such as reintroductions into marginal habitat. Historic data therefore must be incorporated into distribution models for species that have undergone geographic decline. But, given the typically sparse data available to inform historical distributions, how does one ascertain whether a historic dataset is an adequate sample of a species’ formerly occupied environmental niche? In this chapter, I show how environmental niche accumulation curves can be used to indicate sampling adequacy in occurrence datasets. Data for 24 species of threatened Australian marsupials were arranged in three configurations; (i) randomly, (ii) forward and (iii) reverse chronological order. If a niche is well sampled, accumulation curves should approach a clear asymptote. However, oversampling of occurrences after a decline has occurred might be expected to result in a false asymptote emerging at a lower than expected niche space. If no bias exists due to under sampling before the decline, chronologically arranged data should not differ beyond random variation. Divergence between chronologically and randomly arranged data implies underestimated niche volume. I found that pre-decline sampling appeared to be adequate for only 25% of species, and that while accumulation curves cannot discover the underlying niche in the absence of data, they can help assess the adequacy of sampling in species occurrence data for declining species. The method I describe in this chapter provides a framework to assess when these biases may exist for the first time and could therefore be used as an initial step in species distribution modeling applications for species suspected to have undergone a geographic decline.

2.2 Introduction
An ecological niche is the combination of factors, both biotic and abiotic, in which a population of a species may persist and exhibit positive growth (Chase 2011). Estimates of species’ niche are frequently made from correlates of presence and environmental factors (Warren and Seifert 2011). Environmental niche estimates fundamentally underpin studies in ecology and evolution as a predictor of species habitat (Guisan and

One common use of environmental niche estimates is to model the spatial distribution of species based on environmental conditions in currently occupied areas (Phillips and Dudík 2008, Elith and Leathwick 2009). Such ecological niche modelling informs conservation decisions as diverse as assessment of risk status (Sattler et al. 2007, Thorn et al. 2009), selecting priority regions for conservation investment (Runge et al. 2015, Tulloch et al. 2015b), estimating dynamic conservation priorities in a changing climate (Hannah 2008, Maggini et al. 2013, Wauchope et al. 2016), and making decisions about where to undertake translocations or reintroductions of extirpated species’ (Chapter 4). However, misleading conclusions about a species’ environmental niche can result from biased sampling of the environmental conditions in which a species can occur.

Biodiversity survey effort can be highly spatially biased, with uneven sampling across a species’ geographic distribution leaving some regions under-sampled or not sampled at all (Boakes et al. 2010; 2016). Uneven and biased sampling can lead to underestimation of the range of environmental conditions that a species can occupy (Lahoz-Monfort et al. 2014). In this case additional, targeted data can be collected if under-sampled areas are identified, or bias can be partially compensated for by adjusting sampling of background points in model inputs (Raes and ter Steege 2007, Syfert et al. 2013).

A second, more vexing form of sampling bias occurs in declining species. The current geographic distribution of declining species is often a small subset of the environmental conditions that it once occupied (Cowlishaw 1999, Wilson et al. 2004, Boakes et al. 2010). Ecological niche model outputs based on contracted ranges are known to differ to those based on full historical datasets (Hortal et al. 2008, Martínez-Freiría et al. 2015). The impact of most agents of decline causes remnant populations of threatened species to retract to refugial habitats (Cromsigt et al. 2012). These refugia are often inversely correlated with the impact of agents of decline (Cowlishaw 1999, Boakes et al. 2010). Consequently, predictive models might make misleading predictions, such as inadvertently estimating the spatial influence of an agent of decline rather than habitat suitability of the threatened species (Kerley et al. 2012), or substantially underestimating the importance of habitat only occupied prior to the onset of decline (Cromsigt et al. 2012, Kuemmerle et al. 2012).

Conservation actions frequently rely on species distribution models (SDM) to identify likely habitat for target species (Moilanen et al. 2009). But given the nature of pre-decline sampling, it is uncertain how far such models should be trusted. For example, Hunter et. al (2015) created a Maxent habitat suitability model (Phillips and Dudík 2008) for Tasmanian devils on the Australian mainland trained on contemporary occurrence data from Tasmania. Before the arrival of dingoes, devils were widely distributed across Australia, not just constrained to the south-east corner (Dawson 1982, Louys et al. 2014). The SDM in Hunter et. al. (2015) therefore identifies climatic space on the Australian mainland that is most similar to

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Tasmania. However, given their historic occurrence, it seems likely that the model underestimated the full extent of environmentally suitable geographic space that devils historically occupied on the Australian mainland. Greater conservation opportunities would likely arise by considering a more complete description of the devil’s formerly occupied environmental niche. This does not mean the model is not useful, it identifies initially low risk areas for mainland translocations, where environmental space is most likely to be suitable for the Tasmanian genotype.

Ultimately there is a need to balance the risk of error in modelling habitat suitability beyond the currently occupied distribution, against the increased opportunity that a more complete model of environmental niche might afford. If managers knew which models where created using representative samples of historic environmental niches, they could make decisions with a reduced risk of misidentifying suitable habitat. However, no method currently exists to assess the comprehensiveness of pre decline occupancy sampling in historic occurrence datasets for ecological modelling applications.

2.2.1 The case of Australia's declining marsupials

Australia’s mammals are amongst the most threatened in the world (Woinarski et al. 2015). Since European colonisation, 22 mainland species have become extinct: mainly smaller-bodied species that have fallen victim to invasive red foxes (*Vulpes vulpes*) and cats (*Felis catus*; Woinarski et al. 2014). A further 58 Australian mammal species are listed as threatened, with predation from invasive predators recognised as a key cause of decline (Chapter 1.1). One of the key management actions aimed at safeguarding Australian mammal populations is conservation fences (Dickman 2012, Woinarski et al. 2014). Considerable opportunities exist to translocate beyond a species’ current distribution (Chapter 4), but translocations must occur in suitable habitat to improve success (Griffith et al. 1989, Armstrong and Seddon 2008).

Unlike many species which have declined globally, the timing of the recent, rapid decline of Australian mammals shortly after the permanent colonisation of Europeans in the 18th century is relatively well understood. Cats were released shortly after European arrival, and spread rapidly across the continent. Foxes became established in the state of Victoria by the 1860's and reached most of their current range by the early 20th century. The impact of cats and foxes on native wildlife was apparent by the turn of the 20th century (Abbott 2002, 2008, 2011). Australia’s marsupials provide a unique case study to investigate the patterns of historic sampling in declining species against a known timeline of decline.

Accumulation curves are commonly used to estimate total species richness at a site based on the return of new information from repetitive sampling (Colwell et al. 2004, Xuan Mao et al. 2005). In the same way, completeness of environmental niche description for a species could be estimated based on the addition of new occurrence data. In this chapter, I examine the relationship between geographic range collapse and environmental niche contraction in Australia's fast-declining marsupials, and develop a new method for
assessing whether our understanding of environmental niche is likely to be a true representation of the realised niche prior to commencement of the decline. Here I (i) describe the relationship between geographic range decline and the reduction in environmental niche, and (ii) determine whether niche space accumulation curves contain information that helps assess the completeness of niche estimates for species that have undergone rapid declines.

2.3 Methods

2.3.1 Niche accumulation curves

When the first locality for a species is discovered, an estimate of its environmental niche will be a single coordinate in environmental space. As new localities are identified, the estimate of occupied environmental niche will expand each time a locality is discovered that is not environmentally identical to one of the localities already known. As the estimate of niche space approaches the true realised niche, returns on new information diminish. An accumulation curve should therefore approach an asymptote (green line, Figure 2.1), as sampling approaches complete description of the species niche. The presence of an asymptote should suggest that data are approaching a true estimate of the true environmental niche, but if sampling is biased, this asymptote may be misleading.

Where a species has declined spatially, sampling might be incomplete or even absent in the parts of a distribution that are no longer occupied. If the range of occupied environmental conditions in the portion of the range from which the species has now been extirpated were not adequately sampled, an environmental niche estimate will be incomplete (compare green line to black line, Figure 2.1). With limited capacity for retrospective sampling, how is it possible to determine whether the original realised niche has been adequately sampled? One approach is to compare niche space accumulation curves from data arranged in (i) forward and (ii) reverse chronological order. Where local extinctions of a declining species have occurred in a manner which conserves the realised niche with respect to environmental conditions, recently discovered localities will be as informative as older records, and the forward and reverse chronological accumulation curves should show no difference. However, where the species has contracted to an environmentally narrow region of the original realised niche, the earliest known localities will be more informative than more recent localities, as sampling at the oldest time point should be occurring from an overall larger occupied niche space. As a result, a more rapid accumulation of niche space should occur when the data are arranged in forward chronological order (compare red line to blue line, Figure 2.1).
Figure 2.1.
Accumulation curves for two different sampling scenarios for the same hypothetical ecological niche. In the first scenario depicted by the circled line, sampling occurred randomly with equal likelihood across the species entire geographic distribution. In this case chronological ordering of the localities does not change the shape of the accumulation curve. In the second scenario, the species occupies the same ecological niche as in the first scenario but underwent geographic decline during sampling, consequently the contemporary distribution is more frequently sampled. In this scenario, the black line depicts the expected accumulation curve of data arranged randomly with respect to time, the red line depicts data arranged oldest to newest and the blue line depicts data arranged newest to oldest. For data arranged oldest to newest (red line), the accumulation curve initially tracks with the expected accumulation of the circled line, but returns diminish more rapidly as the geographic extent of occurrence of the species begins to decline, and thus sampling occurs in an increasingly constrained geographic space. When data are arranged newest to oldest, the niche space initially accumulates at the rate from the contemporary distribution, as sampling is occurring from a smaller geographic area; the initial accumulation rate is lower. As we move back in time the species occupies more geographic space and the described niche space continues to climb. Despite both scenarios
suggesting asymptotic trajectories in the randomly arranged data, the differences between the accumulation curves with data arranged in forward and reverse chronological order suggests the latter is underestimating the species’ realised ecological niche.

2.3.2 Data

Species distribution and occurrence data

I used two sources of species distribution data for each of 24 critical weight range (35-5500 g) marsupials: (i) the overall geographic distribution of the species at two time points based on maps in a field guide (Van Dyck and Strahan 2008), the first time point prior to permanent settlement by Europeans in 1770 generated via expert assessment, and second, the present area of occurrence, and (ii), a database of occurrence records where the specific locality and year of observation is known. I constructed a database of historic Australian mammal occurrence data using data from the Atlas of Living Australia (accessed 10/09/2015). This dataset was supplemented with an exhaustive search of additional museum specimen records and state government databases (see Appendix 1). Occurrence records were manually vetted, ensuring that each record comprised a recognised species name, a year, and geographic coordinates accurate to within 10 km. All data were matched to a 10 x 10 km grid to identify unique localities where duplicate records falling within the same grid cell were aggregated to first recorded instance.

Environmental niche space calculations

Environmental variables were based on the 19 bioclimatic surfaces from Hijmans (2005), resampled at 10x10 km resolution. These climatic surfaces were subjected to a detrended principal components analysis (DCA, implemented in the vegan R package; (Oksanen et al. 2013). The first two principal components were then used to summarise the main gradients of climatic variation across the continent, creating a two-dimensional environmental space. For comparative purposes, environmental space was assumed to remain constant throughout a species’ occurrence sampling period. Environmental niche space was calculated using convex hulls enclosing the environmental coordinates of species occurrence data from the first two DCA axes (using the hypervolume R package; Blonder et al. 2014). Each species niche size was estimated in relation to the entirety of the Australian continent, avoiding pre-conceived notions of niche limits. Convex hulls were chosen over a density or probabilistic approach to niche space estimation due to the uncertain nature of sampling bias in the occurrence dataset, thus avoiding underestimates in niche size through unsampled holes. This method was used for all environmental niche estimates throughout the analysis.

2.3.3 Analysis

Reductions in geographic space and niche space
For each species I calculated percentage reduction in geographic range space and environmental niche space by dividing present values into historical values from the range maps in Van Dyck and Strahan (2008). From these range maps, I extracted the values of the first two DCA principal components from the environmental data at each 10 km grid cell to calculate the historic and current niche space.

**Comparison of niche accumulation curves under chronological arrangement of data**

To examine the pattern of accumulation of information on species’ environmental niche space, occurrence data were arranged chronologically from (i) most recent to oldest, (ii) oldest to most recent and (iii) in 100 different configurations, randomised by date (henceforth referred to as historic, contemporary and random). Niche space accumulation curves were created for each species by incrementally adding and recalculating niche space for each addition of a grid cell. A thoroughly sampled historic niche should satisfy two criteria. First, accumulation of randomly arranged data should approach an asymptote; second, for datasets approaching an asymptote, the chronological accumulation curves should approximate the random expectation. Where this is not the case, this suggests the estimate of the original environmental niche should be treated with caution. Accumulation curves for all 24 species were visually assessed against these criteria.

### 2.4 Results

Since European settlement, species lost an average of 79% geographic range space and 60% environmental niche space. Species with greater reductions in geographic range also typically showed a greater loss of environmental niche space, with some species maintaining surprisingly high environmental niche space even for geographic range contractions as large as 80% (Figure 2.2). The lower bound of the relationship approximated 1:1, while the upper bound suggested that for some species, environmental niche information may be relatively well conserved despite severe geographic range retraction. This likely relates to the pattern of decline. For instance, species that retracted to multiple locations, which were spread broadly across a large, environmentally homogenous distribution appear more likely maintain a similarly large estimate of niche space (e.g. common brushtail possum Appendix 2).
Figure 2.2.
Change in geographic range size and environmental niche space in 24 Australian mammals between their estimated historical distribution prior to European colonisation (approx. 1770), and their contemporary distribution based on occupancy at the time of publication. Environmental niche space is calculated from bioclimatic conditions within each 10 km grid cell overlapping the historical and contemporary distributions (see text).

2.4.1 Patterns in accumulation curves
Niche accumulation curves varied markedly among species. Five species recorded from fewer than 50 unique localities, exhibited random accumulation curves with a near linear increase - suggesting an under sampled niche space (Appendix 2). Niche space description of the remaining 19 species approached an asymptote to varying degrees, and also varied in their differentiation between randomly and chronologically arranged data. Of these species, eight (33%) demonstrated clear differentiation between randomly and chronologically arranged data, where historic niche space accumulated more rapidly than expected, and contemporary data accumulated more slowly than expected (Appendix 2).

In total, only six (25%) of the 24 species covered in this analysis satisfied the criteria of asymptotic niche accumulation and chronologically arranged accumulation curves that fell within the observed variation in randomly arranged data. One example is the boodie (*Bettongia lesueur*, Figure 2.3), for which historic and
contemporary arrangements of new locality data accumulated niche space at a rate that falls within the 95th percentiles of randomly arranged data. Records of boodie occurrence commenced shortly after European colonisation, with the most of the 104 unique localities recorded between 1870 and 1970 (see histogram in Figure 2.4). The combination of a large proportion of localities recorded before decline, an asymptotic trajectory of randomly arranged data, and chronologically arranged data accumulation within the range of variation of randomly arranged data, implies that the environmental niche space of boodies is likely to be well described, even if its geographic distribution is not.

Accumulations curves for many species failed to approach an asymptote, suggesting an undersampled niche. Small sample sizes were common, with nine of the 24 species included in the analysis (37.5%) recorded from fewer than 100 unique localities. An example of less intensive sampling is the bridled nailtail wallaby (*Onychogalea fraenata*, BNT). Unique localities for the BNT accumulate consistently throughout European history, but from only 42 unique localities. Consequently, the random accumulation curve exhibits a near linear increase (Figure 2.4). Historic and random data accumulate at a comparable rate, with both contemporary and historic accumulation curves falling within the 95% quantiles of randomly arranged data.

Of the more thoroughly sampled species, many exhibited accumulation rates of historic and contemporarily arranged data which implies inadequate pre-decline sampling. The northern quoll (*Dasyurus hallucatus*, Figure 2.5) and eastern quoll (*Dasyurus viverrinus*, Figure 2.6) as examples, exhibit markedly different accumulation curves to the boodie and BNT. Both species exhibit similar sampling histories, with the majority of localities collected in the last 50 years. Both are recorded in twice the number of unique localities as the boodie (northern quoll 247, eastern quoll 207). However, randomly arranged data only appears to approach an asymptote in the northern quoll. Records for the eastern quoll steadily increase until the last locality. For both species, historic data accumulates rapidly at rates much faster than expected based on randomly arranged data, and flatten off within the first 15% of unique localities. Converstely, the contemporary data accumulate more slowly than the 95th percentiles of the randomly arranged data. While the contemporary data for the northern quoll accumulates at a steady rate, the eastern quoll accumulates no additional niche space for over 100 localities, before doubling in size in the last 20 records.
Figure 2.3.
Environmental niche accumulation curve for the boodie (Bettongia lesueur) from the historic occurrence dataset. In plot A, y axis depicts the total described niche space (arbitrary units), the x axis depicts the number of unique geographic location in which B. lesueur was recorded. The black points depict the average accumulation curve from 100 randomised arrangements with respect to the date recorded. The grey bounds depict the 95% quantiles of the randomly arranged data. The blue line depicts the accumulation of data arranged chronologically from oldest to newest. The red line depicts the accumulation of data arranged in reverse chronological order, from newest to oldest. Plot B shows the number of unique localities where the boodie was recorded since European colonisation (1770 to present). The top plot shows the total number of records collected during each time bin. The bottom plot shows the number of new 10x10km cells to acquire a record, starting from the oldest records first.
Figure 2.4.

Environmental niche accumulation curve for the bridled nailtail wallaby (Onychogalea fraenata) from the historic occurrence dataset. In plot A, the y axis depicts the total described niche space (arbitrary units), the x axis depicts the number of unique geographic location in which O. fraenata was recorded. The black points depict the average accumulation curve from 100 randomised arrangements with respect to the date recorded. The grey bounds depict the 95% quantiles of the randomly arranged data. The blue line depicts the accumulation of data arranged chronologically from oldest to newest. The red line depicts the accumulation of data arranged reverse chronological order, from newest to oldest. Plot B shows the number of unique localities where O. fraenata were recorded post European colonisation (1770 to present). The top plot shows the total number of records collected during each time bin. The bottom plot shows the number of new 10x10km cells to acquire a record, starting from the oldest records first.
Figure 2.5.

Environmental niche accumulation curve for the northern quoll (Dasyurus hallucatus) from the historic occurrence dataset. In plot A, the y axis depicts the total described niche space (arbitrary units), the x axis depicts the number of unique geographic location in which D. hallucatus was recorded. The black points depict the average accumulation curve from 100 randomised arrangements with respect to the date recorded. The grey bounds depict the 95% quantiles of the randomly arranged data. The blue line depicts the accumulation of data arranged chronologically from oldest to newest. The red line depicts the accumulation of data arranged in reverse chronological order, from newest to oldest. Plot B shows the number of unique localities where D. hallucatus were recorded post European colonisation (1770 to present). The top plot shows the total number of records collected during each time bin. The bottom plot shows the number of new 10x10km cells to acquire a record, starting from the oldest records first.
Figure 2.6
Environmental niche accumulation curve for the eastern quoll (Dasyurus viverrinus) from the historic occurrence dataset. In plot A, the y axis depicts the total described niche space (arbitrary units), the x axis depicts the number of unique geographic location in which D. viverrinus was recorded. The black points depict the average accumulation curve from 100 randomised arrangements with respect to the date recorded. The grey bounds depict the 95% quantiles of the randomly arranged data. The blue line depicts the accumulation of data arranged chronologically from oldest to newest. The red line depicts the accumulation of data arranged in reverse chronological order, from newest to oldest. Plot B shows the number of unique localities where D. viverrinus were recorded post European colonisation (1770 to present). The top plot shows the total number of records collected during each time bin. The bottom plot shows the number of new 10x10km cells to acquire a record, starting from the oldest records first.
2.5 Discussion

By considering uncertain parts of a species distribution as potential locations for conservation actions, a larger area may result in increased opportunity (Chapter 4) and help to spread risk spatially (Helmstedt et al. 2014). Here, species distribution models (SDMs) can be used as decision support tools (Moilanen et al. 2009, Franklin 2010, Hunter et al. 2015, Kendall et al. 2015), identifying currently unoccupied space of similar environmental niche (Guisan and Zimmermann 2000, Peterson 2001). However, for declining species, the niche that is currently occupied may not represent highly suitable environmental space (Wallace 2002, Cromsigt et al. 2012, Kuemmerle et al. 2012). Typically, species that have contracted in geographic space have similarly retracted in environmental space (Figure 2.2). For models to be useful, biases in contemporary occurrence data inputs must be identified and accounted for (Loiselle et al. 2003, VanDerWal et al. 2009, Martínez-Freiría et al. 2015). Historic data therefore provides a mechanism to account for contemporary sampling bias, assuming sufficiently fine scale spatial resolution of records (Reside et al. 2011).

The findings of this work suggest that incorporating historic occurrence data by itself is inadequate, as sampling bias across environmental space and adequate rigor in historic datasets appears to be common. Before creating a SDM, modellers should first assess how comprehensively their occurrence dataset samples the historic niche to overcome sampling bias. The method described in this paper provides for the first time a framework to assess when these biases may exist.

In the case study, many Australian CWR marsupials have retracted to small proportions of their former realised niche. For some species, such as the common brushtail possum (*Trichosurus vulpecula*), environmental niche space is remarkably well conserved, with almost complete retention of original niche space, despite a nearly 50% contraction in geographic range size (Figure 2.1). This is because the common brushtail possum has retracted to numerous refugial populations that are widely spread across the breadth of its' former environmental niche. In contrast, for species that have retracted to one or two populations in the margins of their former distribution, estimates of niche space are a small fraction of the likely true extent (Figure 2.1). Description of the historic environmental niche in these species depends on pre-decline sampling adequacy, and accumulation curves can demonstrate whether sampling was adequate.

2.5.1 Applying accumulation as a gauge of dataset adequacy

There is a need for improvement in model verification techniques in species distribution modelling (Araujo and Guisan 2006). However, model verification methods typically test how well the model fits the data (Wisz et al. 2008), but not whether the input data is an adequate representation of the species’ niche. For example, at present 50-100 records are generally regarded as adequate to achieve repeatability within a model (Raes and ter Steege 2007), but I have shown here that many species with greater than 100 unique localities defined at relatively coarse resolution, failed to achieve both a strong asymptote in the randomly arranged accumulation curves, and exhibited greater variation than expected in chronologically arranged data. This method provides a mechanism to assess the adequacy of an occurrence dataset before modelling
commences, and suggests that the number of localities is less important than the spatial and temporal biases governing how the species’ distribution has been sampled.

All but two of the 24 species studied here have been translocated for conservation purposes (Short 2009). However, only 25% of the 24 species appear to have a thoroughly sampled historic niche. Ecological niche models based on data for the remaining 75% of species would probably under-predict both the geographic extent of former distribution, and provide misleading inferences about relative suitability based on sampling rate (Maiorano et al. 2013).

The example of the eastern quoll (Figure 2.6) illustrates the utility of accumulation curves in evaluating occurrence datasets. With records from 207 unique localities, total sampling effort for this species is high. However, historic and contemporary configurations of chronologically arranged (red and blue lines, Figure 2.6), varied greatly from random expectation (black line, Figure 2.6). The shape of niche accumulation curves (Figure 2.6) rapid accumulation in historic data and slower than expected accumulation in contemporary data indicates that the final prediction of niche space for the eastern quoll is an underestimate. Eastern quolls formerly occupied the south-eastern corner of mainland Australia, and disappeared from the mainland by the 1960s. The species persists in Tasmania, in the far south of its former range (Strahan and Van Dyck 2008). Only 15% (30) of unique localities were collected before 1950, so little sampling effort had occurred in their mainland niche before extirpation. Despite records from over 200 localities, randomly arranged data did not approach an asymptote (black line, Figure 2.6). Clearly a strong temporal sampling bias has acted upon this dataset. The extent of variation between historic and contemporary accumulation curves (red and blue lines respectively, Figure 2.6) also indicates an underestimate of niche volume. The pattern in the chronologically arranged data (red and blue lines, Figure 2.5), where historic data accumulates rapidly, and contemporary data accumulates more slowly, combined with increased sampling in recent years (histogram, Figure 2.5), tells us that niche space is likely to be underestimated.

2.6 Conclusions

For poorly sampled species, it is imperative to seek a more comprehensive historic occurrence dataset. It is likely that SDM's for these species will over predict the relative importance of niche space similar to that from their contemporary distribution and under predict the importance of some historic habitat types. Here my method can be used to identify which species more detailed historical occurrence data needs to be collected, through means such as more thorough synthesis of museum records, focussed collection of paleontological records (Smith 1977) and utilising indigenous knowledge (Burbidge et. al. 1988). If more data cannot be found, alternative modelling approaches such as mechanistic models may be a more useful alternative (Merow et al. 2014a). For translocations, conducting experimental trials designed to maximize information gain might be a useful way to extend the boundaries of the known environmental niche.
For conservation, the implications of incorrectly identifying habitat for a species of conservation concern are significant. The biogeography of species that have declined as a result of human impacts is perhaps the most uncertain (Wallace 2002, Cromsigt et al. 2012, Kuemmerle et al. 2012), yet species distribution models have seen increased application as decision support tools in conservation (Peterson 2006). The credibility of species distribution models depends on robust verification techniques and capacity to account for biases (Jiménez-Valverde et al. 2008), however, these areas are in the most need of development and refinement (Araujo and Guisan 2006). In adopting the method I have developed, managers can help gauge the adequacy of their historic occurrence datasets, helping to alleviate some of the uncertainty in applied SDMs.
Chapter 3

Movement ecology of reintroduced woylies
(Bettongia penicillata) in adjacent feral predator-free fenced areas
3 Movement ecology of reintroduced woylies (*Bettongia penicillata*) in adjacent feral predator-free fenced areas.

3.1 Abstract

Conservation translocations of threatened animal species often occur on islands or within fenced areas where the limited area potentially constrains the population. A more thorough understanding of the variation of movement ecology of translocated species across their former range can quantify expected variation in populations and assist in the design of future translocation attempts. This chapter reports on the movement ecology of the woylie (*Bettongia penicillata*) in two adjacent 4000 ha predator exclusion fences (‘Stages 1 and 2’) within Scotia Wildlife Sanctuary in south-western New South Wales. Woylies were reintroduced to Stage 1 in 2004 and Stage 2 in 2008; and population density is much higher in Stage 2 than Stage 1. For the first time, I describe the movement ecology of woylies (i) within fences, (ii) using high precision GPS technology, and (iii) towards the arid extent of the species’ historic distribution. In total, 20 woylies were collared and tracked during July-December, 2013. Woylies from the lower density population (Stage 1) occupied larger total foraging ranges (average of 97 ha over three nights) than the higher density population (average of 37 ha over three nights). The woylies in the lower density population achieved larger foraging ranges by venturing further from their nests, covering more ground on a given evening, and covering more unique ground between consecutive nights. They did this despite travelling a similar minimum distance each night to their higher density counterparts. The results highlight the degree of variation in movement ecology that can occur among *ex-situ* translocations, despite relatively similar reintroduction conditions. Future translocations could usefully consider this potential variation in *a-priori* assessments of project feasibility.
3.2 Introduction

Invasive predators are a key driver of species declines globally (Clavero Pineda and García-Berthou 2005), most severely impacting predator-naïve species on islands and continents in the southern hemisphere (Mack et al. 2000). Species impacted by invasive predators are frequently translocated for conservation purposes (Soorae 2008, Short 2009). To be successful, invasive predators must be controlled before a reintroduction can be attempted (Chapter 1.3, Blumstein et al. 2002, Short et al. 2002, Carthey and Banks 2012). However, given the vulnerability of many species to invasive predators, eradication is often necessary, which is often only achievable in spatially-constrained areas, such as on islands or within predator exclusion fences (Parkes et al. 2014). Reintroductions within conservation fences have become increasingly popular due to their high security against threats (Hayward and Kerley 2009). Predator exclusion fencing has been used around the world (Hayward and Somers 2012), particularly when predators cannot be completely eradicated from the broader landscape, as is the case in Australia (Chapter 4, (Short 2009, Dickman 2012) and New Zealand (Burns et al. 2012).

In Australia, introduced cats and foxes have had severe negative impacts on native mammal fauna (Chapter. 1.1, Johnson 2006), contributing to the extinction of at least 21 species and being implicated in the decline of a further 58 species listed under the Environment Protection and Biodiversity Conservation Act (1999). As much as 60% of the original mammal richness has been reported to have been lost throughout the Australian interior (McKenzie et al. 2007). The species most impacted favour semi-arid and arid habitats (McKenzie et al. 2007), tend not to climb trees to escape predators (Johnson and Isaac 2009), and are the preferred prey size for cats and foxes (between 35 g and 5.50 kg; Burbidge and McKenzie 1989). That cats and foxes not only prevent the recovery of extirpated species but continue to increase their decline makes the Australian mammal crisis both an urgent and vexing conservation problem (Woinarski et al. 2015). Some surviving species cannot tolerate the presence of foxes or cats at any density (Blumstein et al. 2002, Short et al. 2002, Carthey and Banks 2012), making translocations into predator exclusion fences or islands the only viable option for stabilising or recovering populations.

A-priori assessments of translocation feasibility are designed to help managers achieve a sufficiently large, viable population (Armstrong and Seddon 2008). In spatially constrained populations such as those on islands or within fences, feasibility assessments are particularly important as maximum population size will ultimately be limited by the area enclosed. Here, carrying capacity estimates can be used to estimate maximum potential population size in predictable ecosystem types (Hayward et al. 2007). However, in stochastic ecosystems, predictions of population size and carrying capacity are highly uncertain (McLeod 1997). As a result, estimates of expected population size and viability at potential translocation sites are also uncertain for many threatened species. Ecological information
from established translocated populations might help managers account for some of this uncertainty in future translocation feasibility assessments (Sutherland 1998), yet such data are seldom reported (Seddon et al. 2007, Sheean et al. 2012).

Here, I report on the movement ecology of two translocated populations of the woylie (*Bettongia penicillata*), a small bodied marsupial endemic to Australia. It was once broadly distributed throughout the south and centre of the continent, including semi-arid, woodland and shrubland communities (Strahan and Van Dyck 2008, Yeatman and Groom 2012). Since European settlement the woylie has declined due to predation from invasive cats and foxes (Woinarski et al. 2014), resulting in near total extirpation. By the 1970s only a few populations remained in Western Australian woodland communities. An extensive aerial baiting program targeting foxes resulted in dramatic population recovery (Morrison 2015) and the temporary delisting of the species. However, after reaching over 200,000 individuals the population crashed to less than 20,000 (Groom 2010), resulting in a re-listing as critically endangered (IUCN, EPBC) as a result of a population decline of >90% in less than 10 years (Woinarski et al. 2014). During the species’ brief recovery, at least 47 reintroductions were attempted across its former distribution, making the woylie one of the most frequently translocated species of Australian mammal (Short 2009). Yet surprisingly little information about movement ecology has been reported for the species from those successful translocations. Furthermore, nearly all of what we know about woylie movement ecology comes from the south-western portion of their original distribution (Groom 2010, Yeatman and Wayne 2015).

In this chapter, I aim to improve our understanding of woylie movement ecology so to assist in future translocation attempts through an exploratory study of woylie movement ecology. For the first time, I report on the movement ecology of the woylie (i) within fences, (ii) using high precision GPS technology with GPS fixes over short time intervals, and (iii) towards the arid extreme of the species’ historic distribution. I test for differences in movement ecology of woylies in two adjacent predator exclusion fences in south-western New South Wales, investigating potential differences in movement ecology between sex, across two seasons, and at different population densities.

### 3.3 Methods

#### 3.3.1 Study context: Scotia Sanctuary endangered species recovery project

**Habitat**

Scotia Wildlife Sanctuary in Western NSW is a 64,000 ha reserve, managed by Australian Wildlife Conservancy (AWC). The predominant vegetation types are mallee (*Eucalyptus spp.*) with an
understorey of spinifex grassland (*Triodia spp.*) or woody shrubs on quaternary dune systems, and belah (*Casuarina pauper*) on loamy soils between dunes. The base geology is calcrete with quaternary sand dunes covering much of the site. Climatic conditions are typical of the Australian arid zone, with temperatures ranging from -5 to 50 °C and highly variable rainfall that averages 250 mm per year.

**Community assemblage**

An AWC reintroduction project at Scotia has established populations of a suite of threatened mammal species within 8000 ha of fenced area, including woylie (*B. penicillata*), boodie (*Bettongia lesueur*), bilby (*Macrotis lagotis*), numbat (*Myrmecobius fasciatus*), and bridled nailtail wallaby (*Onychogalea fraenata*). The fence excludes all feral predators (i.e. cats, dogs, and foxes) and all feral herbivores, with the exception of house mouse (*Mus musculus*), whose population periodically erupts within the sanctuary during periods of high rainfall.

**Translocation sites**

The fence is divided into two adjacent 4000 ha areas, referred to as Stage 1 and Stage 2 (hereafter, S1 and S2). The two stages support broadly similar habitats, although there is more *Casuarina pauper* in S2, while more of S1 has been affected by wildfire in recent decades. Both areas support populations of reintroduced woylies, bridled nailtail wallabies, numbats and bilbies while S1 also contains boodies. The S1 mammal community is older than S2 (reintroductions mostly took place in 2004-2005 in S1 and 2008 in S2). At the time of the study, estimated population sizes of bridled nail-tail wallabies and bilbies were similar in S1 and S2, while S1 supported 1200 boodies. The remaining 56 000 hectares of Scotia does not support translocated mammals; this area is managed to reduce numbers of feral species in the surrounding area through regular baiting and the removal of artificial water points.

**Population data**

Woylie populations have been monitored biannually at Scotia by a mark-recapture study using an array of cage traps spread throughout a network of tracks within the fenced areas. At the time of the study, population estimates were approximately 40 in S1 and 400 in S2, or densities of 1/km² and 10/km², respectively.
3.3.2 GPS deployment

Woylies were captured using cage traps with peanut butter and oats as bait. Owing to the large size of the fenced areas at Scotia, trapping for collar deployment was concentrated within 20 hectare trapping grids within a large, contiguous patch of mallee-Triodia habitat (approx 400 ha S1, 100 ha S2) near the S1 – S2 boundary fence to reduce habitat variability. However, animal capture was later expanded to cover all mallee-Triodia habitat in the northern half of S1 (approx 1500 ha), to capture a sufficient number of individuals. Both male and female woylies were collared, but, females with large pouched young or small animals (<800 grams) were excluded due to ethical concerns.

Archival GPS tags (CatTraq GPS modules, Track My Cat Software Ltd) were deployed as a collar fitted on the neck of each woylie. Woylies in Stage 2 were collared during two distinct periods, 31st July and 17th August (winter) 2013, and 30th October and 14th December (Spring) 2013, while S1 woylies were only collared during the Spring period. Following an approach outlined by (Allan et al. 2013), a SirTrack VHF transponder (SirTrack Ltd, NZ) was incorporated into the tag in the second season of trapping to facilitate tag recovery. Collars were recovered through systematic re-trapping, either using the same trap array used for deployment, or by targeted trapping at a daytime nest site of a VHF-tagged animal.

3.3.3 Analysis of GPS data

All home range areas and distances were calculated in an equal area WGS84 UTM projection. Woylies are nocturnally active, sleeping in regularly used daytime nests and foraging during the night. Collars were programmed to switch on an hour before sunset and switch off an hour after sunrise, and to record a GPS location at minimum 8-minute intervals, which was reduced to 5-minute intervals once battery capabilities were determined. However, the number of points per night varied between individuals as GPS units did not always register a fix when scheduled. Nights with >50% of data points missing were omitted along with the nights of collar deployment and recovery. Only animals with at least three consecutive nights of data were used in the analysis. The 'nightly period' was defined as the interval between dusk and dawn, calculated individually for each night (maptools package; Bivand and Lewin-Koh 2013) at the location of the Scotia fenced areas. Only in S2 were enough woylies collared for comparisons of movement ecology between sexes. Within S2, comparisons were made between season and sex. The effect of stage was tested using data collected during the same spring season.

Nightly foraging range estimates
Foraging range estimates were calculated using kernel utilisation distributions (KUD; Worton 1989) as a standard estimate of foraging range size. Brownian Bridge (BB; Horne et al. 2007) models of occupancy area were used as a comparison and to utilise the additional information from the high frequency recording schedule. These were generated using the AdehabitatHR and AdehabitatHS (Calenge 2011) packages in R (R Core Team 2015). Kernel utilisation distributions are a standard, frequently used method for home range estimation, which estimates occupancy based on the density of records. BB models form a chronological path of concurrent locations and estimate a utilisation density based on the likely path or "bridge" which the animal traversed between fixes. Kernel areas estimate the minimum area that a given proportion of records fall within. 50% and 95% kernel areas were extracted for both KUD and BB models.

Nightly foraging range overlap
The percentage overlap with the foraging range of the previous night was compared for BB95% kernels between consecutive nights.

Minimum nightly distance travelled
An estimate of the minimum nightly distance travelled was calculated from all movements summed across the duration of the night, omitting movements < 10 m (the approximate accuracy of the GPS units).

Average distance from nest
Distance from the nest was calculated by measuring the distance of each GPS fix obtained between dusk and dawn, from the first GPS fix taken approximately 1 hour before dusk (the assumed nest site location). These values were averaged across all fixes made that night to obtain a mean distance from the nest location for a given night.

Three night foraging range estimate
As the number of evenings with data differed between individuals, a 3-night foraging range estimate was calculated using KUDs to standardise the measure. For animals with greater than three nights of data, this value was calculated from the average of each consecutive three night span.

3.3.4 Statistical analysis
I tested for differences among the categories of stage, sex and season for each of the above variables, assuming a null hypothesis of no difference between categories. Low sample size precluded the use of a single multivariate model including each response variable. Instead, separate models were used to test whether variance occurred between treatments. I constructed a general linear mixed model (GLMM) assuming a Gaussian distribution, and the 3-night foraging range comparisons were made
using Linear Models (LM). Nightly comparisons were made using Linear Mixed Effect Models (GLMM) with a random ID term for individual animals using the lme4 (Bates et al. 2014) and multcomp (Bretz et al. 2008) packages in R. Significance was tested using Tukey posthoc analysis with a Bonferroni correction factor. All comparisons made between S1 and S2 were made using data collected in the same spring season only.

3.3.5 Animal ethics clearance
Research was carried out as part of the Scotia Sanctuary endangered species recovery project in accordance with animal ethics clearance number S11152 from the New South Wales Parks and Wildlife Service. This clearance was recognised and approved by the University of Queensland animal ethics committee.

3.4 Results
In total, data for 134 nights (41 in S1 and 93 in S2) were collected between July and December 2013 (Table 1). GPS data were collected from five woylies in S1 (three males, two female) and 15 in S2 (six male, nine female). Fewer woylies were collared in S1 than desired because the much lower density and population size limited the number of individuals able to be captured. Foraging ranges for each individual are summarised in Table 2.
Table 3.1
Details of woylies tracked in S1 and S2.

<table>
<thead>
<tr>
<th>ID</th>
<th>Sex</th>
<th>Season</th>
<th>Stage</th>
<th>Date</th>
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<td>1</td>
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<tr>
<td>B02</td>
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<td>s</td>
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<tr>
<td>B03</td>
<td>m</td>
<td>s</td>
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<td>18/11/2013</td>
<td>5</td>
</tr>
<tr>
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<td>f</td>
<td>s</td>
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<td>17/11/2013</td>
<td>12</td>
</tr>
<tr>
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<td>m</td>
<td>s</td>
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<td>19/11/2013</td>
<td>11</td>
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<tr>
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<td>s</td>
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<td>18/11/2013</td>
<td>9</td>
</tr>
<tr>
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<td>f</td>
<td>s</td>
<td>2</td>
<td>19/11/2013</td>
<td>8</td>
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<td>s</td>
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<td>2/08/2013</td>
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<td>C05</td>
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<td>2/08/2013</td>
<td>3</td>
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<td>12/08/2013</td>
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<td>f</td>
<td>w</td>
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<td>1/08/2013</td>
<td>4</td>
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<td>31/07/2013</td>
<td>5</td>
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<td>29/10/2013</td>
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<tr>
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<td>28/11/2013</td>
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</table>
Table 3.2
A summary of foraging range estimates for each individual woylie in S1 and S2, including average three night KUD’s, nightly KUD’s and nightly BB’s with values given ± 1 SE.

<table>
<thead>
<tr>
<th>ID</th>
<th>3 night KUD50</th>
<th>3night KUD95</th>
<th>KUD50</th>
<th>KUD95</th>
<th>BB50</th>
<th>BB95</th>
</tr>
</thead>
<tbody>
<tr>
<td>B01</td>
<td>6.09 ± 1.26</td>
<td>63.42 ± 13.37</td>
<td>12.31 ± 4.05</td>
<td>49.7 ± 13.73</td>
<td>5.22 ± 1.24</td>
<td>29.36 ± 5.15</td>
</tr>
<tr>
<td>B02</td>
<td>11.29 ± 2</td>
<td>77.85 ± 16.56</td>
<td>17.59 ± 8.52</td>
<td>86.85 ± 44.46</td>
<td>7.96 ± 0.89</td>
<td>51.75 ± 18.17</td>
</tr>
<tr>
<td>B03</td>
<td>14.69 ± 0.37</td>
<td>71.98 ± 1.29</td>
<td>11.8 ± 4.12</td>
<td>48.64 ± 13.98</td>
<td>9.95 ± 1.99</td>
<td>66.08 ± 15.36</td>
</tr>
<tr>
<td>B04</td>
<td>39.16 ± 3.47</td>
<td>168.04 ± 8.11</td>
<td>19.86 ± 5.21</td>
<td>73.57 ± 18.4</td>
<td>7.96 ± 1.12</td>
<td>42.63 ± 5.8</td>
</tr>
<tr>
<td>B05</td>
<td>15.87 ± 0.63</td>
<td>101.25 ± 4.7</td>
<td>21.26 ± 6.34</td>
<td>96.01 ± 28.18</td>
<td>8.87 ± 1.18</td>
<td>66.41 ± 10.75</td>
</tr>
<tr>
<td>C01</td>
<td>5.52 ± 0.32</td>
<td>21.91 ± 0.67</td>
<td>4.08 ± 0.41</td>
<td>16.6 ± 1.27</td>
<td>3.98 ± 0.57</td>
<td>18.36 ± 1.14</td>
</tr>
<tr>
<td>C02</td>
<td>1.81 ± 0.16</td>
<td>10.11 ± 0.17</td>
<td>2.01 ± 0.42</td>
<td>9.03 ± 1.29</td>
<td>4.23 ± 0.59</td>
<td>39.56 ± 6.83</td>
</tr>
<tr>
<td>C03</td>
<td>35.99 ± 1.81</td>
<td>136.73 ± 4.03</td>
<td>22.23 ± 6.6</td>
<td>81.15 ± 22.8</td>
<td>8.25 ± 0.8</td>
<td>46.63 ± 5.69</td>
</tr>
<tr>
<td>C04</td>
<td>4.53 ± NA</td>
<td>18.99 ± NA</td>
<td>4.94 ± 1.31</td>
<td>19.57 ± 4.34</td>
<td>7.96 ± 0</td>
<td>41.8 ± 3.45</td>
</tr>
<tr>
<td>C05</td>
<td>6.13 ± NA</td>
<td>24.85 ± NA</td>
<td>6.89 ± 0.78</td>
<td>29.06 ± 5.58</td>
<td>8.62 ± 2.65</td>
<td>52.41 ± 9.64</td>
</tr>
<tr>
<td>C06</td>
<td>1.61 ± 0.06</td>
<td>17.63 ± 1.88</td>
<td>4.01 ± 1.46</td>
<td>22.42 ± 5.66</td>
<td>8.46 ± 0.95</td>
<td>46.28 ± 8.02</td>
</tr>
<tr>
<td>C07</td>
<td>7.79 ± 0.76</td>
<td>46.76 ± 2.13</td>
<td>9.82 ± 1.66</td>
<td>54.61 ± 7.79</td>
<td>9.62 ± 1.08</td>
<td>72.32 ± 7.55</td>
</tr>
<tr>
<td>C08</td>
<td>6.68 ± 0.08</td>
<td>33.58 ± 0.57</td>
<td>6.21 ± 1.89</td>
<td>27.83 ± 6.28</td>
<td>7.46 ± 1.7</td>
<td>65.68 ± 33.2</td>
</tr>
<tr>
<td>C09</td>
<td>4.29 ± 0.37</td>
<td>16.29 ± 1.38</td>
<td>4.53 ± 0.7</td>
<td>16.98 ± 2.57</td>
<td>6.37 ± 1.16</td>
<td>49.36 ± 10.48</td>
</tr>
<tr>
<td>C10</td>
<td>3.16 ± 0.12</td>
<td>12.75 ± 0.2</td>
<td>3.45 ± 0.46</td>
<td>13.14 ± 1.4</td>
<td>3.13 ± 0.59</td>
<td>17.34 ± 2.29</td>
</tr>
<tr>
<td>C11</td>
<td>8.11 ± 0.26</td>
<td>33.27 ± 0.52</td>
<td>6.34 ± 0.97</td>
<td>29.62 ± 4.03</td>
<td>7.17 ± 0.49</td>
<td>37.42 ± 1.82</td>
</tr>
<tr>
<td>C12</td>
<td>3.32 ± 0.14</td>
<td>13.15 ± 0.12</td>
<td>3.02 ± 0.46</td>
<td>11.89 ± 1.34</td>
<td>2.65 ± 0.66</td>
<td>14.6 ± 1.22</td>
</tr>
<tr>
<td>C13</td>
<td>6.67 ± 0.51</td>
<td>26.81 ± 1.05</td>
<td>8.43 ± 2.05</td>
<td>32.91 ± 8.04</td>
<td>10.45 ± 2.05</td>
<td>65.18 ± 20.34</td>
</tr>
<tr>
<td>C14</td>
<td>4.84 ± 0.02</td>
<td>20.17 ± 0.32</td>
<td>4.29 ± 0.35</td>
<td>16.57 ± 1.29</td>
<td>4.35 ± 0.33</td>
<td>19.78 ± 0.95</td>
</tr>
<tr>
<td>C15</td>
<td>8.98 ± 0.25</td>
<td>42.78 ± 0.51</td>
<td>8.5 ± 2.12</td>
<td>33.32 ± 6.96</td>
<td>4.64 ± 0.84</td>
<td>23.88 ± 4.08</td>
</tr>
</tbody>
</table>
3.4.1  Sex and season comparisons of Stage 2 woylie movement ecology

Differences in movement ecology in S2 woylies were investigated for sex (Table 3) and season (Table 4). Distance travelled per night did not vary between sexes (GLMM, $Z = 0.505$, $p = 0.613$) or between seasons (GLMM, $Z = 0.029$, $p = 0.977$). Similarly, three night range sizes did not vary between the sexes (LM, KUD50% $F_{1,13} = 1.22$, $p = 0.290$, KUD95% $F_{1,13} = 1.70$, $p = 0.215$) or seasons (LM, KUD50% $F_{1,13} = 0.60$, $p = 0.451$, KUD95% $F_{1,13} = 0.336$, $p = 0.572$). No difference in nightly overlap was found for sex (GLMM, $Z = 0.946$, $p = 0.344$), but nightly overlap was greater in winter than in spring (GLMM, $Z = 2.534$, $p = 0.011$).

No difference in nightly BB home ranges was found between males and females (GLMM, BB50%, $Z = 1.569$, $p = 0.399$, KUD95%, $Z = 0.843$, $p = 0.117$), however, a large seasonal difference occurred, with winter nightly ranges being approximately double the size of spring nightly ranges (GLMM, BB50% $Z = 4.56$, $p < 0.001$, BB95%, $Z = 4.345$, $p < 0.001$), but only for BB models, with nightly and three nightly remaining consistent between seasons (Table 4).

Table 3.3

Table 3.3

Movement metrics of male and female S2 woylies, with values given ± 1 SE, along with results of statistical tests for a difference between males and females. See methods for details of statistical tests.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Male (6)</th>
<th>Female (9)</th>
<th>Statistical Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance</td>
<td>3326 ± 287</td>
<td>3557 ± 457</td>
<td>$Z = 0.505$, $p = 0.613$</td>
</tr>
<tr>
<td>Overlap</td>
<td>67.7 ± 6.7</td>
<td>61.4 ± 4.2</td>
<td>$Z = 0.946$, $p = 0.344$</td>
</tr>
<tr>
<td>Distance away</td>
<td>179.6 ± 48.6</td>
<td>218.4 ± 30.5</td>
<td>$Z = 0.798$, $p = 0.425$</td>
</tr>
<tr>
<td>BB50</td>
<td>2.3 ± 0.6</td>
<td>3.9 ± 1.0</td>
<td>$Z = 1.569$, $p = 0.399$</td>
</tr>
<tr>
<td>BB95</td>
<td>18.9 ± 7.3</td>
<td>24.1 ± 5.1</td>
<td>$Z = 0.843$, $p = 0.117$</td>
</tr>
<tr>
<td>KUD50</td>
<td>7.5 ± 2.4</td>
<td>5.3 ± 1.5</td>
<td>$Z = 1.368$, $p = 0.171$</td>
</tr>
<tr>
<td>KUD95</td>
<td>36.1 ± 8.7</td>
<td>21.8 ± 5.8</td>
<td>$Z = 1.633$, $p = 0.102$</td>
</tr>
<tr>
<td>3 night</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>KUD50</td>
<td>10.2 ± 4.3</td>
<td>5.4 ± 2.7</td>
<td>$F_{1,13} = 1.22$, $p = 0.290$</td>
</tr>
<tr>
<td>3 night</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>KUD95</td>
<td>44.2 ± 14</td>
<td>23.4 ± 10</td>
<td>$F_{1,13} = 1.70$, $p = 0.215$</td>
</tr>
</tbody>
</table>
Table 3.4

Movement metrics of winter and spring S2 woylies, with values given ± 1 SE, along with results of statistical tests for a seasonal difference. Values in bold font identify statistical significance of 0.05. See methods for details of statistical tests.

<table>
<thead>
<tr>
<th>Season</th>
<th>Winter (8)</th>
<th>Spring (7)</th>
<th>Statistical Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance</td>
<td>3410 ± 318</td>
<td>3423 ± 454</td>
<td>Z = 0.029, p = 0.977</td>
</tr>
<tr>
<td>Overlap</td>
<td>70.7 ± 5.5</td>
<td>56.7 ± 3.9</td>
<td>Z = 2.534, p = 0.011</td>
</tr>
<tr>
<td>Distance away</td>
<td>218.8 ± 48.3</td>
<td>248.6 ± 34.2</td>
<td>Z = -0.618, p = 0.537</td>
</tr>
<tr>
<td>BB50</td>
<td>8.3 ± 0.6</td>
<td>3.8 ± 0.8</td>
<td>Z = 4.56, p &lt; 0.001</td>
</tr>
<tr>
<td>BB95</td>
<td>54.2 ± 6.6</td>
<td>25.6 ± 4.5</td>
<td>Z = 4.345, p &lt; 0.001</td>
</tr>
<tr>
<td>KUD50</td>
<td>6.4 ± 1.9</td>
<td>6.7 ± 2.7</td>
<td>Z = -0.114, p = 0.909</td>
</tr>
<tr>
<td>KUD95</td>
<td>22.2 ± 10.4</td>
<td>25.8 ± 7.4</td>
<td>Z = 0.346, p = 0.729</td>
</tr>
<tr>
<td>3 night KUD50</td>
<td>5.7 ± 4.3</td>
<td>9.1 ± 3.1</td>
<td>F_{1,13} = 0.60, p = 0.451</td>
</tr>
<tr>
<td>3 night KUD95</td>
<td>27.3 ± 16.4</td>
<td>36.8 ± 12</td>
<td>F_{1,13} = 0.34, p = 0.572</td>
</tr>
</tbody>
</table>

Comparisons between Stage 1 and Stage 2 woylies

Differences in movement behaviour were investigated between spring season S1 and S2 woylies (Table 5). Total distance travelled per night did not differ between S1 and S2 woylies (GLMM, Z = -0.076, p = 0.939), however S1 woylies spent more time further away from their daytime nest (GLMM, Z = -2.7, p = 0.007). Nightly overlap was greater in S2 than S1 animals (GLMM, Z = -2.84, p = 0.005). Three night foraging ranges of S1 woylies were two to three times larger than those of S2 woylies based on 50% and 95% occupancy kernels respectively, however, only for 95% occupancy kernels was this difference significant (LM, KUD50 F_{1,10} = 1.33, p = 0.276, KUD95 F_{1,10} = 5.32, p = 0.044). Nightly BB estimates for S1 woylies were twice the size of S2 animals(GLMM, BB50% Z = -3.436, p < 0.001, BB95% Z = -3.104, p = 0.002). Overall, larger foraging ranges were attained by venturing further from their nests, covering more unique ground between consecutive nights and covering more ground on a given evening (Figure 1). Individuals’ nightly BB kernels are given in Supplementary Table 1.
Table 3.5
Movement metrics of S1 and S2 woylies in spring, with values given ± 1 SE, along with results of statistical tests for a difference between stages. Values in bold font identify statistical significance of 0.05. See methods for details of statistical tests.

<table>
<thead>
<tr>
<th>Stage</th>
<th>S1 (5)</th>
<th>S2 (7)</th>
<th>Statistical Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance</td>
<td>3466 ± 398</td>
<td>3426 ± 520</td>
<td>Z = -0.076, p = 0.939</td>
</tr>
<tr>
<td>Overlap</td>
<td>37.4 ± 5.2</td>
<td>56.8 ± 6.8</td>
<td>Z = -2.7, p = 0.007</td>
</tr>
<tr>
<td>Distance away</td>
<td>442.5 ± 55.6</td>
<td>246.2 ± 72.7</td>
<td>Z = -2.84, p = 0.005</td>
</tr>
<tr>
<td>BB50</td>
<td>7.9 ± 0.8</td>
<td>4.4 ± 1.0</td>
<td>Z = -3.436, p &lt; 0.001</td>
</tr>
<tr>
<td>BB95</td>
<td>50.9 ± 6.2</td>
<td>25.7 ± 8.1</td>
<td>Z = -3.104, p = 0.002</td>
</tr>
<tr>
<td>KUD50</td>
<td>17 ± 2.7</td>
<td>6.6 ± 3.5</td>
<td>Z = -3.003, p = 0.003</td>
</tr>
<tr>
<td>KUD95</td>
<td>72.4 ± 10.4</td>
<td>25.1 ± 13.5</td>
<td>Z = -3.5, p &lt; 0.001</td>
</tr>
<tr>
<td>3 night KUD50</td>
<td>17.4 ± 5.5</td>
<td>9.1 ± 7.2</td>
<td>F_{1,10} = 1.33, p = 0.276</td>
</tr>
<tr>
<td>3 night KUD95</td>
<td>96.5 ± 19.8</td>
<td>36.8 ± 25.89</td>
<td>F_{1,10} = 5.32, p = 0.044</td>
</tr>
</tbody>
</table>

Figure 3.1
Nightly foraging ranges of an individual woylie in S1 and an individual woylie in S2. The figure depicts the BB50% kernels from 9 consecutive nights of a S1 woylie B01 (left, red kernels) and 8 consecutive nights of S2 woylie C01 (right, blue kernels). The many, small, non-overlapping kernels seen for B01 is typical of S1 woylies, while the kernels with high spatial overlap seen for C01 is typical of S2 woylies. Occupancy kernels for all woylies included in the study can be seen in Supplementary 1.
3.5 Discussion

Tagged woylies in the lower population density S1 occupied larger foraging ranges, travelled more broadly and spent more time further away from daytime nests than conspecifics in the higher density S2 population. Individuals in S2 performed more spatially confined movements and often remained in close proximity to their daytime nest. Furthermore, these animals demonstrated higher fidelity to nightly foraging patches.

Telemetry studies of free ranging woylies in the south-western woodlands of Western Australia reported a general tendency for home range areas to be greater at lower densities (Sampson 1971, Groom 2010, Yeatman and Wayne 2015). While these studies used lower frequency, longer duration sampling than that used here, our results conform to this pattern, with the 3-night foraging ranges in S2 being comparable to those reported in Western Australia at a similar population density (Groom 2010). Sampson (1971) reported home ranges of approx 29 ha in the Tutanning population with densities of 10/km², compared with 27-36 ha 3 day foraging ranges at similar densities in the present study (Table 4). However, the density in S2 was relatively low compared to most reported Western Australian populations, and in S1 density was lower still. Here I observed the largest ranges ever reported for woylies of 96 ha over three nights, larger again than Yeatman’s (2015) study reporting 65 ha home ranges from a long term VHF study, suggesting that the tendency for increased home range size with decreased population density continues at very low densities. This study describes the mechanisms by which woylies vary their range size. Woylies at lower densities occupy larger ranges by fanning out over a greater area, spending more time further away from their daytime nest, and covering more unique ground on consecutive evenings.

3.5.1 Interpretation of density related differences in foraging range

Despite apparently similar environmental conditions in the two adjacent fenced areas, S1 woylies showed remarkably larger foraging ranges than S2 animals. Based on my observations and those of other studies (Sampson 1971, Groom 2010, Yeatman and Wayne 2015), it is most likely that population density is interrelated with the described variation in range. Two forces acting from opposite directions determine an individual home range size. By occupying a larger home range, an animal on average will encounter a larger variety and abundance of resources (Pyke et al. 1977). A larger home range is therefore desirable, particularly when resources are limited, yet there are also costs to a larger home range, including increased exposure to predators (Milinski and Heller 1978), increased competition with conspecifics (Ostfeld 1990), and greater exposure to threats (Woodroffe and Ginsberg 1998).

With predation assumedly consistent, from only native, avian predators within the predator controlled areas at Scotia, and population density likely a key driver of range size in woylies, there are two plausible, related factors that could be driving the variation in foraging range between the S1 and S2 woylies. Firstly, resources may be more abundant in S2, reducing the need to occupy larger extents. Second, with a smaller woylie population in S1, density related intraspecific competition might be relaxed, allowing for larger foraging ranges.
The larger foraging ranges of S1 animals could indicate resource limitation, in which S1 individuals must cover a larger area than S2 animals to satisfy their energy intake requirements. This could be driven by either subtle differences in resource availability between the two stages, or increased interspecific competition caused by the different mammal community assemblages. Woylies in S1 have been demonstrated to exhibit no detectable difference in habitat preference (Pizzuto et al. 2007). Conversely, Yeatman (2015) described preferential habitat use in a Western Australian population that occurs in an area of significantly higher rainfall than the Scotia site (800 mm/year cf. 250 mm/year). The S1 population co-occurs with a large number of the closely related boodie, which is absent from S2. While dietary studies have been conducted on woylies in much higher productivity Western Australian woodland (Garkaklis et al. 2004, Murphy et al. 2005, Yeatman and Groom 2012), none has so far been conducted at Scotia. The near absence of food resources such as truffles (pers. obs. Jeremy Ringma) commonly eaten by woylies elsewhere may mean the woylies are forced to have considerable dietary overlap with the boodies at the Scotia site. Intraspecific competition is therefore a plausible cause of differences in resource availability between S1 and S2.

The second possibility is that the differences in S1 and S2 populations are driven by stochastic processes, where the differences in woylie population fall within the expected range of population outcomes. With no causative mechanism for the observed differences, in relaxed density related interspecific competition between woylies might ultimately permits larger foraging ranges. Scotia occurs in a highly environmentally stochastic system, typical for the Australian arid zone. Australian arid and semi-arid mammal populations are strongly affected by stochastic rainfall (Dickman et al. 1999). The S1 reintroduction was undertaken 3-4 years earlier than the S2 translocation, during a different phase of the El Niño southern oscillation cycle.

Prior to recent declines, woylies in more mesic habitats in Western Australia occurred at densities of 20-160/ km² (Wayne et al. 2013). In comparison, woylies at Scotia occur at relatively low densities (1-10/ km²), and occupy relatively large home ranges, perhaps suggesting a more challenging environment. Indeed, Scotia is the most arid region where woylie translocated have occurred, the analysis from Chapter 2 suggests the woylie’s environmental niche is well documented and that Scotia is likely to be the arid extent of their climatic niche (Start et al. 1995), where resources are less abundant than Western Australian woodlands. Hence, S2 woylie foraging effort may already be close to the maximum for the species, if resources were further limited in S1, an increased home range may be necessary to compensate for reduced food availability in the area. However, larger home ranges alone cannot be reliably used as an indicator of resource limitation. It is to be expected that animals will occupy a larger home range at lower density (Groom 2010, Yeatman and Wayne 2015), and there may be little cost for S1 woylies to occupy larger ranges. If resources are limited, one might expect animals to travel a greater distance each night in search of food, but I found that S1 and S2 woylies covered on average a remarkably similar overall distance each night (Table 5).

This raises the possibility that reduced interspecific competition among the low density S1 animals is responsible for their larger home ranges. Differences between community level ecology and innate,
stochastic variability are unlikely to be resolved from a single movement study as conducted here. Ultimately, teasing apart the mechanisms that drive the differences in ecology between the two populations will rely on experimentally manipulating the populations or replicating studies across many more sites. Focused studies will be required in translocated woylie populations with different home range size and population density in regions of different environmental conditions.

3.6 Conclusions
Translocations have become a pivotal conservation tool for Australian predator affected mammals. In this chapter, I aimed to improve our understanding of woylie movement ecology in previously unstudied habitat to assist in future translocation attempts. Using GPS technology at fine resolution sampling intervals revealed that woylies vary the size of their overall foraging range not just by increasing their nightly foraging range, but by covering more unique ground between evenings, and spending more time further away from their nests.

The marked difference in home range size of translocated woylies within these two adjacent fences highlights the uncertainty associated with using observed density information to inform translocation efforts, particularly in environments where habitat suitability and population responses are poorly understood. Targeted translocations aimed at providing new information about species ecology may be required, and in such cases, fences that are adequately large, such as Scotia, may help to improve translocation outcomes, while exploring new boundaries for translocation science.
Chapter 4

Where to put the next conservation fence? Minimizing species extinctions through strategic planning for conservation fencing projects.
4 Where to put the next conservation fence? Minimizing species extinctions through strategic planning for conservation fencing projects.

4.1 Abstract
Conservation fences are an increasingly common management action for mammal species threatened by invasive predators. However, unlike many conservation actions, fence networks are expanding in an unsystematic manner, generally as a reaction to local funding opportunities or threats. In a gap analysis of Australia’s substantial fence network, I found highly uneven protection, with 67% of predator-sensitive species remaining unrepresented. I developed a systematic method that uses viability analysis to minimise expected species’ extinctions, and apply the approach to New South Wales, Australia, where the state government intends to expand the existing conservation fence network. My results show that prioritisation yields substantial efficiencies, reducing the expected number of species extinctions as much as 17 times more effectively than an ad hoc approach. This dramatically superior outcome emphasises the importance of informing future choices using systematic methods rather than opportunistic decisions.

4.2 Introduction
Conservation fencing is a rapidly expanding management action (Hayward and Somers 2012), primarily used to exclude invasive species (Bennett et. al. 2009, Malpas et. al. 2013), game management (Luxmore 1985), and abate human wildlife conflict (Tolhurst et. al. 2008). Fencing creates a physical barrier between conservation assets and threatening agents, providing a higher level of protection than alternative management actions. In many countries, fencing projects are arising rapidly and independently of each other. By considering fences built for similar purposes as a network, rather than individually, systemic conservation planning methods (Margules and Pressey 2000) such as those used for protected area planning could be used to improve the effectiveness of conservation fencing. However, unlike protected areas, fences need to be sited and constructed, the animals often translocated into the area, and populations actively maintained. Bespoke methods are therefore required to identify and prioritise new fencing projects.

Conservation fences are frequently used in Australia (Dickman 2012) and New Zealand (Burns et al. 2012) to exclude invasive predators. Invasive predators are a leading driver of global biodiversity decline and loss (Mack et al. 2000, Clavero and García-Berthou 2005), particularly in ecosystems where prey species are evolutionarily naïve. Introduced predators have been implicated in 60% of mammal extinctions (46 species) and 55% of bird extinctions worldwide (77 species; IUCN 2015), particularly in southern hemisphere ecosystems. Populations of invasive predators are frequently targeted for eradication, but this becomes
infeasible over large areas (Clout and Veitch 2002, Rejmánek and Pitcairn 2002). Australia, New Zealand, and the Pacific nations are increasingly turning to conservation fences to exclude introduced mammalian predators where eradication is impossible, and when prey species cannot tolerate introduced predators at any density.

Compared to ongoing predator control, a fence can be built and maintained in a cost-effective manner comparable to island translocations (Bode et al. 2012, Norbury et al. 2014, Short 2009), allowing conservation organisations to reintroduce species with a higher rate of success. Fences are consequently popular across the conservation sector (Hayward and Kerley 2009), even for small, local organisations. These factors create a highly decentralised fence network, with the majority (58%) of Australian fences being operated by nongovernmental organisations or local councils. The same decentralisation occurs in New Zealand, where 78% of fences are nongovernmental initiatives (Saunders & Norton 2001; Burns et al. 2012). This situation is unusual for conservation in these two countries, whose political systems and history of land tenure has seen the majority of protected area designations undertaken by state or federal governments (Saunders and Norton 2001, Burns et al. 2012).

Economic theory suggests that sectors made up of diverse, independent organisations will be better able to adapt to local environmental and socio-political conditions; to access diverse funding sources and local volunteers; to lower operating and transaction costs; and to experiment and innovate (Bilodeau and Slivinski 1997, Albers and Ando 2003, Armsworth et al. 2012). A network of independently operated fences is therefore a positive reflection of a diverse conservation community. However, decentralisation comes at a cost. Unsystematic and uncoordinated actions in conservation have previously resulted in costly inefficiencies (Pressey et al. 1993), incomplete protection (Margules and Pressey 2000) and enormous legacy costs (Stewart et al. 2007, Fuller et al. 2010). Such inefficiencies are therefore likely to be a feature of existing fence networks. Moreover, compared to reserve systems, the decentralised organisation and funding structure of fence networks mean that any inefficiencies will be difficult to correct using top-down control. Nevertheless, coordination could substantially increase the performance of fence networks.

There are two essential pieces of information required for this coordination to occur, and in this paper I construct a method for providing them. Drawing on theories of population viability and systematic conservation planning, I design a systematic method that evaluates the current performance of a network of fences, and quantifies the relative benefits of alternative future fence projects. To illustrate the approach, I consider Australia’s network of predator exclusion fences built for the conservation of threatened mammals. Australia is a global epicentre of mammal extinctions (Woinarski et al. 2015), driven primarily by invasive foxes (*Vulpes vulpes*) and cats (*Felis catus*; (Abbott 2011, Woinarski et al. 2011). Currently 58 mammal species are recognised in the Environment Protection and Biodiversity Conservation Act 1999 (EPBC) as threatened by invasive predators, many of which might benefit from predator exclusion fences (Chapter 1.1, Woinarski et al. 2014).
First, I review the state and performance of Australia’s existing network of predator exclusion fences and assess whether the network exhibits the inefficiencies expected from such a decentralised structure. Second, I outline and explain a flexible systematic framework for optimally expanding existing fence networks, and apply it to a New South Wales (NSW) case study, where the state government is currently planning two new fence projects. As with systematic conservation planning, the method seeks to construct an efficient and complementary network of fences. However, because fenced populations are small and constrained, methods must explicitly calculate and minimise species extinction probability. This focus on viability is therefore an essential element of fence network planning.

4.3 Methods

4.3.1 Goals and objective function
Systematic planning for conservation fencing differs from standard reserve system design in two important ways. First, locally extirpated species are almost always translocated into the fence (Dickman 2012). As a result, the locations of new projects must be based on the suitability of a site for key species, rather than areas of current occupancy. Second, since fenced populations are often small and spatially constrained, one cannot assume that representation guarantees persistence, and instead fence networks must focus explicitly on population viability. I therefore chose fences with the goal of minimising expected extinctions across a suite of species. All subsequent analyses are assessed against this objective. I focused specifically on the 58 Australian mammal species listed as threatened by invasive predators under EPBC and IUCN red list criteria, 22 of which have suitable habitat in NSW (Table 4.1).
Table 4.1
List of species used in the NSW case study. Species that were chosen had to satisfy three criteria. They must (i) occur or have formerly occurred in the state of NSW, (ii) be listed under either EPBC or IUCN criteria, and (iii) be recognised as threatened by introduced predators.

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
<th>EPBC listing</th>
<th>IUCN listing</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bettongia gaimardi</em></td>
<td>Eastern bettong</td>
<td>Vulnerable</td>
<td>Near Threatened</td>
</tr>
<tr>
<td><em>Bettongia lesueur</em></td>
<td>Burrowing bettong (boodie)</td>
<td>Vulnerable</td>
<td>Near Threatened</td>
</tr>
<tr>
<td><em>Bettongia penicillata</em></td>
<td>Brush-tailed bettong (woylie)</td>
<td>Endangered</td>
<td>Critically</td>
</tr>
<tr>
<td><em>Burramys parvus</em></td>
<td>Mountain pygmy-possum</td>
<td>Endangered</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Dasyurus geoffroii</em></td>
<td>Western quoll</td>
<td>Vulnerable</td>
<td>Near Threatened</td>
</tr>
<tr>
<td><em>Dasyurus maculatus</em></td>
<td>Spotted-tailed quoll</td>
<td>Endangered</td>
<td>Least</td>
</tr>
<tr>
<td><em>Dasyurus viverrinus</em></td>
<td>Eastern quoll</td>
<td>Least Concern</td>
<td>Near Threatened</td>
</tr>
<tr>
<td><em>Isoodon auratus</em></td>
<td>Golden bandicoot</td>
<td>Vulnerable</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Isoodon obesulus</em></td>
<td>Southern brown bandicoot</td>
<td>Endangered</td>
<td>Least Concern</td>
</tr>
<tr>
<td><em>Lasiorhinus krefftii</em></td>
<td>Northern hairy-nosed wombat</td>
<td>Endangered</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Leporillus conditor</em></td>
<td>Greater stick-nest rat</td>
<td>Vulnerable</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Macrotis lagotis</em></td>
<td>Greater bilby</td>
<td>Vulnerable</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Myrmecobius fasciatus</em></td>
<td>Numbat</td>
<td>Vulnerable</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Onychogalea fraenata</em></td>
<td>Bridled nail-tailed wallaby</td>
<td>Endangered</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Perameles bougainville</em></td>
<td>Western barred bandicoot</td>
<td>Endangered</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Petrogale penicillata</em></td>
<td>Brush-tailed rock-wallaby</td>
<td>Vulnerable</td>
<td>Near Threatened</td>
</tr>
<tr>
<td><em>Petrogale xanthopus</em></td>
<td>Yellow-footed rock-wallaby</td>
<td>Vulnerable</td>
<td>Near Threatened</td>
</tr>
<tr>
<td><em>Potorous longipes</em></td>
<td>Long-footed potoroo</td>
<td>Endangered</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Potorous tridactylus</em></td>
<td>Long-nosed potoroo</td>
<td>Vulnerable</td>
<td>Least Concern</td>
</tr>
<tr>
<td><em>Pseudomys fumeus</em></td>
<td>Smokey mouse</td>
<td>Endangered</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Pseudomys novaehollandiae</em></td>
<td>New Holland mouse</td>
<td>Vulnerable</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Pseudomys oralis</em></td>
<td>Hastings river mouse</td>
<td>Endangered</td>
<td>Vulnerable</td>
</tr>
</tbody>
</table>

Based on standard population ecology models (Lande 1993), I adopted a benefit function that predicts the probability of each species becoming globally extinct within the next 20 years, based on the number and size of the species’ constituent populations (fenced and wild), the probability of catastrophic events (e.g., fires, floods), demographic stochasticity, and species’ per-capita growth rates. The function predicts the benefit of a potential fencing project ($X_f^e$), based the reduction in probability of extinction $p_e$, provided by a new translocated population in relation to its existing population structure $N_s$, catastrophic risk and demographic tendencies. The expected return on a new population was scaled by the modelled habitat suitability $K_s^f$, with an expected translocation success rate $q_s$. Each new population reduces extinction risk of the species, but
marginal returns of subsequent populations diminish. Hence, creating a new population for a highly populous species with many discrete populations provides less benefit than a species with few, small populations.

\[
\langle X_f \rangle = \sum_{s=1}^{S} q_s \cdot P_e(N_{s}, K_s^f, T) + \sum_{s=1}^{S} (1 - q_s) \cdot P_e(N_{s}, T)
\]

(Eq. 1)

This benefit function was used to assess the performance of the current fence network and to systematically assess potential additional fences (see Appendix 4 for a full mathematical description and explanation of the function).

4.3.2 Current Australian fence network

Australian conservation fence efforts have been previously summarized, but rapid expansion has made these assessments out of date. Starting with a baseline literature specifically Short (2009), Dickman (2012) and Woinarski et al. (2014) we reviewed the formal scientific literature using Google Scholar and Web of Science searching both the scientific and common names of all listed predator threatened Australian mammals known to have occurred in NSW (Table 4.1). For small nongovernmental fencing organizations, much of the relevant information occurs outside the peer-reviewed literature, and we therefore used internet search engines to search for the scientific name, common name and fence location terms. For each fence location, online search and direct contact were used to determine which species had been translocated into each fence, the outcome of the translocation, and a current population estimate for the species contained provided by fence managers.

I constructed frequency histograms summarising fenced protection for all Australian mammals. Then, I used my benefit function to compare extinction risk of each species to the number of known translocation attempts. If the current fencing network were designed to minimise extinctions, I would expect a positive relationship between extinction probability and attempted fence translocations, since an efficient network would prioritise species whose wild populations are at greater risk of extinction. Finally, I contrast IUCN status with number of translocation attempts, expecting that species with higher threat status should attract a greater number of translocation attempts.

4.3.3 Systematic planning of fence network expansion

I devised a search algorithm for identifying locations for new fences that will produce the greatest expected reduction in the number of threatened species extinctions, based on maximising the marginal benefit of each new fence (Appendix 4). It first calculates the expected marginal benefit for every new candidate location and then selects the best option, adding it to the current network. The marginal benefit is then recalculated
for each of the remaining candidate locations. This process is repeated until the required number of fences is chosen.

I created Maxent habitat suitability models for each of the 22 species of interest known to formerly occur in the state of NSW. Maxent is a widely used presence only method for predictive suitability models. For species known to have declined unevenly across their distribution, using current data only is known to over predict the suitability of regions where the agent of decline are least effective, rather than the intrinsic habitat suitability of the species (Cromsigt et al. 2012). Using a contemporary dataset for predator affected Australian mammals this effect was observed to be strong (Chapter 2). We formed a historical occurrence dataset using atlas of living Australia data cut off at 1970 and historical records from specimen collections from museums dating to the early 1800’s. Models were created for Australia at 5x5 km resolution using bioclim layers 1, 3, 4, 5, 12, 18, (Hijmans et al. 2005) relief (Williams 2011), extreme minimum and maximum temperature variation, and vegetation height (Simard et al. 2011) as predictors. Suitable release sites were estimated for each of the 22 NSW species (Figure 4.1).

The state government in NSW is currently seeking to expand their existing fence network. To apply my algorithm, the state is divided into 30,640 5x5km planning units, each of which could contain a potential new fence project of 2500ha, approximating the NSW proposal for large fences. Large fences provide a number of benefits; they can mitigate some of the uncertainty of translocation outcome by providing more habitat (Chapter 3), and are more efficient in perimeter to surface area ration, reducing material costs. In the first, all land tenure types are considered, but only if the cells contain sufficient intact habitat (specifically, no more than 10% of vegetation cleared, as assessed by NVIS version 4.1). In the second, I limited new fences to intact habitat within the current protected area system (CAPAD, 2014). In both cases I assumed that if a fence is constructed, all species that have suitable and sufficient habitat will be translocated (Figure 4.1), but not that all translocations will be successful, as outcomes from fenced translocations can be highly variable (Chapter 3). The probability of translocation failure modifies the expected benefit of a fence, and I based this probability on each species’ empirical translocation history (Figure 4.2). Therefore, the benefit of a new fence is the expected reduction in extinction probability, aggregated across all translocated species, discounted by the probability of translocation failure. I also considered two different spatial perspectives for the project. The first is focused on NSW, and aims to minimise each species’ probability of extinction from NSW. That is, based only on current populations within the state. The second considers the probability of global extinction, calculated from all known populations of each species.
Figure 4.1
Maps of translocation suitability for each species. Habitat suitability and translocation cut offs for each species. Areas of habitat suitability too low to consider release are light grey and areas too degraded dark grey.
Figure 4.2
Probability of translocation success. This figure shows the beta distribution of translocation success drawn from for each species. Distributions were created based on the unique translocation history of each species.
For each combination of land tenure constraint and spatial scope, I compared a systematic approach to two reasonable alternative strategies. (i) A uncoordinated approach in which new locations are chosen opportunistically based for example on local funding opportunities or by focusing on individual species. I modelled this scenario using random selection of the new fence locations. (ii) A species-richness approach, where a spatially-flexible organisation chooses new fence locations that maximise the number of species that can persist within the new fence. This method ignores complementarity, does not account for the state of the existing fence network, and does not consider the species threat status. All combinations of scenarios and prioritization approaches are summarized in Table 4.2.

Table 4.2.
Summary of each scenario. For each scenario I estimated reduction in extinction risk for a new fence chosen at (i) random (ii) based on species richness and (iii) using a systematic approach.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Population</th>
<th>Protection</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>New South Wales</td>
<td>All land</td>
</tr>
<tr>
<td>B</td>
<td>New South Wales</td>
<td>Protected only</td>
</tr>
<tr>
<td>C</td>
<td>Australia</td>
<td>All land</td>
</tr>
<tr>
<td>D</td>
<td>Australia</td>
<td>Protected only</td>
</tr>
</tbody>
</table>

4.4 Results

4.4.1 State of the current Australian fence network
Currently there are 30 predator exclusion fences larger than 40 hectares operating in Australia, managed by 17 different organisations (6 government; 11 non-government/council) containing 31 species. The number of fenced translocations is highly skewed in favour of certain species and only half the species threatened by introduced predators are represented (Figure 4.3).

Conservation status is not a strong predictor of the species that have been favoured for translocation into fences (Figure 4.3). Total population size is not related to the number of fenced translocation attempts (linear regression, $F_{1,57} = 0.11, P = 0.74$), and the estimated probability of extinction for NSW species is unrelated to the number of attempted translocations (linear regression, $F_{1,22} = 0.35, P = 0.56$; Figure 4.1B). The IUCN red list status is essentially independent of the number of translocation attempts (ordinal regression, $P = 0.75$), with the 5 species that received the most translocations ranging from the Critically Endangered woylie (*Bettongia pencillata*; Chapter 3), to the Least Concern southern brown bandicoot (*Isoodon obesulus*).
Figure 4.3
State of the current Australian fence network. This figure shows the large skew in the representation of species in the current fence network with no apparent trend to IUCN red list threat status (A). There is no clear relationship between extinction probability and the number of translocation attempts (B). These findings indicate a need for systematic planning.

4.4.2 Systematic planning for fence networks
I considered the expansion of the existing fenced network using two different constraints on land tenure (all intact habitat; all protected intact habitat), and with two different objective functions (minimise global extinctions; minimise NSW extinctions). For each of the four scenarios (Figure 4.4, Table 4.2), a systematic approach consistently reduces overall extinction probability more than both random and richness-based (Figure 4.5) fence expansions (Figure 4.6 & 4.7).
Figure 4.4
The five most beneficial fence locations using NSW population status and the five most beneficial fence locations using Australia wide population status. Where (A) considers only protected areas (protected areas where translocations would not occur are dark grey), (B) considers all land with sufficient remaining vegetation as a potential site, (C) considers only protected areas and (D) considers all land with sufficient remaining vegetation as a potential site.
Figure 4.5
Species richness with 5 richest spatially separate locations. The summed probability of occurrence maps of NSW’s threatened species and the five most species-rich locations. If the objective were to simply add as many species as possible to each fenced area, ignoring complementarity with the existing network and subsequent fences, these would be the best five locations. This figure is to provide a systematic but non-complementarity-based contrast to the approach depicted in Figure 4.8.
**Figure 4.6**

Relative performance of different strategies. Change in expected species extinctions after 20 years (y-axis) with additional fences (x-axis) chosen using three methods. Fences are chosen according to my systematic method (black line), to the number of unique species that can persist in each fence (dashed lines), or across the range expected by random chance (grey polygon depicts 95% bounds). Benefit is measured in terms of the number of species persisting within NSW (upper panels, Scenarios A & B), and globally (lower panels, Scenarios C & D), compared to the number expected to exist in the absence of any fencing projects. Fenced areas in left-hand panels are chosen from NSW protected areas only; fenced areas in right-hand panels are chosen from any intact NSW habitat.
Figure 4.7
The number of new fences required to achieve the same benefit as two systematically chosen fences. Black bars 95% bounds of randomly chosen fences, blue x’s choosing species rich fences and the red line two systematic fences.

The systematic approach prioritises fenced sites that support combinations of species with few viable populations elsewhere. Individual species with high returns are characterised by an ability to attain viable populations within the confines of a fence, have a history of successful translocations, and a high risk of extinction. Consequently, a fence site containing only a single, high-risk species can be prioritised over an alternative location containing more species. The construction of a new fence reduces the extinction probability of each translocated species, and this changes the relative value of each potential fence location (Figure 4.8).
Figure 4.8
Benefit map for the first three fences, NSW populations using all land (Scenario B). Colours indicate expected reduction in the number of extinctions if a fence were constructed in each location. The sequence of panels shows how the relative value of locations changes as new fences provide species with protection. For example, locations with the highest initial values become relatively low value after selection of the first fence.
Both spatial scope and land tenure strongly influence new fence locations, and which species will benefit. For example, under the Australia-wide objective (Figure 4.4c-d; Table 4.2c-d), the method frequently selects fences that can support the critically endangered northern hairy-nosed wombat (*Lasiorhinus krefftii*), but never for the NSW objective (Figure 4.4a-b; Table 4.2a-b). This is for three reasons: (1) species extirpated from NSW (but found elsewhere Australia) yield large reductions in extinction probability if a fence creates its first NSW population; (2) the northern hairy-nosed wombat distribution barely overlaps with other threatened species; (3) new wombat populations yield only a low marginal reduction in extinction risk, due to their low population density. Comparatively, the woylie (*Bettongia penicillata*) has little influence over new fence locations, despite also being critically endangered and capable of reaching higher population densities inside fences (Chapter 3) than northern hairy-nosed wombats. This is because despite their dire conservation status, woylies now persist in a large number of geographically distinct locations, limiting the relative impact of a new fence population. Species with the greatest return on investment tend to only have a few, small populations, and likely result in a new, large population if translocated into a fence.

### 4.5 Discussion

Fences, like protected areas, will be inefficient if they are not established in a systematic manner (Stewart et al. 2003, Fuller et al. 2010, Radeloff et al. 2013); indeed, the decentralised nature of conservation fencing projects makes inefficient outcomes rather probable. The current state of Australia’s fence network has many similarities with early, *ad hoc* reserve networks: an over-protection of some species, no representation for others, and overall inefficiency. This does not negate its enormous conservation benefits, but rather it highlights the potential additional benefits of coordination and planning. In these analyses, I demonstrate how tools from systematic conservation planning and population viability analysis can help reduce these inefficiencies in the future.

Compared with two reasonable alternative strategies, an explicit consideration of both species viability and complementarity can more effectively reduce expected extinctions. For an equivalent investment, systematic choices can improve network performance by as much as factor of 1.8 over random choices and by a factor of 17 over decisions based on species richness (Figure 4.3 & 4.5, scenario C). Furthermore, returns asymptote rapidly suggesting that only a small number of systematically allocated fences are needed to achieve most of the potential gain.

The benefits of systematic assessments extend beyond superior performance. A quantitative approach to fence network expansion provides stakeholders with a clear explanation of why a particular choice was made. In an open tender process, an explicit benefit function provides funding organisations with defensibility and rigor, and provides the applicant organisations with a transparent description of the funder’s objectives. State or nation-wide priorities may not be wholly applicable to many funding sources for conservation fences, which are locally constrained. Nevertheless, even in these contexts a systematic
approach can provide benefits, by quantifying how local actions contribute to broader-scale objectives. This can highlight regional priorities, motivate local fundraising, and help attract regionally-flexible resources.

My method focused particularly on two essential features of conservation prioritisation (Margules & Pressey 2000): it seeks to represent a range of biodiversity features, and in so doing, offer adequate protection to each. However, the current formulation does not include variation in project cost between sites. The cost of building and maintaining fences varies at fine spatial resolutions, responding to land prices, accessibility, soil type, flood risk, and predator densities (Bode et al. 2012). Variation in cost is therefore an important consideration for fencing projects, and decision-makers may choose to prioritise projects that return the greatest reduction in extinctions per-unit-investment, or may aim to reduce extinction risk by a specified amount, for the minimum investment. The inclusion of cost will emphasise cheaper species – those that can reach high densities (generally small-bodied), and whose suitable habitat is in low-cost, agriculturally unproductive landscapes. In the absence of data, I did not include variation in cost, but acknowledge that it will affect priorities. In an open-tender process, bidding organisations would propose both a location and size for their fence, and would also indicate the cost. Across a large number of bids, this information would allow a calculation of each project’s return-on-investment, which could be easily incorporated.

My benefit function calculates extinction probability based on both the number of independent populations, and the species’ abundance in each. The probability of each fenced population becoming extinct reflects its abundance, its maximum growth rate, and stochasticity (Lande 1993), but active population management (i.e., managed dispersal) can decouple extinction risk from demographics. In fact, local extirpation of fenced populations generally results from catastrophes (e.g., floods, predator incursions), not demographic stochasticity. My approach can easily consider this alternative, by reformulating the benefit function to equally weight all extant populations. The result is a different set of priority sites (Figure 4.4), but a similar improvement in efficiency resulting from the use of a systematic approach. These differences do not reflect limitations in a systematic approach to conservation fences; they instead stress the importance of correctly formulating the network objectives, and the dynamics of the ecological and economic system.

Conservation actions are expensive and the available resources are severely constrained. As a result conservation decisions are consistently moving in the direction of systematic and transparent prioritisation (Margules and Pressey 2000, Joseph et al. 2009, Januchowski-Hartley et al. 2011, Pannell et al. 2012). My method adds to the existing toolkit, with potential application to any spatially-constrained management action that aims to provide population viability benefits to a limited suite of species such as poison baiting programs (Chapter 5) or island prioritisations. Conservation fencing, an increasingly common threatened species management approach, is an increasingly rare exception to the trend of systematic prioritisation. My Australian case-study highlights the value of applying systematic approaches to networks of conservation fences, with similar benefits likely to be observed across the increasing set of conservation fencing networks across the globe (Hayward and Somers 2012).
Chapter 5

Can dynamic baiting improve conservation outcomes across highly stochastic environmental cycles?
5 Can dynamic baiting improve conservation outcomes across highly stochastic environmental cycles?

5.1 Abstract

Given limited resources, conservation managers seek to achieve cost-effective outcomes from their actions. In ecosystems whose dynamics contain cyclical components, managers could seek to achieve cost-effectiveness by timing their actions according to particular phases of the cycle. However, stochastic elements reduce the predictability of both the timing of the cycles, and the effectiveness of management actions taken at a certain point in the cycle. Under what levels of stochasticity in cycles can outcomes be improved? Using parameterised Lotka-Volterra models, I simulated populations of an invasive predator (red fox, *Vulpes vulpes*), an invasive prey species (rabbit, *Oryctolagus cuniculus*), and a threatened prey species (bilby, *Macrotis lagotis*) under El Niño southern oscillation-like rainfall cycles in semi-arid Australia. I investigated whether dynamic scheduling of baiting across the cycle could reliably improve conservation outcomes for the threatened species when compared to alternative baiting schedules. Previous research has recommended that high intensity baiting be synchronised with the period immediately following rainfall events, with reduced intensity towards the end of extended dry periods. I show that this strategy does not yield efficiencies, when considering management outcomes over the long term. More generally, dynamic optimisation techniques indicate that no baiting schedule outperforms continuous baiting of the same budget. These analyses did indicate that modest improvements in cost effectiveness (cost reductions of 35% with no loss of benefit) could be achieved if managers cease baiting at the end of dry periods, when both foxes and bilbies are at naturally low density. However, this decision simply stops baiting when benefits are unavailable; it is not a synchronised baiting schedule. My research suggests that, in highly stochastic systems, ecological insight offered by deterministic theory and logic has limited management value.
5.2 Introduction

Many ecosystems cycle in natural rhythms, ranging from short diurnal or seasonal patterns, to long-term climatic oscillations. However, stochasticity is overlaid upon these deterministic cycles, which reduces the predictability of interventions and the outcomes of management actions. Long-term, climatic oscillations trigger phenomena such as masting events in New Zealand (Schauber et al. 2002), anchovy fishery collapses in Peru (Gutiérrez et al. 2007), coral bleaching (Webster et al. 1999), and boom-bust herbivore eruptions in arid landscapes (Holmgren et al. 2006). The variation caused by these cycles is problematic for managers (Bakun and Broad 2003), however must be incorporated into action plans since their influence is enormous. If the timing and intensity of stochastic cycles are a challenge for managers, can the dynamic allocation of action in accordance with these cycles yield efficiencies and improve outcomes?

Invasive predators pose a significant threat to evolutionarily-naive prey species, particularly on islands (Hilton and Cuthbert 2010) and geographically-separated landmasses in the southern hemisphere (Mack et al. 2000). Managers regularly utilise ecological cycles to improve the effectiveness of invasive predator control and eradication efforts (Brown and Urlich 2005, Robley 2008). Australian mammals have been severely impacted by predation from invasive cats (Felis catus) and foxes (Vulpes vulpes), and are amongst the globe’s most threatened groups of mammals (Chapter 1.1, IUCN, 2014). Interactions between invasive predators and the El Niño southern oscillation (ENSO) cycle has directly contributed to both decline, and complications in management of Australian mammals. ENSO is a stochastic, long-term weather pattern that drives ecological fluctuations throughout the globe (Barber and Chavez 1983). Researchers have suggested that managers can improve the effectiveness of baiting programs by synchronising management with particular phases in the climatic and ecological cycles (Letnic and Dickman 2006).

Along with predator exclusion fencing (Chapters 3 & 4), lethal control through poison baiting is amongst the most popular methods for invasive predator control (Short and Smith 1994). Poison baiting programs are frequently adopted, as they provide a cost effective mechanisms for predator control over large spatial scales (Kinnear et al. 2002). Patterns of implementation in the conservation sector range between ad hoc, random schedules (Gentle et al. 2007), to uniform schedules over extended periods (Bailey 1996, Armstrong 2004). While baiting in Australia might be common practice, the response of threatened species is highly uncertain. Although baiting programs often have measurable impacts on the target predator (Thompson and Fleming 1994, Marlow et al. 2000, Thomson et al. 2000), responses from the species of conservation concern do not necessarily result from the reductions in predator numbers. This could arise from an inability to reduce predator populations below a level tolerable to the threatened species (Walsh et al. 2012), an insufficient spatial scale (Thomson et al. 2000) or inconsistent implementation (Gentle et al. 2007). Baiting can
also result in unanticipated perverse outcomes, such as the triggering of trophic cascades or the release of other predators in the system (Ritchie et al. 2012). Despite these drawbacks, well-implemented baiting programs often achieve positive conservation outcomes.

Decline in Australia's threatened mammals has been most pronounced in regions of semi-arid and arid rainfall (McKenzie et al. 2007). The variation in these systems is dictated by large-scale climatic drivers such as the ENSO cycle. In Australia, ENSO manifests as pulsed El Niño and La Niña episodes that interrupt periods of “normal” rainfall. This cyclic, stochastic rainfall pattern triggers boom-bust periods in Australia's biota over large proportions of the continent (Stafford Smith et al. 1990, Ludwig et al. 1996). Irruptive prey species such as introduced rabbits (Oryctolagus cuniculus) and native long-haired rats (Rattus villosissimus) feed the growth of both native (Pavey et. al. 2008) and invasive predator populations (Southgate and Masters 1996). Once the eruptive prey populations crash, the now abundant invasive predator switches to consuming low-abundance, often threatened species (Sinclair et al. 1998), leading to periods of intense predation pressure and ultimately the resultant extirpation and extinction of Australian mammals (Letnic and Dickman 2006). It has been hypothesised that the periods immediately in the wake of high rainfall are when the threat to native mammals from invasive predators is most intense. It is at this precise point in the cycle that ecologists have suggested management actions be focused (Letnic and Dickman 2006). However, given the systems intrinsic variability and unpredictability, do generalisation for management hold, and can efficiencies be made?

In this paper, I investigate whether conservation managers can improve the efficiency or effectiveness of their actions by synchronising them with ecological cycles. Dynamic action over long cycles places considerable demands on management. Varying management intensity requires greater logistic capacity; responsive, state-dependent decisions need ongoing monitoring; and scheduling variation requires dynamic planning and flexible budgets (McCarthy and Possingham 2007). Clear evidence of increased efficiency over status quo is needed to justify dynamic decision-making. I build a model to test if more efficient and effective baiting schedules can be developed for an ENSO driven system. I consider two questions. First, can an ENSO-synchronised management schedule deliver conservation benefits, given that the cycles are complicated by stochasticity and uncertainty? Second, given the range of management budgets available to different managers, are efficiencies budget dependent?
5.3 Methods

5.3.1 System dynamics:

I used a discrete time model to simulate an Australian semi-arid, ENSO driven system with an eruptive prey species, an invasive predator and a threatened, native prey species. The system was based on the dynamics of a previously described and calibrated population model (Pech and Hood 1998) (hereafter the PH model, see Appendix 5 for details of how I adapted this model for the question). The PH model demonstrates a clear boom-bust cycle, where rabbit abundance was observed to increase 300 fold in response to stochastic rainfall event, triggering growth in fox populations.

In our model, both vegetation (V) and invertebrates (I) were regulated by rainfall (R). Vegetation and invertebrates were eaten by rabbits (N) and bilbies (M). The population dynamics of foxes (P) were driven by the abundance of their main prey: invasive rabbits, and native bilbies. Vegetation growth is rainfall dependent (at rate \( r_V \)), and also reflects consumption by rabbits (\( g_N \)). Similarly, invertebrates respond to rainfall (at rate \( r_I \)), and consumption by bilbies (\( g_M \)). Rabbit and bilby abundance respond to the abundance of vegetation and invertebrates respectively (at rates \( r_N \) and \( r_M \)), and to predation by foxes (\( g_P \)). Foxes increase (at rate \( r_P \)) by consuming rabbits and bilbies, and by density-dependent immigration (\( X(P, P_E) \)) from neighbouring populations. Foxes are also controlled through baiting, which removes a proportion of the population (\( u \)) at each time step, depending on the intensity of control. These responses were modelled using modified Lotka-Volterra models (Volterra 1926, Lotka 1927). See Appendix 5 for the formulation details and parameterization values:

Vegetation:

\[
\frac{dV}{dt} = r_V(V, R) - g_N(V)N
\]

Invertebrates:

\[
\frac{dI}{dt} = r_I(I, R) - g_M(I)M
\]

Rabbits:

\[
\frac{dN}{dt} = r_N(V)N - g_P(N)P
\]

with a Holling type III consumption of rabbits by foxes such that

\[
g_P(N) = \frac{k_NN^2}{N^2 + D_{III}}
\]

Bilbies:

\[
\frac{dM}{dt} = r_M(I)M - \frac{h_P(M)}{1 - g_P(N) / k} P
\]

with a Holling type II consumption of bilbies by foxes such that

\[
h_P(M) = \frac{k_MM^2}{M^2 + D_H}
\]

Foxes:

\[
\frac{dP}{dt} = (r_P(N, M)P + X(P, P_E))(1 - u)
\]
5.3.2 Parameter details:

Rainfall
In the model, rainfall follows an ENSO-like cycle, where 2 years of high rainfall are followed by 5 years of low rainfall. Although the ENSO duration varies between cycles, assuming a fixed period enabled us to compare the impact of baiting schedules over consecutive cycles. Rainfall was calibrated to data gathered in the region where the PH population parameters were estimated. I used an average rainfall from Hillston airport of \((200 \pm 100)\) mm/year during a year of low rainfall, and \((700 \pm 200)\) mm/year during a year of high rainfall (Commonwealth of Australia, 2015)

Invertebrates
Bilbies are omnivorous, however, they feed predominantly on invertebrates (Gibson 2001, Bice and Moseby 2008). I modelled invertebrate abundance using the same rainfall response dynamics as vegetation. While resource competition and other forms of competition between rabbits and bilbies are likely to exist, it remains unquantified (Cooke 2012). The original configuration of the PH model had both herbivores competing for the same food resource. Given the uncertainty of competition, the proportion of bilby diet consisting of invertebrates and vegetation was subject to sensitivity analysis.

Bilbies
The maximum annual bilby population growth rate was estimated at 3.06 (0.24 - 12.59) per annum (Hone et al. 2010), and this declined with decreasing vegetation availability, falling to zero at the same point as rabbits (402 kg/ha of vegetation; Pech & Hood 1998).

Fox Immigration
The PH model assumed that the fox population could not decline below 0.001/ha based on observations from their study site. I modified this assumption by allowing managed (i.e., baited) populations to decline below this floor, and also by allowing immigration from the surrounding landscape. Immigration has a significant influence on the population dynamics of foxes (Thomson et al. 2000, Gentle et al. 2007). In baited landscapes, foxes immigrate from the surrounding, unmanaged landscape to rapidly recolonise the low density, baited territories. In my model, the rate at which foxes increase from very low densities was determined by density dependent immigration up to the floor value. In order to simulate this, I generated a parallel system containing only foxes, rabbits, and vegetation (assuming no bilbies are in this region, Appendix 5), and used the size and growth rate of this population to determine the immigration rate. When the growth rate of the external fox population is negative, I assumed a low random number of foxes will immigrate into the baited region (0 - 5% of the difference between the populations, Appendix 5). Conversely, if the growth rate of the external fox population is positive, I assume a high random immigration rate due to a surplus production of pups (5 - 15% of the difference between the populations, Appendix 5). These immigration rates are a
conservative estimate as studies have shown this rate to be as high as 45% per annum (Thomson et al. 2000).

5.3.3 Management objectives
A successful management action should improve the population viability of a threatened species over a relevant timeframe. Population size is an important factor in determining the risk of population failure (Lande 1993). Therefore, the relative success of the conservation outcome was measured against two population size metrics; firstly, the abundance of bilbies summed over the period (total bilbies, TB). The model maintains bilbies at a floor level so they continue to exist in the environment for future simulations, the fox population would in reality be able to reduce the bilby population below this level, ultimately resulting in extirpation. The likelihood that bilbies become extripated was assumed to correlate with time spent at the floor value. Therefore, the second population metric was calculated from the total number of quarters that bilbies spent above their population floor value (time above floor, TAF). Cost-effective baiting strategies should either provide higher returns on these metrics for a given budget, or provide a comparable level of benefit for a reduced cost. I considered these population metrics over 3 ENSO cycles (21 years) as a realistic but sufficiently long-term timeframe to measure the management objective.

5.3.4 Baiting schedules and budgets
I assumed that managers would implement either an efficient form of manually deployed or of aerial broadcast baiting technique (Moseby and Hill 2011) over an area large enough to prevent immediate immigration (Thompson et. al. 2000). I modelled four different fox baiting intensities, each with a different cost (relative units) that removes a different proportion of the population of foxes calibrated on a common observation that approximately 95% of foxes can be removed from high intensity baiting (Dexter and Meek 1998, Thompson and Algar 2000). The lower cost baiting actions were based on a diminishing returns function described by (Rout et al. 2014; Table 5.1). Baiting is undertaken at the end of each time step, after the population dynamics have been simulated for all populations. Some proportion of the population is removed based on baiting intensity a described in Table 5.1. Management budgets are made available for a 7 year (28 quarter) ENSO cycle. I tested different budgets, ranging from very low budgets which did not allow ongoing baiting in every quarter, to very high budgets, allowing ongoing, high intensity baiting. For a given budget, this total effort could be distributed at varied intensities at different points of the ENSO cycle, forming the basis for different schedule types (Table 5.2):
**Table 5.1.**

Units of baiting effort, where each baiting intensity corresponds with a cost and likely impact as described in Rout et. al. (2014).

<table>
<thead>
<tr>
<th>Baiting intensity</th>
<th>Cost (relative units)</th>
<th>Proportion of population removed (%)</th>
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<td>4</td>
<td>75 - 95</td>
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</table>

**Constant schedule:** baiting effort was allocated uniformly across the span of the ENSO cycle. This schedule was used as a baseline schedule to simulate ongoing programs.

**Random schedule:** baiting timing and intensity was allocated randomly across the ENSO cycle.

**Optimal schedule:** baiting timing and intensity was chosen to maximise returns through 10,000 iterations of a simulated annealing function (Hwang 1988).

**Gradual pulse:** baiting intensity that is increased gradually from low to high, followed by a mirrored reduction in intensity of high to low.

**Short pulse:** applied only to small budgets. Baiting effort is allocated at the highest intensity possible over consecutive quarters until the budget is exhausted.

**Long pulse:** applied only to small budgets. Baiting effort is allocated as slowly as possible by baiting at the lowest intensity possible over consecutive quarters until the budget is exhausted.

5.3.5 **Scenarios tested**

I refer to baiting allocations by the schedule followed by budget. For example a uniform schedule with a budget of 28 is referred to as “constant 28”. Baiting schedules are summarised in Table 5.2.

**Test 1. Dynamic vs. constant.** I wanted to determine the effect size of budget size and dynamic scheduling on management outcomes. I compared a constant 28 (continuous low intensity), a constant 56 (continuous medium intensity) and a constant 112 (continuous high intensity) schedule, to random 28 and 56 schedules, and the optimal 28 schedule. For budgets of 28, baiting frequency was tested within the constant schedule, with conducted quarterly, biannually and annually.

**Test 2. Pulse baiting.** I wanted to test if pulsing baiting intensity can harmonise with the natural cycle and result in efficiencies. The peak of the pulse schedules was shifted across all 28 quarters, so to test
the importance of the timing of the pulse. To test the impact of the timing of baiting pulses within the cycle against a constant baiting schedule of 28, I compared the timing of gradual pulse 28 and short pulse 28 pulse schedules.

Managers often lack the resources to bait constantly over long periods, such as the duration of an ENSO cycle. Therefore, I also considered the importance of timing for smaller budgets. I compared constant schedules of budgets 7 (lowest intensity, once a year), 14 (lowest intensity, twice a year) and 21 (lowest intensity, three times a year) against short and long pulse schedules of the same budget. For pulse schedules, the timing of the middle of the pulse was shifted across each of the 28 quarters in order to assess whether an optimal timing for pulses exists.

Test 3. Reduced cost. Finally, by examining the long pulse schedule in test 2 I devised a likely cost-effective schedule which saves money without compromising outcomes. The schedule starts baiting with the onset of high rainfall, and continues to bait through the bust period at the lowest intensity until the budget is spent. The benefits of continuing baiting for each consecutive quarter are compared against a constant 28 schedule.
Table 5.2
This table depicts different baiting schedules over a seven year ENSO cycle, where the first two years (blue) are high rainfall and the last five years (brown) are low rainfall. The number in each quarter is the corresponding baiting intensity (see Table 5.1). The budget of each schedule is the sum of the cost of all baiting action across the ENSO cycle.

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76
5.3.6 Tests of cost-effectiveness
My population model was simulated using Matlab version 8.5.1 (MATLAB 8.5.1 2015). Plots of model outputs were generated using R version 3.1.3 (R 2015). The 95% range of outcomes for TB and TAF measures of effectiveness were generated from 1000 simulated runs of each baiting schedule.

5.3.7 Model sensitivities
Sensitivity analyses were conducted on three key sources of parametric uncertainty: (i) the duration and severity of ENSO cycle (with La Niña period ranging from 1-3 years in 7), (ii) the proportion of bilby diet that is invertebrate and vegetation (from 100% vegetation to 100% invertebrates), and (iii) the immigration rate of foxes (from 0% to 20% of the external population size pa).

5.4 Results

5.4.1 Model sensitivities, calibration process and variation
My model recreates qualitative dynamics and responses that are observed in the natural system (Figure 5.1). Vegetation and invertebrate density closely follow rainfall levels. Rabbit and bilby population growth are driven by the intensity of rainfall in previous quarters, while the growth and decline of fox populations lags behind the rabbit population. After rainfall ceases and the food sources are exhausted, rabbits experience a much stronger reduction than bilbies. Most importantly, the model recreates the dynamics that Letnic et al. (2007) use to argue that baiting should be synchronised with ENSO cycles. Foxes persist at elevated levels during the vulnerable periods for native bilby populations. Indeed rapid decline of bilbies occurs immediately after the onset of bust periods.
Figure 5.1.
A sample run of the full model with no baiting for 120 periods (disregarding the first 20 periods). Each population is normalized to be within a range of [0,1]. Rainfall in each quarter is overlain by the population dynamics.

5.4.2 Test 1. Dynamic vs constant
The majority of benefit was achieved by a continuous low intensity baiting schedule, with no predictable benefit afforded through strategic timing of varied baiting intensity. Constant, high intensity baiting further increased the upper bounds of benefit, particularly for the TB metric (Figure 5.2), however returns rapidly diminish, with the majority of benefit realised under a constant 28 schedule. For a budget of 28, neither benefit metric differed when baiting effort was spent quarterly, biannually, annually, or in an ad hoc manner (Figure 5.3). Simulated annealing did suggested a tendency to increase baiting effort during the onset of the bust period (Figure 5.4); however, the result of this effect did not equate to an increase in outcome metrics between the optimal 28 and constant 28 schedules (Figure 5.2).
Figure 5.2
This figure shows the relative benefit of different budgets and schedules. In both time above floor and total bilbies metrics, the majority of the return is afforded from baiting at constant low, although higher budgets did provide improvement to the top end of total bilbies outcomes. The range of returns from the simulated annealing result did not differ from random or constant schedules of budget 28 (low intensity baiting, Table 5.2).
Figure 5.3.
The relative benefit of different spending patterns for a budget of 28 compared to no action. Little difference exists between baiting randomly, quarterly, biannually or annually for either metric.
Figure 5.4
This figure shows the optimal baiting schedule as identified from 10,000 runs of simulated annealing for a budget of 28. The y axis indicates the baiting intensity while the x axis indicates timing over the 7 year period. The black dashed line depicts a uniform baiting schedule of intensity 1, every quarter. The red line and polygon depict the mean and 95% confidence intervals for average baiting intensity for each rainfall quarter. The grey polygon depicts the 95% bounds of relative bilby abundance for each rainfall quarter. The vertical blue line depicts the end of the high rainfall period (onset of the bust period), with rainfall quarter 8 and below of above average rainfall. The average optimal schedule according to the simulated annealing program is to bait at a higher intensity during quarters 11 and 12 (immediately after the end of high rainfall) and to bait at a lower intensity during quarters 20-28, when bilbies are of naturally low abundance.
5.4.3 Test 2. Pulse baiting

At no point did any pulse baiting scenario outperform a constant 28 schedule for either benefit measure (gradual 28 represented in green, short pulse represented in red, Figures 5a, 6a). Short duration, high intensity pulses (e.g., Fast pulse 14 in Table 5.2) consistently performed worse than any constant 28 outcomes.

Long pulse schedules, where the effort was allocated over consecutive quarters, performed best when the peak of the pulse overlapped the onset of the bust period (depicted by the vertical blue line, figures 5 & 6). However, even these superior pulse schedules were generally outperformed by a continuous low intensity schedule of the same budget. Only when the peak of long pulse schedules overlapped with the bust period (the 8th quarter of the cycle, depicted by the vertical blue line, figures 5 & 6) did pulse schedule perform in a similar level to a constant schedule of the same budget. This effect was most pronounced in budgets of 14 and 21, however, the long pulse 14 schedule (represented in blue, Figures 5c, & 6c) outperformed a constant schedule of the same budget.
Figure 5.5
Relative comparison of uniform baiting for total bilbies metric compared to dynamic baiting scenarios, depicting 95% quantiles of the sum of bilby density over ENSO cycles (21 years). In these plots, the x axis relates to each quarter of a 7 year ENSO cycle, where the first two years exhibit “boom” like rainfall followed by five years of “bust” like low rainfall. The transition between these two periods is depicted by the vertical blue line. The variation in returns relates to the shifting peak of the dynamic schedule. For example the values that fall on the vertical blue line relate to baiting schedules whose “pulse” peaks on the 8th rainfall quarter of the ENSO cycle. Figure 5.4A compares uniform, low intensity baiting of budget of 28 (depicted by the light grey band); a rapid, high intensity pulse (red band); and a graduated pulse (see Table 5.2, green band). Figures 4B-D compares budgets 7, 14 and 21 respectively, with uniform and dynamic schedules. Each plot depicts the upper or lower bounds of the uniform 28 schedule (light grey dashed lines), uniform baiting of the given intensity (dark grey band), a rapid, high intensity pulse (red band), and a long, low intensity pulse (blue band).
5.4.4 Test 3. Reduced cost

If a low intensity baiting schedule commenced during the onset of high rainfall and ceased spending after 18 quarters (Figure 5.7), outcomes are comparable to that of the constant 28 schedule (both for the TAF metric and TB metric), but with a 35% saving. That is, the same outcomes at a lower cost.
**Figure 5.7**

This plot identifies a potential mechanism for efficiency. Here, baiting commences during the first quarter and ceases at the related x axis quarter. The 95% quantiles TAF (red polygon) and TB (blue polygon) metrics. The vertical blue line depicts the end of the high rainfall period, with rainfall quarter 8 and below of above average rainfall. Here, baiting that ceases at the 18th quarter (vertical red line) does not differ from the lower bounds of a constant 28 schedule, depicted by the grey polygon.
5.4.5 Sensitivities

The three uncertain parameters yielded large differences in the absolute value of the two outcome metrics, however the relative response to different management schedules remained consistent. For instance, if changing bilby diet increased bilby abundance, this increase was consistent and proportional across different management schedules. Since in comparison to eachother the model outcomes remained consistent, I used the most likely values of these parameters, as described in Appendix 5, instead of a range.

5.5 Discussion

5.5.1 Key findings

I investigated whether management efficiencies could be achieved through dynamic allocation of resources in a long term, highly stochastic cycle driven by ENSO weather patterns. Stochasticity within the system hindered the ability to achieve management efficiencies through dynamic scheduling. An overall increase in budget does improve management outcomes, however, the majority of benefit is afforded with a modest budget of 28 (with 112 being the highest possible budget). In terms of timing of action, the majority of improvements in management outcomes were afforded from consistent, ongoing action, with no discernible difference between schedules of the same budget so long as action was applied throughout the cycle. Optimal scheduling performed comparably to constant, even though simulated annealing detected a tendency for dynamic allocation of resources (Figure 5.4), the degree of expected variation in outcomes meant that the effect size was intangible (Figure 5.2). Hence, constant baiting remains the preferred schedule due to its innate simplicity. Overall, the most cost effective schedule is to bait at low intensity, in a constant manner until both fox and bilby numbers are naturally low in the driest part of the cycle. Only for modest budgets, when mangers have enough money and flexibility to bait continuously at low intensity can a more cost effective, dynamic schedule (Figure 5.7) be considered as a viable option. By utilising the natural fluctuations of the system, an approximately 35% saving can be made while still maintaining equivalent threatened species outcomes (Figure 5.7). Ceasing baiting when both the bilby population and external fox population have naturally reached low levels results in little additional risk, while maintaining expected returns. During these periods there is little population effect from the management action, and therefore no benefit to bilbies. So while ecological insight may help us to understand the mechanism by which species are threatened, in highly stochastic systems, it provides little benefit in terms of our capacity to improve management effectiveness.
5.5.2 Budgets

For very small budgets, dynamic schedules, if timed correctly, performed comparably to constant schedules (Figure 5.5c, blue band quarters 5-10). However, poorly timed dynamic schedules performed significantly worse (Figure 5.5c, blue band quarters 15-20). The added complexities and information limitations of a real management program are additional complications, adding uncertainty to the correct timing of dynamic actions. It is likely that spreading action evenly across the cycle remains the best solution as it introduces no risk of mistimed action.

When efficiencies were possible, (Figures 5.5c & 5.6c, Figure 5.7) it was due to improvements of cost effectiveness through inaction in periods where populations are naturally suppressed. Intensified baiting during vulnerable periods yielded no additional benefit, because continuous action over extended periods is required to ensure against immigration of foxes from outside the managed area (Gentle et al. 2007). Rather than a positive pulse of intensified action around the vulnerable bust period (Letnic et al. 2007), efficiencies were observed in a negative pulse, where money could be saved through inaction during periods where management has little impact.

Efficiencies cannot be realised with short-term annual budgets (Figure 5.3). Similarly ad-hoc, high intensity spending when money is available is the worst performing schedule for a given budget (depicted in red, Figures 5.5 and 5.6).

5.5.3 Synthesis

The central justification for applied ecology is that ecological understanding will improve management efficiency. For example aligning baiting with the predictable annual cycle of fox breeding has been identified as a mechanism for increased bait uptake (Robley and Wright 2002). However, the specific conservation goal is not to control foxes numbers, although low fox numbers may be desirable, but instead deliver an action that improves the conservation outcome of improved bilby population viability. I tested if an understanding of the underlying, cyclical dynamics of an ecosystem can achieve management efficiencies. In the case of highly stochastic, cyclic systems, the inability to improve effectiveness of actions is due to the fact that stochastic systems are intrinsically uncertain, where the effect size of generalisations attained through greater understanding is overshadowed by the innate variation within the system. What efficiencies were revealed from my analysis were modest and circumstance dependant. Other than diminishing returns on increased investment and a necessity for maintained, ongoing action, managers have little capacity to improve conservation outcomes through clever temporal allocation of resources.
5.5.4 Comparisons
Optimal allocation of management resources in uncertain systems often requires a dynamic approach (Williams and Johnson 2013), where the timing, duration and intensity of action is varied to improve conservation outcomes (Bode et al. 2015). In dynamic systems where predators require management, the timing can influence the impact of the action on the predator population (Short et al. 1997, Balogh et al. 2001, King and Powell 2011). This is likely due to the importance of scale and immigration. The increased removal of foxes from high intensity baiting coinciding with vulnerable periods, if not continued for sufficient duration, are only short term and might not protect threatened species from subsequent immigration. Action over a sufficiently large area that extends well beyond the extent of the bilby population may be less susceptible to the short term effects of dispersal (Thomson et al. 2000), and perhaps here larger budgets are better spent increasing extent rather than intensity.

5.5.5 Applied implications
What can a manager do with these efficiencies? During the cost effective negative pulse (Figure 7), risk averse managers might continue annual maintenance baits to provide an insurance mechanism hedging against the risk of ceasing baiting altogether. Savings could be used to bait a larger area, improving the effectiveness of the baiting program generally by reducing dispersal potential of foxes from surrounding habitat (Saunders et al. 1995, Thomson et al. 2000). However, for any benefit to arise from these efficiencies, managers require the financial flexibility to budget over the long term, in accordance with the duration of the systems cycle.

5.5.6 Limitations
There are a number of notable exclusions of factors which might influence my model. In my model, I do not consider the added complexity of spatial extent. ENSO cycle duration was a fixed value, despite varying widely in a real system. Only through a fixed cycle duration were like for like comparisons of different baiting schedules possible, so this additional stochasticity was removed. Baiting campaigns over different areas are likely influenced by economies of scale in their application, and are subject to differences in dispersive rate. The added complication of scale was not included as a variable as a model parameter, instead it was assumed that the baited area would be sufficiently large to exclude immediate dispersal recorded from baiting over small spatial extents.

Compared to the real system my model simulates, I only model 5 interacting species (however the vegetation and invertebrates have many species nested within these categories), real systems have thousands of interacting species. The most notable exclusion is feral cats (*Felis catus*), a predator of bilbies, whose populations are thought to strongly interact with targeted fox baiting (Marlow et al. 2015). In a system with
both foxes and cats, a resultant release of cats after fox control might strongly influence conservation outcomes for bilbies for a given baiting schedule. In which case baiting might not be an appropriate management action (Doherty and Ritchie 2016). However, each of these simplifications reduces the number of stochastic interactions, meaning in a real system changes in outcomes from management actions are even less deterministic. The degree of variation expected in my model is likely a conservative estimate, and my conclusions in this regard should be robust against the models simplicity. In fact, that other systems might exhibit greater stochasticity only reinforces my findings: that stochasticity reduces the utility of mechanistic models in designing management plans.

5.6 Conclusions
My recommendations to managers of highly stochastic systems are simple. Regardless of budget, action applied evenly over the duration of long term cycles are consistent and low-risk. Despite their logical plausibility, more complicated dynamic schedules are unlikely to improve outcomes in the long term, and add additional risk if timing of pulses do not precisely overlap with risk periods. In cyclic systems with low stochasticity, the predictability of management outcomes might be greater and the value of ecological insight is likely to improve. However, even when predicted outcomes from dynamic baiting are comparable to uniform, a uniform approach is a superior option as it is simpler to implement, making it robust to staff turnover and short term funding cycles. The implications of these findings role over to funders. In stochastic, cyclic systems, managers require budget stability over consecutive years with ongoing commitment in order to achieve long term, outcome based goals in species conservation.
Chapter 6

General Discussion
6 General Discussion

6.1 Overview

Australian mammals are amongst the most threatened in the world. Predation from invasive cats and foxes has driven many to extinction and caused rapid declines and extirpations in many of the remaining species. The most severely impacted extant species now only persist in a small number of refugial populations of few individuals. For these species, there is a very real risk of extinction from demographic population failure and catastrophic events. Existing populations need to be increased to more viable levels and new populations need to be created to prevent further extinctions. The persistence of many Australian mammal species now depends on continuous active management, and the creation of new populations is now almost exclusively achieved by way of translocations into predator-controlled areas. Predator exclusion fences have become an important tool, providing a highly effective form of threat abatement for remnant populations in situ, and for translocations of animals into new sites. However, translocations are failure prone, and the limited availability of founder individuals makes it particularly important to identify projects that maximize the likelihood of translocation success. A-priori assessments of project feasibility are therefore crucial, but knowledge is often lacking to make thorough assessments. In this thesis, I have enhanced conservation decision making in this area by addressing key knowledge gaps associated with translocation and predator management for Australian mammals.

In this thesis, I have focused principally on challenges associated within translocation of Australian threatened mammals with a particular focus on predator exclusion fences. I developed methods for locating new predator exclusion fences and filled some key knowledge gaps required to inform decision frameworks. I developed a method to assess our knowledge of the environmental niche space occupied by marsupial species that have contracted in geographic range (Chapter 2), identified important new information on habitat requirements for woylies (Chapter 3), developed a framework for deciding where to put new fences with regard to the existing network (Chapter 4), and investigated how cost effectiveness might be improved in long term predator baiting programs (Chapter 5).

Mammal translocations need to occur in suitable habitat, yet the pattern of occupancy across a species’ historic distribution is often poorly understood for threatened species, rendering our knowledge of their environmental niche space incomplete at best, and misleading at worst. To describe a species’ environmental niche, occurrence data from a broadly representative sample across the full range of conditions occupied by the species is required. For species that have been extirpated from large areas of their former distribution, our present understanding of its niche can be highly biased, and quantifying this bias is difficult. Without a thorough understanding of what constitutes suitable habitat for a species, conservation practitioners might inadvertently translocate animals into marginal or unsuitable habitat. Additionally, the risk averse approach of only translocating animals into environments similar to those that remain occupied by remnant extant
populations might severely constrain the number of translocation opportunities. To make informed reintroduction decisions based on predicted habitat suitability, I needed to know how thoroughly a species’ historic distribution was sampled and recorded before it began to decline. In Chapter 2, I proposed and tested a method for determining whether a species’ niche is well sampled by historical data by comparing niche volume accumulation curves under different chronological arrangements. Species whose distribution was sampled during geographic range contraction typically have poorly sampled ecological niches. Unrepresentative niche sampling can be identified by comparing environmental niche volume accumulation curves when data are arranged (i) randomly, and in (ii) forward and (iii) reverse chronological order. The greater the divergence between chronologically and randomly arranged data implies an increased likelihood of underestimated niche volume (Chapter 2). This method can be used as a basis to assess uncertainty in species distribution models. While it does not resolve the underlying problem, it does provide a mechanism to assess how far environmental niche models for translocation candidate species can be trusted.

Conservation fences, into which translocated mammals are often introduced to shield them from predators, are expensive to build and maintain. Fences that are built at a small size to reduce cost potentially limit the size and viability of a translocated population. A good understanding of how translocated animals use the space within a fence is crucial in making choices about its size. In Chapter 3, I investigated the spatial use of woylies (*Bettongia penicillata*) at the Australian Wildlife Conservancy’s Scotia Sanctuary. Woylies are the most frequently translocated Australian mammal species and are of acute conservation concern, yet their movements within conservation fences remains poorly understood. Using GPS tracking devices, I measured animal movements in two adjacent fenced populations in the arid extreme of their historic distribution. While the habitat characteristics and size of both fenced areas were comparable, the two populations differed greatly in density, and number of additionally translocated species of other mammals. As previously reported, home range size varied with population density. In the higher density stage 2, woylies exhibited home ranges of sizes similar to those previously reported of a similar density (kernel utilisation density (KUD) estimates 50-95%, 7.5-35 ha). The lower density stage 1 woylies had home ranges 2-4 times greater than in stage 2, (KUD estimates 50-95%, 20-140 ha). Total home range size in the low population density stage 1 was higher because animals covered more unique ground each evening, and spent more time further away from their daytime nest. Explanations for variation between the two stages include (i) competition for resources, and (ii) stochastic variation due to the timing of release. The example of Scotia demonstrates the unpredictable nature of translocation outcomes. Unexplained, potentially stochastic, variability in spatial requirements needs to be incorporated into risk assessments of translocation project feasibility.

In Chapter 4, I set about developing a framework for identifying and prioritizing new, highly beneficial fence translocation projects. Instead of the standard representation problem often used in conservation prioritisations, sites were instead prioritised using a population viability approach. This approach is far more appropriate given the somewhat inconsistent nature of threat listing for Australian mammals and the crisis circumstances of Australian mammal populations. The approach is also explicitly pragmatic, and considers
the conservation community’s priorities, capacity to act, and the limitations of a decentralised network to prioritise new fences locations using a complementarity framework. I demonstrated that conservation planned strategically using this framework is 17 times more efficient than an *ad hoc* approach, suggesting a high return for prioritisation frameworks in guiding conservation fencing programmes.

While fences form an effective, high security form of protection for Australian mammals, to many, the ultimate conservation goal for Australian mammals is to re-establish fully wild and unrestricted populations. Feral predators therefore need to be managed effectively in a broader landscape. In Chapter 5, I investigated whether utilising underlying ecological cycles could improve conservation outcomes for a predator-affected mammal. Poison baiting is a frequently adopted management action for the control of feral predators. Over the long term, implementation can range from uniform, consistent programs to ad-hoc, spontaneous pulses. In Chapter 5, I tested whether dynamic baiting schedules could improve cost-effectiveness with an outcome oriented conservation objective. I modeled populations of rabbits (*Oryctolagus cuniculus*), foxes (*Vulpes vulpes*) and bilbies (*Macrotis lagotis*) in a semi-arid community across the full duration of the El Niño Southern Oscillation (ENSO) cycle. I found that the stochastic nature of the Australian climate overshadowed most of the potential benefit from dynamic baiting over the duration of the ENSO cycle. While some modest savings can be made by baiting dynamically in accordance with the ENSO cycle, the majority of conservation benefit comes from consistent baiting that is maintained over the long term, meaning that to be most effective, baiting must be sufficient, ongoing and consistent. These findings highlight that the value of ecological insight in improving management outcomes can be limited in highly stochastic systems.

### 6.2 The importance of fences for conservation

Conservation fencing is a rapidly growing management action in Australia and elsewhere around the world. Matt Hayward’s recent book “Fencing for Conservation” (Hayward and Somers 2012), lists examples from South Africa, Poland, Australia, New Zealand, Tanzania, Namibia, Botswana, Scotland, Canada and Brazil. The narrower definition of “predator exclusion fences”, has examples from Australia (Dickman 2012), New Zealand and its offshore islands (Burns et al. 2012), Hawaii (Young et al. 2012), and some Portuguese islands (Cooper 2013). Networks within these countries are rapidly expanding, as is interest for application in new regions. However, there is a gap between existing prioritisation protocols and the requirements for efficient conservation fencing networks.

The planning of protected areas and fence construction are similar in that they are both spatial conservation actions, however, there are fundamental differences that are not encapsulated by existing reserve design methods. The standard representation approach (Cocks and Baird 1989, Ball et al. 2009) for systematic conservation planning is not a particularly useful tool for prioritising crisis conservation actions requiring translocations because the fencing problem has a different dimensionality. Fenced areas need to be sited and
constructed, the animals translocated into the area, and populations actively maintained. These actions take time and are limited to incremental addition, therefore importance lies in the sequence of each additional fence that augments the existing set of populations. These actions, while sometimes applied to protected areas, are not characteristic, and are certainly not a primary consideration in the majority of existing systematic conservation planning tools. Prioritisations for such translocations need to recognize this reality, thus an alternative planning approach to existing methods is required. In the case of fences, a factor of importance is in the timing and sequence of new actions, a factor which is not encapsulated by methods which provided returns on area coverage or total number of individuals.

Through management action, conservation managers are ultimately trying to improve the likelihood of a species’ persistence. The framework I produced for Chapter 4 seeks to directly improve the probability of persistence across a suite of threatened species. The method estimates the reduction in the expected number of extinctions that will occur if a particular suite of new fences is added to the current set. This prediction is calculated by running a stochastic metapopulation PVA for each species, and then aggregating across all species that would benefit from predator exclusion fencing. Not only does this stochastic metapopulation model consider the specific abundance of each existing and fenced population (as opposed to applying a simple MVP threshold), but it also explicitly incorporates the risk of failure, calculating the benefit of spreading effort over numerous, spatially-separated populations. This is an important consideration when spatially isolated populations are continually threatened by environmental catastrophes and feral predator breaches as illustrated by examples such as the cat breach of the Currawinya bilby fence (Williams 2012) and recent catastrophic fires in Western Australia impacting populations of Gilbert’s potoroo (*Potoroos gilberti*; De Poloni 2015).

Persistence is a longstanding goal of conservation planning, although in multi-species reserve systems it has only ever been quantitatively estimated for hypothetical cases (Nicholson et al. 2006). This is because quantitative estimates of persistence while ideal, can be difficult to calculate. Instead objectives are often based on arbitrary abundance thresholds (Jamieson and Allendorf 2012, Frankham et al. 2014). The implications of this framework are the most significant component of my thesis in terms of its contribution to conservation science. This method estimates species’ persistence probabilities in an explicit, species-comparable, and theoretically justifiable manner using pre-existing, recognised methods (Lande 1993, McCarthy et al. 2005). While its immediate application is well suited to fencing networks, the general applicability of my method to a large range of management actions gives it potential for much broader use in future.

The method I developed in Chapter 4 measures extinction risk directly. It is therefore a significant advancement on existing systematic conservation planning methods, providing a novel approach to prioritising conservation actions, not just protected area selection. This analysis revealed that many commonly translocated species are overrepresented within the existing fence network, with little additional
benefit arising from creating new populations. For these species, we would be better served attaining a more complete understanding of factors that affect their demographic viability (such as habitat and spatial use, Chapter 3) than to create additional fenced populations. An even more robust assessment would also incorporate the risk of population decline under different management regimes, and the capacity to manage fenced populations as quasi metapopulations through targeted re-stocking programs.

A series of assumptions underpins the optimisation. If the problem was addressed from a different perspective or with a different objective, the approach would need to be modified to account for its limitations. The fixed value of cost and fence size in Chapter 4 is however a clear limitation. The approach considered cost as a “per fence” value and that fences were a single, fixed size. The cost of building and maintaining fences varies spatially (Bode et al. 2012) and allowing fences to vary between a range of practical sizes may yield greater efficiencies (Bode and Wintle 2010). The decision to consider size and cost to be a fixed value was due to a number of management objective related complications that arise when cost is explicitly considered. Here I was limited in reporting of fence costs in real monetary values. Even in relative cost terms, there is limited capacity to remotely predict numerous factors that might influence construction and maintenance costs, such as erosion, soil acidity and vegetation density.

The benefits of variable fence size were not included in my analysis as they cannot be accurately considered without including a true cost estimate. For variable fence size to be integrated into the calculus, all possible new fence combinations must be assessed, to achieve target reductions in extinction risk for each species for the lowest cost. While this approach would yield a solution that is nearer to optimal, it does not accurately reflect the nature of governance in the currently decentralised fencing network, and is therefore probably less useful for independently acting managers than a sequential, greedy approach. Given the real-world context where an unknown number of fences will be built by an unknown number of managers, the greedy function identifies the next best fence in sequence. Including an estimated cost of the fence triages timely action for species that live in more expensive habitat types. A greedy function which chooses cost-effective solutions would inadvertently delay action for more expensive species until a point where the marginal return on cheaper species is sufficiently low.

Prioritisations are only as accurate as their data inputs. In estimating an expected return on a given fence location, I incorporated several elements that might determine the likely population size a species might attain within a fence, and the probability that a given translocation attempt might be successful. The most influential are the species' spatial requirements, and how this changes across a species distribution.

In Chapter 2, I attempted to address the uncertainty of unknown habitat suitability which in turn affects our capacity to prioritise action spatially. Maps of species’ distributions are an important decision support tool for translocations, as identifying suitable habitat is a critical component of maximizing translocations success (Seddon et al. 2007, Armstrong and Seddon 2008). However, our capacity to accurately predict habitat suitability is limited to the proportion of a species' historic released niche as described by pre-decline
occurrence data. A more thorough understanding of a species’ environmental niche can result in increased opportunity, and an increased capacity to spread risk spatially. As illustrated recently by two populations of Gilbert’s potoroo affected by the same fire, the costs of failing to spreading risk spatially can be acute.

Spatial risk spreading also comes with a cost. A fence, while separating predators from threatened species, simultaneously restricts growth of the confined population, limiting the size and viability of the translocated population. It is therefore important that fence sizes are appropriate for the spatial requirements of the species. The optimal size of a fence is dependent on many factors (Bode and Wintle 2010), and while building a large fence provides economies of scale resulting in a larger total of individuals per dollar spent, building a single large fence fails to spread risk spatially. Multiple smaller fences enclosing a smaller total of individuals may ultimately better protect a species (Helmstedt et al. 2014). While the minimum size of a fence is defined by demographic population viability, the decision to build a single large fence or multiple small fences is a trade-off between the potential for larger, more viable populations and spreading risk spatially (Helmstedt et al. 2014). For example, a translocation of northern hairy-nosed wombat into Richard Underwood Reserve, Queensland, occurred inside a fence of just 130 hectares (DEHP 2016a). While the decision to create an insurance population is sound, given the spatial requirements of northern hairy-nosed wombats and densities observed at the Epping population (DEHP 2016b), the new population at Richard Underwood reserve will be severely limited in its capacity to grow to a size where risk of demographic failure is acceptably low. In Chapter 3, I demonstrated how the movement ecology of woylies can vary dramatically not only across a species’ geographic range, but in two comparable populations. This uncertainty needs to be incorporated into predictions of population size for a new project, so that demographic viability is enhanced through conservative predictions of population size.

6.3 Managing mammals in a broader landscape
Many critical weight range mammals are fossorial, and played important ecosystem roles of increasing soil turnover (James and Eldridge 2007, James et al. 2009, James et al. 2010). These species were once widespread, and their disappearance has left much of Australia depauperate of its original mammal species richness (McKenzie et al. 2007b). While fences may be highly effective at abating the threat of predation and provide a mechanism for securing species from the immediate threat of extinction, implementation at a scale that represents even a fraction of many species’ former distribution is logistically infeasible. Due to the ongoing legacy costs of the Australian fencing network, ideally no more fences than what is absolutely necessary to secure Australian mammals against immediate extinction risk will be constructed. Landscape scale recovery of Australia’s mammals therefore requires alternative predator control methods to fencing alone.

Poison baiting campaigns can reduce feral predator abundance and lead to recovery of threatened species across the landscape (Glen et al. 2007). Currently, large scale baiting programs such as Western Shield
(Armstrong 2004) in the south-western corner of Western Australia are the only predator control strategy operating on landscape scales. While baiting, in comparison with fencing, offers a chance of operating at a landscape scale, it is beset by variable and uncertain predator control outcomes. To be effective, baiting programs must operate at a sufficient spatial scale as to cover immediately dispersing predators (Thomson et al. 2000), and be consistent in their application (Gentle et al. 2007). They must therefore be implemented through structured, systematic programs, requiring considerable logistic and financial coordination and commitment over the long term. My work in Chapter 5 further supports these findings as spontaneous, ad hoc baiting provided relatively little benefit in the long term compared to structured, ongoing baiting programs.

While often effective, fencing and baiting are not the only mechanisms for controlling invasive predators. The current debate around top down predator control shows promise under specific circumstances. When and where this might be effective needs to be further investigated before it can be implemented widely or considered in an overall threatened species management strategy. For example, it has been discovered that predator control through poison baiting can lead to cats being released from suppression and predation by the higher order predators and actually increase in number in the wake of baiting programs (Priddel and Wheeler 2004, Groom 2010, Moseby et al. 2011, De Tores and Marlow 2012). As a consequence, many baiting programs have been less successful at averting native mammal declines than expected. Cats, unlike foxes, cannot be reliably controlled using conventional baiting methods (Doherty and Algar 2015, Letnic et al. 2015), and a single cat can cause the failure of a translocation or disproportionately impact established populations (Johnson et al. 1996). Therefore, while foxes may have caused the decline of many species (Woinarski et al. 2015), cats are perhaps rather widely preventing their recovery. Clearly, innovative solutions are required in systems where cats occur. For example, there is a suggestion that dingoes could be used as a control method for lower trophic level predators (Fleming et al. 2006, Claridge and Hunt 2008, Johnson and VanDerWal 2009, Allen et al. 2011a, b, Letnic et al. 2011).

Dingoes can suppress cats and foxes, both through direct predation and by influencing their behaviour (Newsome et al. 2001, Letnic et al. 2009). The supposition is that in the presence of dingoes, foxes and cats are controlled and that this will have meaningful implications for native threatened wildlife (Ritchie et al. 2012). While they almost certainly caused extinction and extirpation when they arrived 3500 years ago (Johnson 2006), the remaining species left in the landscape assumedly reached equilibrium with dingoes where they were able to persist in their presence.

While the idea of encouraging dingo populations across the broader landscape is gaining momentum (Glen 2012), there are some concerns. The preferred prey range of dingoes falls within the top end of the critical weight range (Corbett and Newsome 1987, Allen and Fleming 2012). Evidence for positive effects only exists in arid environments for in-situ populations of small prey weight species (Letnic et al. 2011). Dingoes have been observed to have direct negative impacts of larger prey species such as briddled-nailtail wallabies.
(Onychogalea fraenata). Finally, the equilibrium state that previously existed has been disrupted. For example, the maximum distance to water in east Australia is typically less than 10 km (Fensham and Fairfax 2008), where previously there would have been no permanent water across expansive landscapes. Extensive areas have been cleared for grazing, promoting populations of large macropods (Jonzén et al. 2005), which in turn influence dingo populations (Pople et al. 2000). The landscape first observed by European settlers is a distant memory of a former ecological system where relationships and ecological balances cannot be assumed to persist in the current context; such is the degree of European influence.

To many, dingoes are most likely a less objectionable choice than cats and foxes. The cost of promoting dingoes as a management action is also very low, given that with careful control of shooting and baiting, dingo populations will recover, thus providing a considerable opportunity for widespread, cost effective management. Also, threatened mammals are already extirpated from most of the landscapes in which we might encourage dingoes, such that the risk to remaining biodiversity is low. However, in the context of predator control for reintroduction purposes the use of offshore islands and the increasingly popular option of predator exclusion fencing remains the most reliable method of predator abatement.

6.4 Synopsis of research and future direction

My thesis demonstrates that significant improvements in cost-effectiveness for management of Australian mammals could be made through systematic conservation planning, and by strategic collection and incorporation of new ecological information. By treating fence translocations as a portfolio rather than a set of individual units, we can achieve significant improvements in conservation outcomes. Yet, the effect of environmental stochasticity and species interactions, particularly in multi-species translocations within fences, remains poorly understood. Furthermore, in these stochastic systems, increased ecological knowledge may not equate to a capacity to improve management effectiveness.

The way we currently implement baiting has almost certainly not been optimized for cost effectiveness. Some programs are overzealous in bait deployment, while others are too sporadic or insufficient in their spatial extent to be beneficial in terms of threatened species outcomes. Baiting practices in Australia generally need to be reviewed and assessed with best practice recommendations made at sufficient resolutions for practitioners to make informed decisions about how they bait. Furthermore, sporadic, short term baiting is a wasteful use of resources if positive long-term outcomes for threatened species are intended.

While this is the conclusion of my thesis, it is by no means the final chapter in Australian mammal conservation. Systematic conservation planning can greatly increase the efficiency of our conservation actions. A truly optimal management plan requires higher level governance and cooperation across organisations conducting building fences and managing across large landscapes to prevent wasteful redundancy and incomplete action across the full suite of threatened mammals. Uncertainties need to be
recognised and incorporated into management plans. An integrative action plan for the recovery of Australian mammals needs to be devised, starting with an Australia wide fence prioritization, and expanding to a multiple action recovery plan. Finally, greater collaboration between managers is required, where individual agencies act in manner that is complimentary to existing efforts, action needs to be implemented with long-term mindsets. Only when these factors are considered can we truly expect positive outcomes for Australia's mammals.
7 References


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## 8 Appendices

### 8.1 Appendix 1

List of databases used to create the historic occurrence dataset.

<table>
<thead>
<tr>
<th>Data source</th>
<th>URL (where applicable)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Museum of Victoria</td>
<td>NA</td>
</tr>
<tr>
<td>NT fauna database</td>
<td>NA</td>
</tr>
<tr>
<td>South Australian Museum</td>
<td><a href="http://www.environment.sa.gov.au/Science/Information_data/Biological_databases_of_South_Australia">http://www.environment.sa.gov.au/Science/Information_data/Biological_databases_of_South_Australia</a></td>
</tr>
<tr>
<td>Database</td>
<td>nasurveypublic</td>
</tr>
<tr>
<td>OZCAM: Online Zoological Collections of Australian Museums) Online national fauna database administered by the Australian Museum and contributed to by the major State and Territory museums</td>
<td><a href="http://www.ozcam.org.au/ozcam-data/">http://www.ozcam.org.au/ozcam-data/</a></td>
</tr>
<tr>
<td>Pers. comm. Ian Abbott (bridled nailtail wallaby records) and Ian Abbott’s publications on historical distributions of mammals</td>
<td>NA</td>
</tr>
<tr>
<td>British Museum of Natural History</td>
<td>NA</td>
</tr>
<tr>
<td>Liverpool Museum (UK)</td>
<td>NA</td>
</tr>
<tr>
<td>The Macleay Museum (University of Sydney)</td>
<td>NA</td>
</tr>
</tbody>
</table>
8.2 Appendix 2

(A) 

(B) 

(A) 

(B) 

(A) 

(B) 

(A) 

(B) 

Aepyrprymnus rufescens

Bettongia gaimardi

Bettongia penicillata
Dasyurus geoffroii

Isoodon auratus

Isoodon obesulus
Macrotis lagotis

Myrmecobius fasciatus

Perameles bougainville
(A) 

(Petrogale penicillata) 

(Niche Volume) 

(# Unique Locations) 

(B) 

(Petrogale xanthopus) 

(# New Unique Locations) 

(Year) 

1800 1850 1900 1950 2000 

122
Phascogale tapoatafa

Pseudocheirus occidentalis

Thylogale billardierii
Environmental niche accumulation curves (plot A) and new sampling information through time (plot B). The y axis of plot A depicts the total described niche space (arbitrary units), the x axis depicts the number of unique geographic location the species was recorded. The black points depict the average accumulation curve from 100 randomised arrangements with respect to the date recorded. The grey bounds depict the 95% quantiles of the randomly arranged data. The blue line depicts the accumulation of data arranged chronologically from oldest to newest. The red line depicts the accumulation of data arranged reverse chronological order, from newest to oldest. Plot B shows the number of unique localities where the species was recorded since European colonisation (1770 to present). The top plot shows the total number of records collected during each time bin. The bottom plot shows the number of new 10x10km cells to acquire a record, starting from the oldest records first.
8.3 Appendix 3
Nightly BB50 kernels for each woylies over the same spatial extent. The black bar is 1km.

B01 Brownian bridge nightly 50% kernels

B02 Brownian bridge nightly 50% kernels
B03 Brownian bridge nightly 50% kernels

B04 Brownian bridge nightly 50% kernels
C12 Brownian bridge nightly 50% kernels

C13 Brownian bridge nightly 50% kernels
C14 Brownian bridge nightly 50% kernels

C15 Brownian bridge nightly 50% kernels
Appendix 4
Mathematical definition of the benefit function

We need to choose the fence locations that will provide the greatest aggregate benefit to conservation. Clearly fences should be sited in areas that would provide suitable habitat for a large number of species that are threatened by invasive predation (Figure 4.1). However, the optimal choice is not as simple as overlaying suitability maps and choosing a set of hotspots. The current levels of overrepresentation in the fence portfolio can only be rectified, and future issues avoided, if the presence of each species is modified by a series of filters. First, we need to modify the value of each species by taking into account their current conservation status. Second, we need to correct the species richness of each site by the existing representation of those species in conservation management projects elsewhere – that is, we need to take complementarity into account. Finally, we need to consider the risk of full or partial project failure, a serious and acknowledged problem for threatened species translocations (IUCN/SSC, 2013; Short 2009). In the section following, we integrate each of these factors into a single benefit function for a proposed fence.

Current conservation status: The benefits provided by a candidate fencing project can be measured in different ways. In general, we assume that the primary purpose of the fence is to minimise the extinction risk of species that are threatened by invasive predators. This goal is explicitly stated in the relevant state (the NSW National Parks & Wildlife Act 1974), federal (The Environment Protection and Biodiversity Conservation Act 1999) threatened species policy, and international protocols (the IUCN Red List of threatened species, Criterion E). We acknowledge, however, that fences can have other goals, such as the provision of ecosystem services (Miller et al. 2010), the recreation of extirpated communities (Shorthouse et al. 2012), or as ecotourism attractions (Daily and Ellison 2012).

We therefore define an extinction probability function \( P_e(N_s, T) \) that translates the current distribution of each threatened species to its probability of extinction over a given time period of \( T \) years. The vector \( N_s \) indicates the current population and distribution of each species:

\[
N_s = \{K_s^1, K_s^2, K_s^3, \ldots, K_s^{M_s}\}.
\]

(Eq. 1)

Each of the \( K_{s}^{m} \) values describes the carrying capacity of species \( s \) is the \( m^{th} \) population, where \( M_s \) is the number of existing populations of species \( s \). Ideally the function \( P_e(N_s, T) \) would be defined by species- and site-specific population viability analyses, but these are rarely available for even the best-researched threatened species (Reed et al. 2002). In their absence, we choose a general model of species extinction that includes both environmental and demographic stochasticity (Lande 1993; McCarthy et al. 2005). The constant annual probability of extinction of a single population with carrying capacity \( K \) is:

\[
P_e(N_s = (K), T = 1) = \frac{\sigma^2 b^2}{2K^b}
\]

(Eq. 2)

where \( \sigma^2 \) is the variance in the population growth rate (which has a mean of \( r \) and \( b = (2r/\sigma^2) - 1 \). By assuming that each population is independent, and that the populations are exposed to
uncorrelated catastrophic failure (e.g., fence breach, large fire or flood) with annual probability \( p_c \), we can calculate that the probability \( P_s \) of a set of populations \( N_s \) going extinct in \( T \) years is:

\[
P_s(N_s, T) = \prod_{m=1}^{M_s} \left( 1 - \left( 1 - \frac{\sigma^2 b^2}{2(K_s^m)^2} \right)^T \right) (1 - p_c)^T
\]

(Eq. 3)

We note that, in extending Eq. 2 to Eq. 3 we have assumed that all the populations are independent, and that the species’ extinction will occur when each local population has gone independently extinct. This assumption will be invalid if translocation is commonly used to re-colonise locally extirpated populations – that is, for managed metapopulations. If this assumption does not hold, our estimates of extinction probability will likely be over-estimates. We show this function in Figure S.1 for a range of population sizes, project times and catastrophic extinction probabilities \( p_c \).

Throughout the analyses that follow we have assumed a catastrophe probability of \( p_c = 0.05 \), an environmental variance of \( \sigma^2 = 1 \), a project period of 20 years, and a maximum per-capita population growth rate based on the estimates of Hone et al. (2010). For those NSW species where data did not exist, we substituted values from similar taxa provided by Hone et al. (2010).

Existing representation: Although we perform our analysis at the scale of NSW, we consider the distribution and abundance of each species across Australia in our assessment of complementarity. However, we acknowledge that the NSW government may have different values for species representation within NSW and outside. For example, the distribution of the greater bilby (\( Macrotis lagotis \)) historically extended into western NSW. Although the species is well represented in Australia’s fence portfolio and persists in portions of its historical habitat and therefore considered a low priority, it does not currently persist in the state of NSW. A decision-maker who was only interested in NSW representation could therefore legitimately consider greater bilbies a high priority for a new fence.

We include the existing distribution of each species in other locations by including extant populations of each species in the vector \( N_s \), used in Eq. 6. For example, western barred bandicoot (\( Perameles bougainville \)) are currently extant in four populations across Australia, with populations of 350, 900, 1500 and 500. For this species, this means \( M_s = 4 \) and \( N_s = \{350, 900, 1500, 500\} \).

Probability of translocation failure: We note that the additional fenced population will only contribute to the population viability if the translocation there is successful, and that this is not guaranteed. We therefore estimate for each candidate species, a probability of translocation success \( q_s \). We will assume that this value does not vary between fence sites, but does vary between species. We calculate each species’ probability of success based on the observed outcomes of all translocations of that species to date, using the mean value of the beta distribution \( B(1 + \theta, 1 + \phi) \) where \( \phi \) is the number of successful translocations and \( \theta \) is the number of failed translocations (Rout et al. 2009). For those species that have never been translocated, we use the mean probability
of the remaining species ($q = 0.73$). The probability of successful translocation for each species is shown in Figure 4.2.

**Integrating the elements of the benefit function:** The expected number of extinctions in $T$ years, across the set of threatened mammal species is calculated as:

$$\langle X \rangle = \sum_{s=1}^{S} P_e(N_s, T)$$

(Eq. 4)

where $S$ is the total number of listed species. Each candidate conservation fence will create new populations of a number of species (the ones that are suitable for the chosen location), of particular sizes (depending on the suitability of the fenced habitat for those species). This will effectively add a new element to the $N_s$ vectors that correspond to those species for which the fence contains suitable habitat. These new elements, $K_{sf}$, are based on the modelled habitat suitability of each candidate fence location, as described in Eq. X.

Substituting the new abundance vector into Eq. 1, conditional on successful translocation, we can calculate the expected number of extinctions in the presence of the new fence:

$$\langle X_f \rangle = \sum_{s=1}^{S} q_s \cdot P_e\left(\{N_s, K_{sf}\}, T\right) + \sum_{s=1}^{S} (1 - q_s) \cdot P_e(N_s, T)$$

(Eq. 5)

The optimal decision is therefore to fence the location $f$ that maximises:

$$\max_f [\langle X \rangle - \langle X_f \rangle]$$

(Eq. 6)

Because there are a reasonable and finite number of fence locations, it is possible to identify a single optimal fence location for Eq. 6 by exhaustive search. However, if managers plan to build multiple fences, finding the true optimal solution becomes difficult because the number of options increases combinatorially. When siting multiple fences, we use a greedy search heuristic, re-calculating each of the problem parameters each time. Specifically, after we identify the single best fence, we update the list of each species’ populations $N_s$ by adding the new fenced population. We then recalculate the predicted probability of extinction for each species, with and without all possible new fences. However, we no longer consider the site of the first chosen fence, on the assumption that managers will not want to site multiple fences close together, in case a single large-scale stochastic disturbance damages a large part of the portfolio. In our NSW example we exclude any locations within 25 km of a fence from the analyses.
References


### 8.5 Appendix 5

**Part A - Table of Values**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Value</th>
<th>Description</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rainfall</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R_{low}$</td>
<td>50</td>
<td>Average rainfall in a low rainfall year (mm quarter$^{-1}$)</td>
<td>Hilston Airport data</td>
</tr>
<tr>
<td>$\delta_{low}$</td>
<td>25</td>
<td>Variance of rainfall in a low rainfall year (mm quarter$^{-1}$)</td>
<td>Hilston Airport data</td>
</tr>
<tr>
<td>$R_{high}$</td>
<td>175</td>
<td>Average rainfall in a high rainfall year (mm quarter$^{-1}$)</td>
<td>Hilston Airport data</td>
</tr>
<tr>
<td>$\delta_{high}$</td>
<td>50</td>
<td>Variance of rainfall in a high rainfall year (mm quarter$^{-1}$)</td>
<td>Hilston Airport data</td>
</tr>
<tr>
<td><strong>Initial Values</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$V_0$ &amp; $V_0'$</td>
<td>300</td>
<td>Initial vegetation biomass (kg ha$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$I_0$</td>
<td>300</td>
<td>Initial invertebrate biomass (kg ha$^{-1}$)</td>
<td>Same value as vegetation</td>
</tr>
<tr>
<td>$N_0$</td>
<td>0.15</td>
<td>Initial baited rabbit population (rabbits ha$^{-1}$)</td>
<td>PH Model with no bilbies</td>
</tr>
<tr>
<td>$N_0'$</td>
<td>0.15</td>
<td>Initial surrounding rabbit population (rabbits ha$^{-1}$)</td>
<td>PH Model with no bilbies</td>
</tr>
<tr>
<td>$M_0$</td>
<td>0.08</td>
<td>Initial bilby population (bilbies ha$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$P_0$ &amp; $P_0'$</td>
<td>0.001</td>
<td>Initial fox populations (foxes ha$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td><strong>Change in Vegetation and Invertebrate Biomass</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$V_1(t)$ (and $I_1(t)$)</td>
<td>$-55.12 - 0.0153V(t-1) - 0.00056V(t-1)^2 + 2.5R(t)$</td>
<td>PH Model</td>
<td></td>
</tr>
<tr>
<td><strong>Foxes</strong></td>
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</tr>
<tr>
<td>$a_F$</td>
<td>0.56</td>
<td>Maximum rate of fox population decrease (quarter$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$c_F$</td>
<td>0.77</td>
<td>Sets maximum rate of fox population increase (quarter$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$d_F$</td>
<td>3.2</td>
<td>Demographic efficiency of foxes</td>
<td>PH Model</td>
</tr>
<tr>
<td>$P_{min}$</td>
<td>0.001</td>
<td>Minimum fox population (ha$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$i$</td>
<td>9.7</td>
<td>Fox immigration from surrounding region per quarter (%)</td>
<td>Thomson et al. 2000</td>
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<td>Variable</td>
<td>Value</td>
<td>Description</td>
<td>Source</td>
</tr>
<tr>
<td>----------</td>
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<tr>
<td>$k_N$</td>
<td>1096</td>
<td>Upper limit of fox consumption of rabbits (g day$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$w_N$</td>
<td>782</td>
<td>Average rabbit weight (g)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$D_{III}$</td>
<td>1.32</td>
<td>Density of rabbits at inflection point (rabbits ha$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$a_N$</td>
<td>4.6</td>
<td>Maximum rate of rabbit population decrease (quarter$^{-1}$)</td>
<td>PH Model</td>
</tr>
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<td>$c_N$</td>
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<td>Sets maximum rate of rabbit population increase (quarter$^{-1}$)</td>
<td>PH Model</td>
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<td>$d_N$</td>
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<td>Demographic efficiency of rabbits</td>
<td>PH Model</td>
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<td>$N_{min}$</td>
<td>0.08</td>
<td>Minimum rabbit population (ha$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$N'_{min}$</td>
<td>0.17</td>
<td>Minimum surrounding rabbit population (ha$^{-1}$)</td>
<td>PH Model</td>
</tr>
</tbody>
</table>

**Bilbies**

<table>
<thead>
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<th>Variable</th>
<th>Value</th>
<th>Description</th>
<th>Source</th>
</tr>
</thead>
<tbody>
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<td>$k_M$</td>
<td>1096</td>
<td>Upper limit of fox consumption of bilbies (g day$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$w_M$</td>
<td>782</td>
<td>Average bilby weight (g)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$D_{II}$</td>
<td>0.99</td>
<td>Constant determining slope for small $M$ (bilbies ha$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$a_M$</td>
<td>4.6</td>
<td>Maximum rate of bilby population decrease (quarter$^{-1}$)</td>
<td>PH Model</td>
</tr>
<tr>
<td>$c_M$</td>
<td>4.94</td>
<td>Sets maximum rate of bilby population increase (quarter$^{-1}$)</td>
<td>Hone 2010</td>
</tr>
<tr>
<td>$d_M$</td>
<td>0.0067</td>
<td>Demographic efficiency of bilbies</td>
<td>Calculated using 402 kg ha$^{-1}$ (from PH Model), $a_M$, and $c_M$</td>
</tr>
<tr>
<td>$M_{min}$</td>
<td>0.01</td>
<td>Minimum bilby population (ha$^{-1}$)</td>
<td>PH Model</td>
</tr>
</tbody>
</table>
Part B - Sequence of Calculations for Each Iteration of the Model

We describe here the calculations required for each iteration of the model, after rainfall data is generated. Each iteration represents 3 months.

Dynamics of surrounding habitat:

1. Vegetation growth \( (V') \)
   (i) Change in ungrazed pasture biomass per quarter
   \[
   V'_1(t) = -55.12 - 0.0153V'(t - 1) - 0.00056V'(t - 1)^2 + 2.5R(t)
   \]
   (ii) Normally distributed change in biomass \( \Delta V'(t) \) drawn from a normal distribution with a mean of \( V'_1(t) \) and standard deviation of 52 kg ha\(^{-1}\)
   (iii) Total ungrazed pasture biomass
   \[
   V'_2(t) = V'(t - 1) + V'_1(t) + \Delta V'(t)
   \]
   (iv) Pasture removed by rabbits
   \[
   C'_V(t) = (w_N)^{0.75} \times 0.068 \left(1 - e^{-V'_2(t)/138}\right) \times N'(t - 1) \times \left(\frac{365}{4}\right)
   \]
   (v) Pasture biomass at time \( t \)
   \[
   V'(t) = \max\left(0, V'_2(t) - C'_V(t)\right)
   \]

2. Rabbit population \( (N') \)
   (i) Predation rate per fox per day
   \[
   g'_P(t) = \left(k_N/w_N\right)N'^2(t - 1)/(N'^2(t - 1) + D'_{II})
   \]
   (ii) Total predation rate per rabbit per quarter
   \[
   G'_P(t) = \left(\frac{365}{4}\right)\left(g'_P(t)P'(t - 1)\right)/N'(t - 1)
   \]
   (iii) Net per capita rate of increase
   \[
   r'_{N,net} = -a_N + c_N \left(1 - e^{-d_NV'(t-1)}\right) - G'_P(t)
   \]
   (iv) Rabbit density at time \( t \)
   \[
   N'(t) = \max(N'_{min}, N'(t-1)e^{r'_{N,net}})
   \]

3. Fox population \( (P') \)
   (i) Rate of increase
   \[
   r'_P = -a_P + c_P \left(1 - e^{-d_PN'(t-1)}\right)
   \]
   (ii) Fox density at time \( t \)
   \[
   P'(t) = \max(P'_{min}, P'(t-1)e^{r'_P})
   \]
Dynamics of baited region:

4. Vegetation growth (V)
   (i) Change in ungrazed pasture biomass per quarter
   \[ V_1(t) = -55.12 - 0.0153V(t - 1) - 0.00056V(t - 1)^2 + 2.5R(t) \]
   (ii) Normally distributed change in biomass \( \Delta V(t) \) drawn from a normal distribution with a mean of \( V_1(t) \) and standard deviation of 52 kg ha\(^{-1}\)
   (iii) Total ungrazed pasture biomass
   \[ V_2(t) = V(t - 1) + V_1(t) + \Delta V(t) \]
   (iv) Pasture removed by rabbits
   \[ C_V(t) = (w_N)^{0.75} \times 0.068(1 - e^{-V_2(t)/138}) \times N(t - 1) \times (365/4) \]
   (v) Pasture biomass at time \( t \)
   \[ V(t) = \max(0, V_2(t) - C_V(t)) \]

5. Invertebrate growth (I)
   (i) Change in invertebrate biomass per quarter
   \[ I_1(t) = -55.12 - 0.0153I(t-1) - 0.00056I(t-1)^2 + 2.5R(t) \]
   (ii) Normally distributed change in biomass \( \Delta I(t) \) drawn from a normal distribution with a mean of \( I_1(t) \) and standard deviation of 52 kg ha\(^{-1}\)
   (iii) Total invertebrate biomass
   \[ I_2(t) = I(t - 1) + I_1(t) + \Delta I(t) \]
   (iv) Invertebrates removed by bilbies
   \[ C_I(t) = (w_N)^{0.75} \times 0.068(1 - e^{-I_2(t)/138}) \times M(t - 1) \times (365/4) \]
   (v) Invertebrate biomass at time \( t \)
   \[ I(t) = \max(0, I_2(t) - C_I(t)) \]

6. Rabbit population (N)
   (i) Predation rate per fox per day
   \[ g_P(t) = \frac{(k_N/w_N)N^2(t-1)/(N^2(t-1)+D_{III}^2)}{N(t-1)} \]
   (ii) Total predation rate per rabbit per quarter
   \[ G_P(t) = (365/4)\left(g_P(t)P(t-1)\right)/N(t-1) \]
   (iii) Net per capita rate of increase
   \[ r_{N,net} = -a_N + c_N(1 - e^{-d_NV(t-1)}) - G_P(t) \]
   (iv) Rabbit density at time \( t \)
   \[ N(t) = \max(N_{min}, N(t - 1)e^{r_{N,net}}) \]
7. Bilby population (M)
   (i) Predation rate per fox per day
       \[ h_P(t) = \frac{(k/w)M(t-1)}{(M(t-1) + D_{II})} \]
   (ii) Total predation rate per bilby per quarter
       \[ H_P(t) = \frac{(365/4)(h_P(t)P(t-1))(1 - g_P(t)/k_N)}{M(t-1)} \]
   (iii) Net per capita rate of increase
       \[ r_{M,net} = -a_M + c_M \left(1 - e^{-d_M(t-1)}\right) - H_P(t) \]
   (iv) Bilby density at time \( t \)
       \[ M(t) = \max(M_{min}, M(t-1)e^{r_{M,net}}) \]

8. Fox population (P)
   (i) Rate of increase
       \[ r_P = -a_P + c_P \left(1 - e^{-d_P N(t-1)}\right) \]
   (ii) Density dependent immigration rate
       if \( r'_P(t) > 0 \), then \( Ef = \Delta_1 \left(P'(t-1) - P(t-1)\right) \),
       otherwise \( Ef = \Delta_2 \left(P'(t-1) - P(t-1)\right) \)
   (iii) Altered minimum density of foxes
       if \( P(t-1) > P_{min} \), then \( P^*_{min} = P_{min} \),
       otherwise \( P^*_{min} = P(t-1) + Ef \)
   (iv) Fox density at time \( t \)
       \[ P(t) = \max(P^*_{min}, P(t-1)e^{r_P}) \]

Baiting control

9. Reduction of fox population (P)
   Define \( Prop[a,b] \) to be a continuous uniform distribution between \( a \) and \( b \).
   Reduction of fox population:
   if low, \[ P(t) = P(t) \times \left(1 - Prop[30, 50]\right) \]
   if medium, \[ P(t) = P(t) \times \left(1 - Prop[50, 70]\right) \]
   if high, \[ P(t) = P(t) \times \left(1 - Prop[75, 95]\right) \]
   otherwise \( P(t) \) unchanged