

# Is vegetation change a legacy of native mammal decline?

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Mills, Charlotte

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# **Is vegetation change a legacy of native mammal decline?**

Charlotte Helen Mills

A thesis submitted in fulfilment of the requirement for the degree of  
Doctor of Philosophy



School of Biological, Earth and Environmental Sciences

Faculty of Science

UNSW Sydney

Australia

**September 2019**

# Thesis Sheet

Surname/Family Name	: <b>MILLS</b>
Given Name/s	: <b>CHARLOTTE</b>
Abbreviation for degree as give in the University calendar	: <b>PhD</b>
Faculty	: <b>Science</b>
School	: <b>Biological, Earth and Environmental Sciences</b>
Thesis Title	: <b>Is vegetation change a legacy of native mammal decline?</b>

## Abstract 350 words maximum:

In this thesis, I discuss the global mammal extinction crisis and the role of rewilding programs in restoring ecological function to landscapes (Chapter 1). I draw attention to functional extinction and rewilding in an Australian context because the Australian arid zone mammal fauna has been decimated in the past 200 years. Consequently, our understanding of ecosystem function in Australian deserts is prone to shifting baselines because many paradigms were developed within depauperate mammal assemblages.

I used reserves to which functionally extinct mammals have been reintroduced to revisit paradigms about mammals being unimportant seed predators. I found that mammals were important seed predators, and that existing paradigms on seed fate (Chapter 2 & 3), shrub encroachment (Chapter 2) and myrmecochory (Chapter 3) are legacies of mammal functional extinction.

I used exclusion experiments to determine how rewilded and refuge populations of rare mammals influence the vegetation community (Chapter 4 & 5). I found that interactions between mammals and vegetation were more complicated than predicted from prior knowledge of these species' functional roles (Chapter 4) and that omnivores had unexpectedly strong effects on multiple food resources of varying protein content (Chapter 5).

Overall, I found that paradigms describing the function and organisation of Australia's deserts are legacies of mammal extinction and that the flow-on effects of mammal decline on vegetation and ecosystem function have been overlooked. However, I also found that the interactions between mammals, vegetation and the seedbank were complex.

To synthesise the findings within this thesis, I introduce the Resource-Pulse-Consumer-Compartment model to describe the multiple pathways by which omnivorous consumers influence resources, especially vegetation, in the Australian arid zone (Chapter 6). I recommend that future research investigating consumer – vegetation interactions do so across a variety of mammal assemblages and densities.

It is impossible to discuss the functional roles of mammals without considering the role that shifting baselines have played in our understanding of arid Australian ecosystems. With this in mind, I suggest that rewilding and other ecosystem restoration programs embrace the novel ecosystems that they are creating, instead of seeking a past for which there is no baseline.

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## **Preface**

This thesis consists of six chapters including an introductory chapter providing a background and context for the research which follows, four data chapters providing detailed original research completed as part of this doctoral thesis, and a concluding discussion chapter which summarises the research presented within the thesis.

Research chapters in this thesis are either published or submitted for publication in scientific journals. This has led to slight differences in the formatting of each chapter and repetition of the references as each chapter has its own reference list.

This research was conducted in accordance with UNSW ACEC approval (# 18/20A) and under South Australian DEW Scientific Licence (M26749-1).

This research was made possible through a Research Training Program Scholarship to CM. Funding for this research was provided by the Hermon Slade Foundation, the Ecological Consultants Association, the Ecological Society of Australia and the Holsworth Wildlife Endowment Fund.

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Finally, thank you to my supervisor, Mike. It has been a pleasure working with you for the past six years. Thank you for this opportunity, for your guidance, and for teaching me everything from crafting beautiful sentences to ocean fishing.



Mike and I never did get these buckets apart.

Photo credit: Nick Chu

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## **Abstract**

In this thesis, I discuss the global mammal extinction crisis and the role of rewilding programs in restoring ecological function to landscapes (Chapter 1). I draw attention to functional extinction and rewilding in an Australian context because the Australian arid zone mammal fauna has been decimated in the past 200 years. Consequently, our understanding of ecosystem function in Australian deserts is prone to shifting baselines because many paradigms were developed within depauperate mammal assemblages.

I used reserves to which functionally extinct mammals have been reintroduced to revisit paradigms about mammals being unimportant seed predators. I found that mammals were important seed predators, and that existing paradigms on seed fate (Chapter 2 & 3), shrub encroachment (Chapter 2) and myrmecochory (Chapter 3) are legacies of mammal functional extinction.

I used exclusion experiments to determine how rewilded and refuge populations of rare mammals influence the vegetation community (Chapter 4 & 5). I found that interactions between mammals and vegetation were more complicated than predicted from prior knowledge of these species' functional roles (Chapter 4) and that omnivores had unexpectedly strong effects on multiple food resources of varying protein content (Chapter 5).

Overall, I found that paradigms describing the function and organisation of Australia's deserts are legacies of mammal extinction and that the flow-on effects of mammal decline on vegetation and ecosystem function have been overlooked. However, I also found that the interactions between mammals, vegetation and the seedbank were complex.

To synthesise the findings within this thesis, I introduce the Resource-Pulse-Consumer-Compartment model to describe the multiple pathways by which omnivorous consumers influence resources, especially vegetation, in the Australian arid zone (Chapter 6). I recommend that future research investigating consumer – vegetation interactions do so across a variety of mammal assemblages and densities.

It is impossible to discuss the functional roles of mammals without considering the role that shifting baselines have played in our understanding of arid Australian ecosystems. With this in mind, I suggest that rewilding and other ecosystem restoration programs embrace the novel ecosystems that they are creating, instead of seeking a past for which there is no baseline.

## **Chapter 1: Introduction**

### **1.1 The global extinction crisis**

Global biodiversity is declining at an unprecedented pace (Bar-On, Phillips, & Milo, 2018; Seddon, Griffiths, Soorae, & Armstrong, 2014). The functional extinction of many keystone bird and mammal species has induced trophic cascades and evolutionary shifts with profound impacts on ecosystems (Anderson, Kelly, Ladley, Molloy, & Terry, 2011; Estes et al., 2011; Galetti et al., 2013; Lacher et al., 2019). Mammal extinction rates are accelerating and projected losses of not only species diversity, but also phylogenetic diversity (Davis, Faurby, & Svenning, 2018) and diversity in ecological strategies (Cooke, Eigenbrod, & Bates, 2019) further reduces the chance of recovery.

The current extinction rate is primarily due to anthropogenic impacts (Ceballos et al., 2015; Dirzo et al., 2014). Human activities and population growth have driven shifts in the biomass distribution on Earth from being dominated by wild animals, to being dominated by humans and the livestock that feed them (Bar-On et al., 2018). The wildlife which remains responds to the ubiquity of humans in the environment by shifting its behaviour to increase nocturnality (Gaynor, Hojnowski, Carter, & Brashares, 2018), reduce long-range movements (Tucker et al., 2018), reduce foraging time and increase cautious behaviour (Suraci, Clinchy, Zanette, & Wilmers, 2019) in areas of high human activity.

#### **1.1.1 Shifting baselines**

Shifting baseline syndrome, first coined by Pauly (1995), is a term used to describe the idea that accepted standards in ecosystem condition decline with each generation,



as people rely on their own experience as a baseline (Papworth, Rist, Coad, & Milner-Gulland, 2009; Soga & Gaston, 2018). In species conservation programs, the development of baselines or goals to which success is measured may be subject to shifting baselines (Soga & Gaston, 2018). This is especially the case where the historical ranges and abundances of locally extinct species are poorly understood, or where introduced species have become established and exert strong interactions within the remnant ecosystem (Estes et al., 2011; Legge et al., 2018).

Just as human activity has been the driver of global biodiversity loss, so too are humans best placed to halt or reverse biodiversity loss through conservation (Ceballos et al., 2015; Seddon et al., 2014). The success of contemporary conservation activities depends on active engagement and management by humans (Lacher et al., 2019; Shackelford et al., 2013) and therefore any definitions of baselines and goals are at inherent risk of shifting baselines. Paradoxically, one of the main mechanisms proposed to combat shifting baseline syndrome is to increase conservation activities, including rewilding (Soga & Gaston, 2018).

### 1.1.2 Rewilding

Rewilding is growing in popularity around the world as a strategy for restoring ‘wildness’ to a human dominated landscape (Fernández, Navarro, & Pereira, 2017; Svenning, Pedersen, Donlan, Ejrnæs, et al., 2015; Sweeney et al., 2019). In this thesis, “rewilding” is defined as the process of reintroducing species in order to restore ecosystem function (Seddon, Griffiths, Soorae, & Armstrong, 2014). Examples of rewilding in this context include: the reintroduction of wolves to their former range to restore their functions as apex predators (Ripple & Beschta, 2003); the use of ecological replacements such as replacing extinct tortoises in Mauritius

with ecologically similar species (Griffiths et al., 2010); and the reintroduction of digging animals to restore their soil turnover functions (James, Eldridge, & Hill, 2009). In situations such as those described above, rewilding is considered an important tool which conservation practitioners can use to address the direct and indirect effects of widespread species extinctions (Svenning, Pedersen, Donlan, Ejrnæs, et al., 2015).

However, since the term's original introduction (Soule & Noss, 1998), rewilding has been redefined several times and is now associated with several different ideas including: "passive rewilding", where ecosystems are left to grow without human intervention; "Pleistocene rewilding" (Donlan et al., 2005) where the baseline is set to a system many millennia ago; and "trophic rewilding" which explicitly refers to the restoration of top-down interactions (Svenning, Pedersen, Donlan, Ejrnæs, et al., 2015). There are voices of dissent who believe rewilding, with its range of definitions and very little empirical research, is a distraction from conservation endeavours (Rubenstein & Rubenstein, 2015) and only serves to cause confusion in the field of restoration (Hayward et al., 2019).

Another factor in rewilding which can cause confusion is that the baselines or goals used to monitor the success of rewilding programs are often unrealistic, unclear or entirely undefined (Seddon et al., 2014). Models which predict distributions and interactions can serve to inform rewilding programs but must be used with caution as it is impossible to know in advance what the outcomes of a project might be (Hunter, Britz, Jones, & Letnic, 2015). This is particularly the case for rewilding programs which include species that became functionally extinct before we understood their ecological functions, or where rewilding efforts involve the re-establishment of

multiple species into novel contexts (Fernández et al., 2017; Hunter et al., 2015). As such, there have been calls for increased empirical research (Svenning, Pedersen, Donlan, Ejrnaes, et al., 2015), closer monitoring (Schweiger, Boulangeat, Conradi, Davis, & Svenning, 2019), and increased caution as outcomes are difficult to predict when undertaking rewilding programs (Nogués-Bravo, Simberloff, Rahbek, & Sanders, 2016).

Of existing rewilding programs, much of the focus has been on returning large charismatic mammals, such as wolves, bears and bovids, to ecosystems. Owing to the high metabolic demands of individuals, these large animals have strong per capita effects as consumers and well documented ecological roles (Ripple et al., 2014; Seddon et al., 2014). In contrast, small mammals with low per capita metabolic demands but high population densities have largely been overlooked in rewilding efforts. However, there is growing evidence that the functional extinction of granivores, pollinators and ecosystem engineers, such as small mammals and birds, can reshape ecosystems because they can be important drivers of ecosystem dynamics (Anderson et al., 2011; Davidson, Detling, & Brown, 2012; Gordon & Letnic, 2016; James et al., 2009).

## 1.2 Mammal extinction in arid Australia

Australia has an appalling record of mammal extinctions. Since European arrival 230 years ago, around 30 mammal species have become extinct and many more have undergone dramatic range declines (Woinarski, Burbidge, & Harrison, 2015). Mammal extinction in Australia has been attributed to several inter-related factors. These include the introduction of novel predators the red fox (*Vulpes vulpes*) and cat (*Felis catus*) which decimated naïve native mammal species; competition and

destruction of habitat by introduced herbivores including European rabbits (*Oryctolagus cuniculus*), sheep, and cattle (Burbidge & McKenzie, 1989; Woinarski et al., 2015); and trophic cascades associated with the dogged extirpation of the top predator, the dingo (*Canis dingo*), particularly from the south east of the continent (Letnic, Ritchie, & Dickman, 2012).

Australia's mammal declines have been most severe in arid regions, where numerous species of native mammals, weighing between 35 - 5,500g, have become rare or extinct since European arrival. Two potentially important groups of mammals that have become functionally extinct across much of the Australian arid zone are digging marsupials and native rodents (Fleming et al., 2014; Woinarski et al., 2015).

Rodents and digging mammals are recognised globally as keystone species (Davidson et al., 2012; Delibes-Mateos, Smith, Slobodchikoff, & Swenson, 2011; Prugh & Brashares, 2012) for their role as herbivores, prey, and as ecosystem engineers (Davidson et al., 2012; Delibes-Mateos et al., 2011). Mammals that are now rare or extinct may once have been similarly important in Australia (Gordon & Letnic, 2016); however, we have very little knowledge of their functional roles in arid Australia.

#### 1.2.1 Shifting baselines in Australian ecology

The decimation of mammal fauna in the Australian arid zone preceded any contemporary understanding of their densities or functional roles. Consequently, our understanding of Australian desert ecosystems is prone to shifting baselines because it often relies on observations made in depauperate species assemblages (Caughley, Grigg, Caughley, & Hill, 1980; Morton, 1985). Legislative responsibilities for land

management programs in Australia are primarily state-based (Lockwood & Davidson, 2010), and because of the bureaucratic burden of duplicating applications for research permits in several states, most ecological research projects are conducted within only one state. It follows therefore that paradigms describing arid and semi-arid Australia may be informed by experiences that are isolated within one management area.

For example, in the sand-ridge habitats studied in this thesis, there are three alternate states of mammal assemblages, divided by state boundaries or rewilding programs. The first of these alternate states is depauperate of small and medium sized mammals (Chapters 2, 3) and is representative of much of the arid areas in south-eastern Australia. Here, the extirpation of the dingo has resulted in abundant large native herbivores (*Macropus* spp.; *Dromaius novaehollandiae*; Caughley et al., 1980), higher abundances of introduced predators such as foxes (*Vulpes vulpes*; Letnic, Koch, Gordon, Crowther, & Dickman, 2009), and the proliferation of introduced herbivores such as goats (*Capra hircus*) and European rabbits (Forsyth et al., 2019; Wallach, Johnson, Ritchie, & O'Neill, 2010). In turn, the release of mesopredators and large herbivores from top-down control by dingoes has contributed to the functional extinction of most small marsupial and native rodent species in the area through loss of habitat and elevated predation rates (Johnson, Isaac, & Fisher, 2006; Letnic, Koch, et al., 2009).

The second alternate state (Chapter 5) is one mediated by the top predator, the dingo. Where dingoes persist, large native and feral herbivores (*Macropus* spp., *D. novaehollandiae*, *C. hircus*) are scarce (Wallach et al., 2010), and mesopredators are suppressed (Letnic & Koch, 2010; Letnic, Koch, et al., 2009). Due to mesopredator

suppression, small marsupials and native rodents are released from predation and occur in relatively high abundances (Contos & Letnic, 2019; Johnson et al., 2006; Letnic, Crowther, & Koch, 2009). The introduced herbivore, the European rabbit, is also present.

The third state (Chapters 2, 3 & 4) is one where locally extinct native mammals have been intentionally rewilded into a reserve surrounded by a predator-proof fence.

Predator-proof fences demarcate a distinct management area within which introduced herbivores and predators are removed and native mammals are reintroduced, and is the main defence used to counter the ongoing threat to native mammals posed by introduced predators (Legge et al., 2018; Moseby & Read, 2006; Sweeney et al., 2019). Due to the depauperate nature of the surrounding landscape, the mammal assemblages within these rewilded reserves are often restricted to those which have been intentionally reintroduced, although in some cases there are pre-existing populations of mammals which also benefit from the absence of predators (Moseby, Hill, & Read, 2009).

### 1.2.2 Functional roles of mammals in arid Australia

The two most conspicuous changes in the Australian arid zone since European arrival are the loss of small and medium sized native mammals and the increase in kangaroos (Silcock & Fensham, 2019). Many paradigms describe the role of small and medium-sized mammals in arid zone seed and vegetation dynamics as unimportant (Brown, Reichman, & Davidson, 1979; Davidson & Morton, 1984; Morton, 1985). However, we have little understanding of the functional role that small and medium-sized mammals played in Australian desert ecosystems and therefore what changes may have occurred in the landscape as a legacy of their loss.

By comparison, there is now a considerable body of literature which describes the keystone role that the dingo plays in arid Australia, and the extensive trophic cascades that have resulted from its extirpation (Contos & Letnic, 2019; Fillios, Gordon, Koch, & Letnic, 2010; Gordon et al., 2017; Letnic, Koch, et al., 2009; Lyons, Mills, Gordon, & Letnic, 2018; Morris & Letnic, 2017; Rees, Kingsford, & Letnic, 2017; Rees, Rees, Kingsford, & Letnic, 2019).

The weak role played by mammals as seed predators in Australian desert ecosystems has previously been attributed to the absence of dietary specialist consumers with strong ecosystem effects (Murray, Dickman, Watts, & Morton, 1999). Instead, most Australian desert rodents are small-bodied omnivores (Van Dyck & Strahan, 2008) which feed across multiple trophic levels (Pimm & Lawton, 1978; Polis & Strong, 1996) and therefore are not expected to have strong effects on any one food resource (McCann & Hastings, 1997). In addition, small-bodied mammals are often overlooked as important consumers despite the marked ecosystem effects that small mammals can have when they occur at high densities (Davidson & Lightfoot, 2006; Gordon & Letnic, 2016; Olofsson, Hulme, Oksanen, & Suominen, 2004; Short, 1998).

Indeed, there is a considerable body of evidence showing that many species of now rare digging marsupials are ecosystem engineers which have important effects on soil health (Decker, Eldridge, & Gibb, 2019; Fleming et al., 2014). As digging marsupials forage for invertebrates, fungi and roots under the soil surface they create foraging pits which act as sinks for litter, nutrients and seeds (James et al., 2009; Valentine et al., 2017). Additionally, the soil disturbance and creation of foraging pits by digging marsupials improves soil function by reducing soil hardness,

increasing moisture retention and increasing litter turnover (Davies, Kirkpatrick, Cameron, Carver, & Johnson, 2019; Hayward et al., 2016; Valentine et al., 2017).

With increased nutrients and moisture, foraging pits are ideal sites for seed germination and seedling growth (James et al., 2009; Valentine et al., 2018).

However, very little is known about the functional role of digging marsupials as consumers. Similarly, little is known regarding how their functional roles as consumers and diggers interact (Silvey, Hayward, & Gibb, 2015; Verdon, Gibb, & Leonard, 2016).

In arid Australia, the endangerment and extinction of medium-sized marsupials and native rodents has coincided with an increase in density and cover of woody shrubs (Gordon et al., 2017; Noble, Hik, & Sinclair, 2007; Short & Smith, 1994). The cause of shrub encroachment is usually attributed to combined pressures of over-grazing by livestock, changed fire regimes and increasing CO<sub>2</sub> levels favouring the growth of shrubs over grasses (Archer, Schimel, & Holland, 1995). However, recent research shows that where native rodents persist, they are significant consumers of shrub seeds (Gordon & Letnic, 2016). Hence it has been hypothesised that the functional extinction of omnivorous mammals and resulting relaxation of granivory by these consumers may have relaxed a recruitment bottleneck that once limited shrub populations (Gordon et al., 2017; Noble et al., 2007). It is conceivable then, that current paradigms regarding the functional roles of now rare native mammals are a legacy of mammal declines (Morton, 1985). Therefore, it is possible that the functional extinction of small-bodied omnivorous mammals from the Australian arid zone has had widespread but previously unrecognised effects on vegetation communities (Gordon et al., 2017).



### 1.2.3 Rewilding in arid Australia

Rewilding efforts in arid Australia have focused on two main objectives which counteract the threats posed to native mammals by introduced predators (Sweeney et al., 2019). Firstly, the rewilding of the apex predator, the dingo, and restoration of mesopredator suppression effects it provides; and secondly the re-establishment of populations of medium-sized marsupials and native rodents within reserves enclosed by predator-proof fences (Legge et al., 2018; Moseby et al., 2009).

The rewilding of the dingo into parts of its former range consists primarily of proposals (Dickman, Glen, & Letnic, 2009; Newsome et al., 2015) which detail the benefits to wildlife and landscape function of reintroducing the dingo to south-eastern Australia. Benefits include the reinstatement of the dingo's mesopredator suppression effects, in turn releasing small mammals and reptiles from predation by foxes and cats (Letnic, Koch, et al., 2009), and the control via predation of overabundant native and feral herbivore populations (Morris & Letnic, 2017).

Top predators have documented strong effects in ecosystems (Letnic et al., 2012; Ripple & Beschta, 2003) and their widespread extirpation (Ripple et al., 2014) makes predators a popular target for rewilding projects globally (Ripple et al., 2014; Svenning, Pedersen, Donlan, Ejrnaes, et al., 2015). However, the most common driver for the initial extirpation of top predators, namely the predation of livestock, is often not resolved prior to the commencement of rewilding (Rubenstein & Rubenstein, 2015) and ongoing conflict can obstruct or delay rewilding efforts. This is certainly the case in Australia, where ongoing persecution of dingoes (Letnic et al., 2012) will continue to prevent the fruition of rewilding proposals for the foreseeable future.

Rewilding in arid Australia is focused on the restoration of medium-sized marsupials and native rodents and their ecological functions to predator-free fenced reserves (Legge et al., 2018; Sweeney et al., 2019). Predator-proof fencing is used as introduced predators are a continued threat to the survival of many native mammals (Legge et al., 2018; Woinarski et al., 2015). Many rare, medium-sized marsupials such as the Greater bilby (*Macrotis lagotis*), bettongs (*Bettongia* spp.) and bandicoots (Family: Peramelidae) are valued for the soil turnover functions described in the previous section (Fleming et al., 2014; James et al., 2009) and are a popular target of rewilding programs (Legge et al., 2018; Sweeney et al., 2019). In contrast, very little is known about the functional role of rodents in Australia (Gordon & Letnic, 2016) and they are under-represented in rewilding projects (Legge et al., 2018).

Many rewilded reserves in arid Australia are described as attempts to reconstruct mammal assemblages as they may have existed prior to European arrival (Moseby, Lollback, & Lynch, 2018). However, there are several factors which suggest that this may not be the case. Firstly, because many of these landscapes became depauperate rapidly after European arrival, we simply do not know the assemblages or densities at which these mammals once occurred. Indeed, a number of species in arid Australia are now completely extinct and cannot be replaced. Secondly, the ecosystems in which many predator-proof reserves are located have depauperate mammal assemblages and small native rodents especially are functionally extinct. As small native rodents are often overlooked in rewilding programs, many rewilded reserves have a marked absence in this functional group. However, where small mammal species persist, they benefit significantly from predator exclusion (Moseby et al., 2009).

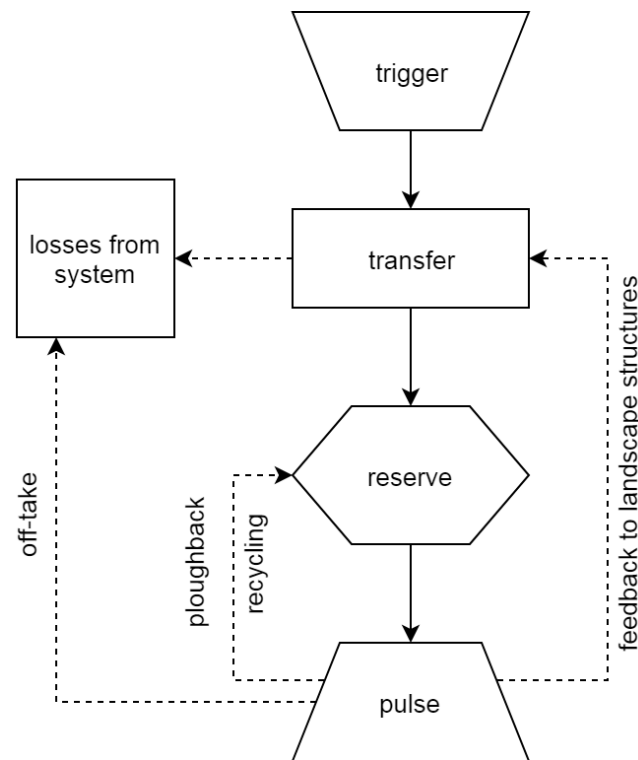
Finally, as a result of the risk posed to already limited populations of endangered wildlife, the small size of most reserves, and the depauperate condition of much of the arid zone, native mammalian predators such as dingoes and dasyurids (Family: Dasyuridae) are often absent from these predator-proof reserves (Moseby, Blumstein, & Letnic, 2016; Sweeney et al., 2019). Nonetheless, rewilded fenced exclosures provide important insights into the assemblages and functions of ecosystems prior to the declines of small and medium sized mammals.

### 1.3 Landscape function

In arid Australia, as in most deserts, rapid pulses of primary productivity are driven by irregular and unpredictable rainfall events which stimulate vegetation growth from a reserve of seeds and nutrients (Letnic & Dickman, 2010; Morton et al., 2011). Our current understanding of the function of arid landscapes is encapsulated by the trigger-transfer-reserve-pulse model (TTRPM; Noy-Meir 1973; Tongway & Ludwig 1997) which provides a framework for understanding how wind- and water- borne nutrients and litter can be transferred across the landscape during productivity pulses (Tongway & Ludwig, 1997). In the TTRPM (Fig. 1.1), the flow of nutrients and litter through the landscape is interrupted by vegetation patches which capture particles as they are carried past by wind or water. The vegetation patches then function as sinks for nutrients and litter to return to the reserve, and therefore the distribution of vegetation across the landscape can determine the distribution of resources and the ability of the landscape to respond during resource pulses.

The TTRPM is a useful tool to inform our knowledge of how animals interact with resource pulses (Morris & Letnic, 2017). By removing vegetation through herbivory, consumers such as large herbivores or rewilded mammals reduce the capacity for the

landscape to capture nutrients. Indeed, an overabundance of kangaroos and the consequent complete removal of ground cover has been associated with a reduction in soil nutrient pools in arid Australia (Morris & Letnic, 2017). On the other hand, rewilded digging mammals such as bettongs and bilbies may also increase the nutrient holding capacity of the landscape through the creation of foraging pits as detailed in section 1.2.2 (Decker et al., 2019; James et al., 2009; Valentine et al., 2018).



*Figure 1.1* The Trigger-Transfer-Reserve-Pulse framework describing the function of arid landscapes (Tongway & Ludwig, 1997).

## 1.4 Project aims and objectives

In this thesis, I aim to address the shifting baselines that apply to our understanding, or absence of understanding, of the functional role of mammals in arid Australia.

Many species of digging marsupials and native rodents became functionally extinct before we understood the roles they played in the ecosystem. By conducting foraging tray and exclosure experiments within areas that have been rewilded, areas that are depauperate, and areas within which small native mammals persist at high densities, I tease apart some of the complex interactions between now rare native mammals and vegetation dynamics in the Australian arid zone.

I use opportunities afforded by rewilding programs and natural refuges to reassess paradigms which were developed in depauperate ecosystems and which form the foundation of our understanding of the function and organisation of arid Australia (Davidson & Morton, 1984; Morton, 1985). I unravel the relationships between mammal assemblages and each species' effects on the vegetation community, and, I uncover how mammals in Australia's arid zone interact and adapt to the resource pulses which frame our current understanding of the desert (Letnic & Dickman, 2010; Morton et al., 2011; Tongway & Ludwig, 1997). My approach transcends the boundaries and alternate states which have until now produced isolated experiences of the Australian arid zone.

The experiments in this thesis are designed to partition the roles of different functional groups at my study sites, namely, native rodents, digging marsupials, and ants. To do this I make use of randomised block design in both my foraging tray and experimental exclosure experiments. The randomised block method provides a robust experimental test of my hypotheses about the impact of rare mammals on

plants and seeds. This design is practical in the field and is fully factorial to ensure that the effects of interest will be detected. In addition to the randomised block experimental design which features in all chapters, in Chapter 2 I compare results from the randomised block design across two contrasting mammal communities, providing a robust assessment of the functional roles held by taxa of interest.

In Chapters 2 and 3, I conduct foraging tray experiments inside and outside of fenced rewilded reserves in arid Australia to compare shrub seed removal in areas with abundant and areas with depauperate mammal assemblages. These experiments address long-standing paradigms concerning seed predation in the arid zone which describe mammals as insignificant seed predators in the deserts of Australia (Morton, 1985) and posit that the prevalence of ant-plant mutualisms (myrmecochory) in Australian plant species is not an adaptation to avoid seed predation (Davidson & Morton, 1984). Both of these paradigms are at odds with our understanding of similar systems overseas where mammals are important seed predators (Brown et al., 1979) and where myrmecochory is generally considered to be an adaptation to escape seed predation (Giladi, 2006). I hypothesise that paradigms describing mammals as unimportant seed predators in Australian deserts were artefacts of shifting baselines due to the functional extinction of mammals. In Chapter 2 I also relate mammal communities to the abundances of shrub seedlings to address the hypothesis that shrub encroachment may be a legacy of native mammal decline as mammals may have provided a recruitment bottleneck which once limited shrub populations (Gordon et al., 2017; Noble et al., 2007).

In Chapter 4, I use an exclusion experiment to investigate the effects that rewilding populations of the digging marsupial the burrowing bettong (*Bettongia lesueur*

*lesueur*) and the rodents, the spinifex hopping-mouse (*Notomys alexis*) and the plains mouse (*Pseudomys australis*) have on above ground vegetation and the seed bank using selective exclosure experiments in a rewilded reserve in arid Australia. I use prior knowledge of the role these mammals play as creators of foraging pits (James et al., 2009; Valentine et al., 2018) and the knowledge gained in Chapter 2 and 3 about their role as seed predators to inform the hypothesis that rewilded mammal activity would lead to greater vegetation cover but decrease the height of vegetation and cover of woody shrubs. This experiment provides a robust experimental test of the functional roles of omnivorous rewilded mammals as consumers and includes insights on the interspecific interactions which drive the observed patterns.

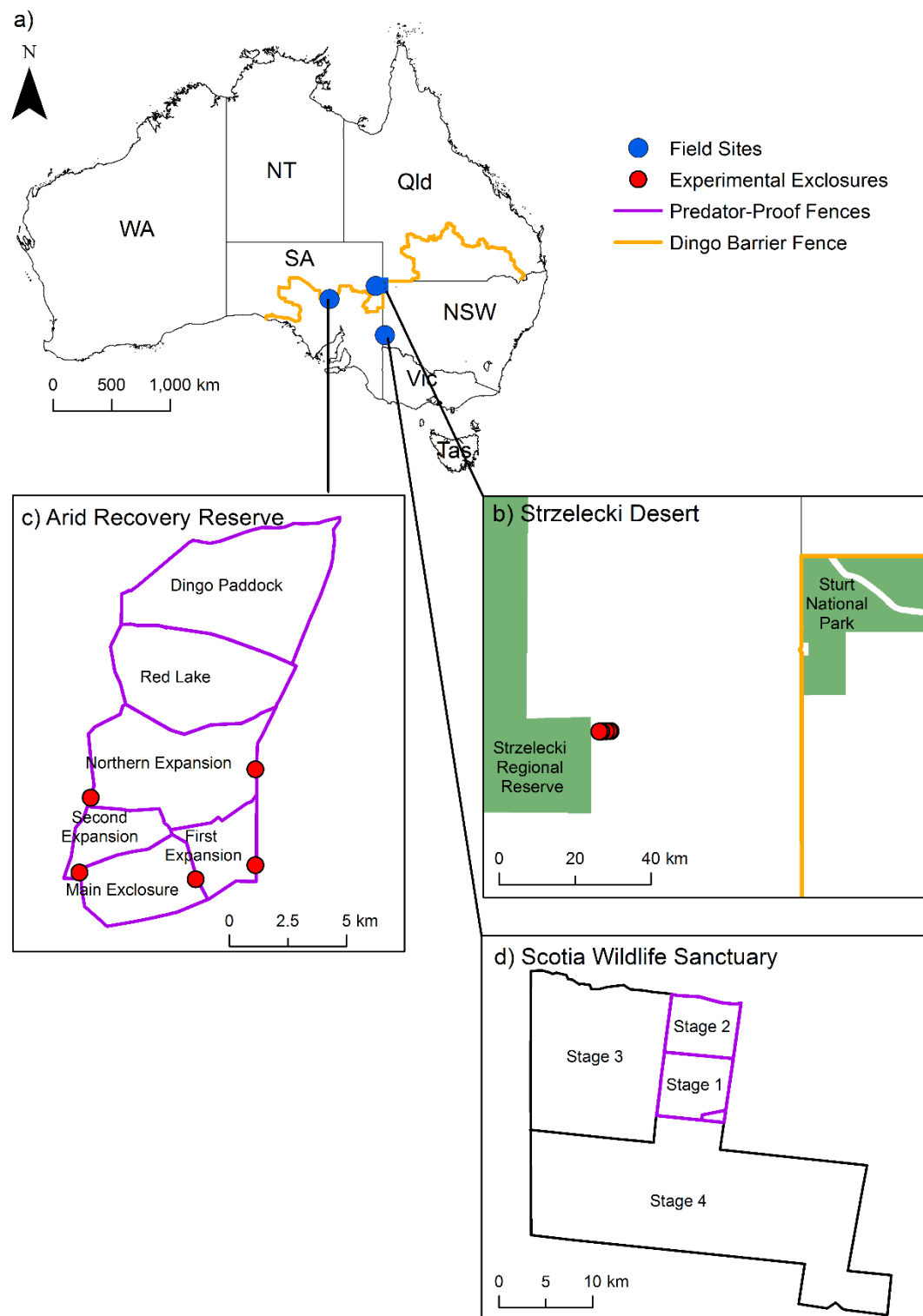
In Chapter 5, I test the strength of interactions between the omnivorous dusky hopping-mouse (*Notomys fuscus*) and its food resources to inform our understanding of how an omnivorous feeding strategy may confer benefits in a highly pulsed landscape (Murray & Dickman, 1994). Using an in-situ selective exclosure experiment and foraging tray experiments, I investigate the effects that the dusky hopping-mouse has on the composition of the seed bank, the composition of above ground vegetation, and the abundance of invertebrates, as well as potential macronutrient drivers for the observed effects. I hypothesise that the dusky hopping-mouse has strong effects on high protein food resources and weak effects on low protein food resources. Understanding the strength and drivers of interactions between omnivores and their prey is fundamental to understanding the functional role of omnivores within ecosystems (McCann & Hastings, 1997; Wootton, 2017) and therefore the potential for the loss of omnivorous mammals to drive vegetation change.

Finally, in Chapter 6, I summarise and synthesise my findings from each Chapter, discuss the limitations of the work in this thesis, and provide recommendations for future research into the interactions between native mammals and the vegetation community in arid Australia. The research contained within this thesis has significant implications for our understanding of shifting baselines and the consequences stemming from the functional extinction of native mammals in arid Australia. Therefore, I conclude this thesis with a discussion of how we can frame our understanding and perception of baselines, rewilding, and mammal assemblages in arid Australia going forward into the future.

#### 1.4.1 Study sites

The work in this thesis was conducted at three study sites (Fig 1.2): Scotia Wildlife Sanctuary (Chapters 2 & 3), Arid Recovery Reserve (Chapters 3 & 4) and in the Strzelecki Desert (Chapter 5). These locations offer unique opportunities to study the effects of mammals which have become extinct across the majority of the Australian arid zone. Both Scotia Wildlife Sanctuary and Arid Recovery are rewilded reserves surrounded by predator-proof fences inside of which locally extinct native mammals have been reintroduced after the eradication of introduced predators. The Strzelecki Desert is a natural refuge for a diverse range of native mammals, primarily due to the mesopredator and herbivore suppression effects of the apex predator, the dingo (Letnic et al., 2009). In many other places the dingo is subject to lethal control (as mentioned in Section 1.2) and mesopredators and herbivores are released from the top-down control the dingo provides.





*Figure 1.2* Map of study sites showing a) study site location within Australia; b) location of experimental enclosures in the Strzelecki Desert relative to conservation areas and the dingo barrier fence; c) Layout of Arid Recovery Reserve and location of experimental enclosures within the reserve; and d) Layout of Scotia Wildlife Sanctuary.

#### 1.4.1.1 Scotia Wildlife Sanctuary

Scotia Wildlife Sanctuary (Scotia) is operated by the not-for-profit organisation Australian Wildlife Conservancy in south-western New South Wales. Scotia is semi-arid with hot summers and cool winters (mean annual rainfall 286.5 mm; Wentworth; Australian Bureau of Meteorology 2016). Average daily minimum and maximum temperatures for March were 22 °C and 37 °C and for August 5.6 °C and 17 °C (Australian Bureau of Meteorology 2016). The dominant landforms of the fenced area and surrounding lands at Scotia are longitudinal sand dunes and loamy plains with an overstorey of basally sprouting *Eucalyptus* spp. (mallee) or *Casuarina pauper*, a midstorey of perennial shrubs and an understorey of *Triodia scariosa* or forbs (Fig. 1.3).

Scotia covers 650 km<sup>2</sup>, of which 80 km<sup>2</sup> is arranged into two predator-proof exclosures. Five species of medium sized mammals (300 - 600 g) have been successfully rewilded to Scotia: *Onychogalea fraenata*, *Bettongia lesueur*, *Bettongia penicillata*, *Macrotis lagotis* and *Myrmecobius fasciatus*. Local rodent fauna is depauperate. Small mammals (body mass < 30 g) present are the insectivorous dasyurids *Ningaui yvonneai* and *Sminthopsis* spp., the uncommon rodent *Pseudomys bolami* and the introduced *Mus musculus*. All areas of Scotia have been destocked since its establishment in 1994 as a wildlife sanctuary.



*Figure 1.3* Vegetation and landform typical of Scotia Sanctuary, with predator-proof fence featuring in left-hand side of photo.

#### *1.4.1.2 Arid Recovery Reserve*

Arid Recovery is situated near Roxby Downs in arid South Australia (mean annual rainfall 149.9 mm; Roxby Downs; Australian Bureau of Meteorology 2016).

Average daily minimum and maximum temperatures during the March survey period were 16 °C and 29.5 °C and during August 6.3 °C and 24 °C (Australian Bureau of Meteorology 2016). Dominant landforms at Arid Recovery include longitudinal sand dunes with clay swales. Vegetation in the exclosures and surrounding areas consists of perennial shrubs with grass and forb understorey (Fig. 1.4). The land encompassing Arid Recovery and its immediate surroundings is on a mining lease that has been destocked for over 20 years.

The fenced area at Arid Recovery Reserve encompasses a total area of 123 km<sup>2</sup>, split into six separate exclosures of varying dimensions. Of this, 60 km<sup>2</sup> is the main reintroduction area and is completely free of introduced mammals including *Vulpes vulpes*, *Felis catus* and *Oryctolagus cuniculus* (European rabbit). Four mammal species have been successfully rewilded to Arid Recovery (*Bettongia lesueur*, *Macrotis lagotis*, *Leporillus conditor*, *Perameles bougainville*) and a number of others such as *Notomys alexis* and *Pseudomys australis* have benefited from the exclusion of predators (Moseby et al. 2009).



*Figure 1.4* Vegetation and landform typical of Arid Recovery, with predator-proof fence featuring in left-hand side of photo.

#### *1.4.1.3 Strzelecki Desert*

Our study sites in the Strzelecki Desert are located on the cattle stations Lindon (29.127069° S, 140.901921° E) and Quinyambie (29.670592° S, 140.528015° E), in the Simpson-Strzelecki Dunefield in north-east South Australia (mean annual rainfall 200 mm; Australian Bureau of Meteorology 2016). The paddocks in which we

conducted our research were used for grazing cattle at low densities (0.1-2.85 cattle per km<sup>2</sup>). The mean annual maximum and minimum temperatures at the closest weather station (Tibooburra Airport, 29.43° S, 142.01° E) are 28 °C and 15 °C respectively (Australian Bureau of Meteorology 2016). The dominant landforms in the Strzelecki Desert are longitudinal sand dunes with clay swales. Vegetation consists of perennial shrubs with grass and forb understorey (Fig. 1.5).



*Figure 1.5* Vegetation and landform typical of the Strzelecki Desert.

The most abundant small mammal species present at the Strzelecki Desert study sites is *Notomys fuscus* (body mass 35 g), occurring at abundances 20 – 70 times higher than any other small mammal species (Rees, Rees, Kingsford, & Letnic, 2019). Other small mammals that occur in the study sites include the native rodents *Pseudomys australis*, *Pseudomys hermannsbergensis*, *Pseudomys desertor* and *Rattus villosissimus*, the marsupial Dasyurids *Sminthopsis crassicaudata*, *Sminthopsis macroura* and *Dasycercus cristicauda*, and the introduced rodent *Mus*

*musculus*. The introduced herbivore the European rabbit (*Oryctolagus cuniculus*) is also present.

## 1.5 References

- Anderson, S. H., Kelly, D., Ladley, J. J., Molloy, S., & Terry, J. (2011). Cascading effects of bird functional extinction reduce pollination and plant density. *Science*, **331**, 1068–1071. doi: 10.1126/science.1199092
- Archer, S., Schimel, D. S., & Holland, E. A. (1995). Mechanisms of shrubland expansion: land use, climate or CO<sub>2</sub>? *Climatic Change*, **29**, 91–99.
- Australian Bureau of Meteorology (2016). Retrieved from <http://www.bom.gov.au/> (Accessed 20 June 2016)
- Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences*, **115**, 6506–6511. doi: 10.1073/pnas.1711842115
- Brown, J. H., Reichman, O. J., & Davidson, D. W. (1979). Granivory in desert ecosystems. *Annual Review of Ecology and Systematics*, **10**, 201–227.
- Burbidge, A. A., & McKenzie, N. L. (1989). Patterns in the modern decline of western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation*, **50**, 143–198. doi: 10.1016/0006-3207(89)90009-8
- Caughley, G., Grigg, G. C., Caughley, J., & Hill, G. J. E. (1980). Does dingo predation control the densities of kangaroos and emus? *Wildlife Research*, **7**, 1–12. doi: 10.1071/WR9800001
- Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances*, **1**, 9–13. doi: 10.1126/sciadv.1400253
- Contos, P., & Letnic, M. (2019). Top-down effects of a large mammalian carnivore in arid Australia extend to epigeic arthropod assemblages. *Journal of Arid Environments*, **165**, 16–27.

- Cooke, R. S. C., Eigenbrod, F., & Bates, A. E. (2019). Projected losses of global mammal and bird ecological strategies. *Nature Communications*, **10**, 2279. doi: 10.1038/s41467-019-10284-z
- Davidson, A. D., Detling, J. K., & Brown, J. H. (2012). Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment*, **10**, 477–486. doi: 10.1890/110054
- Davidson, A. D., & Lightfoot, D. C. (2006). Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography*, **29**, 755–765.
- Davidson, D. W., & Morton, S. R. (1984). Dispersal adaptations of some Acacia species in the Australian arid zone. *Ecology*, **65**, 1038–1051. doi: 10.2307/1938312
- Davies, G. T. O., Kirkpatrick, J. B., Cameron, E. Z., Carver, S., & Johnson, C. N. (2019). Ecosystem engineering by digging mammals: effects on soil fertility and condition in Tasmanian temperate woodland. *Royal Society Open Science*, **6**, 180621. doi: 10.1098/rsos.180621
- Davis, M., Faurby, S., & Svenning, J.-C. (2018). Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proceedings of the National Academy of Sciences*, **115**, 11262–11267. doi: 10.1073/pnas.1804906115
- Decker, O., Eldridge, D. J., & Gibb, H. (2019). Restoration potential of threatened ecosystem engineers increases with aridity: broad scale effects on soil nutrients and function. *Ecography*, **42**, 1–13. doi: 10.1111/ecog.04259
- Delibes-Mateos, M., Smith, A. T., Slobodchikoff, C. N., & Swenson, J. E. (2011). The paradox of keystone species persecuted as pests: A call for the conservation of abundant small mammals in their native range. *Biological Conservation*, **144**, 1335–1346. doi: 10.1016/j.biocon.2011.02.012
- Dickman, C. R., Glen, A. S., & Letnic, M. (2009). Reintroducing the dingo: can



- Australia's conservation wastelands be restored? In M. W. Hayward & M. J. Somers (Eds.), *Reintroduction of Top-Order Predators* (pp. 238–269). doi: 10.1002/9781444312034.ch11
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, **345**, 401–406. doi: 10.1126/science.1251817
- Donlan, J., Greene, H. W., Berger, J., Bock, C. E., Bock, J. H., Burney, D. A., ... Soulé, M. E. (2005). Re-wilding North America. *Nature*, **436**, 913–914.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, **333**, 301–306. doi: 10.1126/science.1205106
- Fernández, N., Navarro, L. M., & Pereira, H. M. (2017). Rewilding: a call for boosting ecological complexity in conservation. *Conservation Letters*, **10**, 276–278. doi: 10.1111/conl.12374
- Fillios, M., Gordon, C., Koch, F., & Letnic, M. (2010). The effect of a top predator on kangaroo abundance in arid Australia and its implications for archaeological faunal assemblages. *Journal of Archaeological Science*, **37**, 986–993. doi: 10.1016/j.jas.2009.11.031
- Fleming, P. A., Anderson, H., Prendergast, A. S., Bretz, M. R., Valentine, L. E., & Hardy, G. E. S. (2014). Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Review*, **44**, 94–108. doi: 10.1111/mam.12014
- Forsyth, D. M., Latham, A. D. M., Davis, N. E., Caley, P., Letnic, M., Moloney, P. D., ... Woolnough, A. P. (2019). Interactions between dingoes and introduced wild ungulates: Concepts, evidence and knowledge gaps. *Australian Mammalogy*, **41**, 12–26. doi: 10.1071/AM17042
- Galetti, M., Guevara, R., Cortes, M. C., Fadini, R., Von Matter, S., Leite, A. B., ... Jordano, P. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, **340**, 1086–1091.



- Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, **360**, 1232–1235. doi: 10.1126/science.aar7121
- Giladi, I. (2006). Choosing benefits or partners: A review of the evidence for the evolution of myrmecochory. *Oikos*, **112**, 481–492. doi: 10.1111/j.0030-1299.2006.14258.x
- Gordon, C. E., Eldridge, D. J., Ripple, W. J., Crowther, M. S., Moore, B. D., & Letnic, M. (2017). Shrub encroachment is linked to extirpation of an apex predator. *Journal of Animal Ecology*, **86**, 147–157. doi: 10.1111/1365-2656.12607
- Gordon, C. E., & Letnic, M. (2016). Functional extinction of a desert rodent: implications for seed fate and vegetation dynamics. *Ecography*, **39**, 815–824. doi: 10.1111/ecog.01648
- Griffiths, C. J., Jones, C. G., Hansen, D. M., Puttoo, M., Tatayah, R. V., Muller, C. B., & Harris, S. (2010). The use of extant non-indigenous tortoises as a restoration tool to replace extinct ecosystem engineers. *Restoration Ecology*, **18**, 1–7. doi: 10.1111/j.1526-100X.2009.00612.x
- Hayward, M. W., Scanlon, R. J., Callen, A., Howell, L. G., Klop-Toker, K. L., Di Blanco, Y., ... Weise, F. J. (2019). Reintroducing rewilding to restoration – rejecting the search for novelty. *Biological Conservation*, **233**, 255–259. doi: 10.1016/j.biocon.2019.03.011
- Hayward, M. W., Ward-Fear, G., L’Hotellier, F., Herman, K., Kabat, A. P., & Gibbons, J. P. (2016). Could biodiversity loss have increased Australia’s bushfire threat? *Animal Conservation*, **19**, 490–497. doi: 10.1111/acv.12269
- Hunter, D. O., Britz, T., Jones, M., & Letnic, M. (2015). Reintroduction of Tasmanian devils to mainland Australia can restore top-down control in ecosystems where dingoes have been extirpated. *Biological Conservation*, **191**, 428–435. doi: 10.1016/j.biocon.2015.07.030
- James, A. I., Eldridge, D. J., & Hill, B. M. (2009). Foraging animals create fertile

patches in an Australian desert shrubland. *Ecography*, **32**, 723–732. doi: 10.1111/j.1600-0587.2009.05450.x

Johnson, C. N., Isaac, J. L., & Fisher, D. O. (2006). Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 341–346. doi: 10.1098/rspb.2006.3711

Lacher, T. E., Davidson, A. D., Fleming, T. H., Emma, P. G., Gary, F., Owen-Smith, N., ... Wall, S. B. Vander. (2019). The functional roles of mammals in ecosystems. *Journal of Mammalogy*, **100**, 942–964. doi: 10.1093/jmammal/gyy169

Legge, S., Woinarski, J. C. Z., Burbidge, A. A., Palmer, R., Ringma, J., Radford, J. Q., ... Tuft, K. D. (2018). Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. *Wildlife Research*, **45**, 627–644. doi: 10.1071/WR17172

Letnic, M., Crowther, M. S., & Koch, F. (2009). Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? *Animal Conservation*, **12**, 302–312. doi: 10.1111/j.1469-1795.2009.00250.x

Letnic, M., & Dickman, C. R. (2010). Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews*, **85**, 501–521. doi: 10.1111/j.1469-185X.2009.00113.x

Letnic, M., & Koch, F. (2010). Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology*, **35**, 167–175. doi: 10.1111/j.1442-9993.2009.02022.x

Letnic, M., Koch, F., Gordon, C., Crowther, M. S., & Dickman, C. R. (2009). Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3249–3256. doi: 10.1098/rspb.2009.0574

- Letnic, M., Ritchie, E. G., & Dickman, C. R. (2012). Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews*, **87**, 390–413. doi: 10.1111/j.1469-185X.2011.00203.x
- Lockwood, M., & Davidson, J. (2010). Environmental governance and the hybrid regime of Australian natural resource management. *Geoforum*, **41**, 388–398. doi: 10.1016/j.geoforum.2009.12.001
- McCann, K., & Hastings, A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society B: Biological Sciences*, **264**, 1249–1254.
- Morris, T., & Letnic, M. (2017). Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20170111. doi: 10.1098/rspb.2017.0111
- Morton, S. R. (1985). Granivory in arid regions: comparison of Australia with North and South America. *Ecology*, **66**, 1859–1866. doi: 10.2307/2937381
- Morton, S. R., Stafford Smith, D. M., Dickman, C. R., Dunkerley, D. L., Friedel, M. H., McAllister, R. R. J., ... Westoby, M. (2011). A fresh framework for the ecology of arid Australia. *Journal of Arid Environments*, **75**, 313–329. doi: 10.1016/j.jaridenv.2010.11.001
- Moseby, K. E., Blumstein, D. T., & Letnic, M. (2016). Harnessing natural selection to tackle the problem of prey naïveté. *Evolutionary Applications*, **9**, 334–343. doi: 10.1111/eva.12332
- Moseby, K. E., Hill, B. M., & Read, J. L. (2009). Arid Recovery - A comparison of reptile and small mammal populations inside and outside a large rabbit, cat and fox-proof enclosure in arid South Australia. *Austral Ecology*, **34**, 156–169. doi: 10.1111/j.1442-9993.2008.01916.x
- Moseby, K. E., Lollback, G. W., & Lynch, C. E. (2018). Too much of a good thing; successful reintroduction leads to overpopulation in a threatened mammal. *Biological Conservation*, **219**, 78–88. doi: 10.1016/j.biocon.2018.01.006

- Moseby, K. E., & Read, J. L. (2006). The efficacy of feral cat, fox and rabbit exclusion fence designs for threatened species protection. *Biological Conservation*, **127**, 429–437. doi: 10.1016/j.biocon.2005.09.002
- Murray, B. R., & Dickman, C. R. (1994). Granivory and microhabitat use in Australian desert rodents: are seeds important? *Oecologia*, **99**, 216–225. doi: 10.1007/BF00627733
- Murray, B. R., Dickman, C. R., Watts, C. H. S., & Morton, S. R. (1999). The dietary ecology of Australian desert rodents. *Wildlife Research*, **26**, 857–858. doi: 10.1071/WR97046\_CO
- Newsome, T. M., Ballard, G.-A., Crowther, M. S., Dellinger, J. A., Fleming, P. J. S., Glen, A. S., ... Dickman, C. R. (2015). Resolving the value of the dingo in ecological restoration. *Restoration Ecology*, **23**, 201–208. doi: 10.1111/rec.12186
- Noble, J. C., Hik, D. S., & Sinclair, A. R. E. (2007). Landscape ecology of the burrowing bettong: fire and marsupial biocontrol of shrubs in semi-arid Australia. *The Rangeland Journal*, **29**, 107–119.
- Nogués-Bravo, D., Simberloff, D., Rahbek, C., & Sanders, N. J. (2016). Rewilding is the new Pandora's box in conservation. *Current Biology*, **26**, R87–R91. doi: 10.1016/j.cub.2015.12.044
- Noy-Meir, I. (1973). Desert ecosystems: environment and producer. *Annual Review of Ecology and Systematics*, **4**, 25–51.
- Olofsson, J., Hulme, P. E., Oksanen, L., & Suominen, O. (2004). Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos*, **106**, 324–334. doi: 10.1111/j.0030-1299.2004.13224.x
- Papworth, S. K., Rist, J., Coad, L., & Milner-Gulland, E. J. (2009). Evidence for shifting baseline syndrome in conservation. *Conservation Letters*, **2**, 93–100. doi: 10.1111/j.1755-263X.2009.00049.x
- Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution*, **10**, 430.

- Pimm, S. L., & Lawton, J. H. (1978). On feeding on more than one trophic level. *Nature*, **275**, 542–544. doi: 10.1038/275542a0
- Polis, G. A., & Strong, D. R. (1996). Food web complexity and community dynamics. *The American Naturalist*, **147**, 813–846.
- Prugh, L. R., & Brashares, J. S. (2012). Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. *Journal of Animal Ecology*, **81**, 667–678. doi: 10.1111/j.1365-2656.2011.01930.x
- Rees, J. D., Kingsford, R. T., & Letnic, M. (2017). In the absence of an apex predator, irruptive herbivores suppress grass seed production: implications for small granivores. *Biological Conservation*, **213**, 13–18. doi: 10.1016/j.biocon.2017.06.037
- Rees, J. D., Rees, G. L., Kingsford, R. T., & Letnic, M. (2019). Indirect commensalism between an introduced apex predator and a native avian predator. *Biodiversity and Conservation*, **28**, 2687–2700. doi: 10.1007/s10531-019-01787-8
- Ripple, W. J., & Beschta, R. L. (2003). Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*, **184**, 299–313. doi: 10.1016/S0378-1127(03)00154-3
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484. doi: 10.1126/science.1241484
- Rubenstein, D. R., & Rubenstein, D. I. (2015). From Pleistocene to trophic rewilding: A wolf in sheep's clothing. *Proceedings of the National Academy of Sciences*, **113**, 201521757. doi: 10.1073/pnas.1521757113
- Schweiger, A. H., Boulangeat, I., Conradi, T., Davis, M., & Svenning, J. C. (2019). The importance of ecological memory for trophic rewilding as an ecosystem restoration approach. *Biological Reviews*, **94**, 1–15. doi: 10.1111/brv.12432

- Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, **345**, 406–412. doi: 10.1126/science.1251818
- Shackelford, N., Hobbs, R. J., Burgar, J. M., Erickson, T. E., Fontaine, J. B., Laliberté, E., ... Standish, R. J. (2013). Primed for change: developing ecological restoration for the 21st century. *Restoration Ecology*, **21**, 297–304. doi: 10.1111/rec.12012
- Short, J. (1998). The extinction of rat-kangaroos (Marsupialia: Potoroidae) in New South Wales, Australia. *Biological Conservation*, **86**, 365–377.
- Short, J., & Smith, A. (1994). Mammal decline and recovery in Australia. *Journal of Mammalogy*, **75**, 288–297. doi: 10.2307/1382547
- Silcock, J. L., & Fensham, R. O. D. J. (2019). Degraded or just dusty? Examining ecological change in arid lands. *BioScience*. doi: 10.1093/biosci/biz034
- Silvey, C. J., Hayward, M. W., & Gibb, H. (2015). Effects of reconstruction of a pre-European vertebrate assemblage on ground-dwelling arachnids in arid Australia. *Oecologia*, **178**, 497–509. doi: 10.1007/s00442-014-3189-y
- Soga, M., & Gaston, K. J. (2018). Shifting baseline syndrome: causes, consequences, and implications. *Frontiers in Ecology and the Environment*, **16**, 222–230. doi: 10.1002/fee.1794
- Soule, M. E., & Noss, R. E. (1998). Rewilding and biodiversity: complementary goals for continental conservation. *Wild Earth*, **8**, 18–28.
- Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*. doi: 10.1111/ele.13344
- Svenning, J.-C., Pedersen, P. B. M., Donlan, C. J., Ejrnæs, R., Faurby, S., Galetti, M., ... Vera, F. W. M. (2015). Reply to Rubenstein and Rubenstein: time to move on from ideological debates on rewilding. *Proceedings of the National Academy of Sciences*, **113**, 201521891. doi: 10.1073/pnas.1521891113
- Svenning, J.-C., Pedersen, P. B. M., Donlan, J., Ejrnaes, R., Faurby, S., Galetti, M.,

- ... Vera, F. W. M. (2015). Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences*, **113**, 898–906. doi: 10.1073/pnas.1502556112
- Sweeney, O. F., Turnbull, J., Jones, M., Letnic, M., Newsome, T. M., & Sharp, A. (2019). An Australian perspective on rewilding. *Conservation Biology*, **33**, 812–820. doi: 10.1111/cobi.13280
- Tongway, D., & Ludwig, J. (1997). The conservation of water and nutrients within landscapes. In J. Ludwig, D. Tongway, D. Freudenberger, J. Noble, & K. Hodgkinson (Eds.), *Landscape Ecology Function and Management* (pp. 13–23). Collingwood, Australia: CSIRO Publishing.
- Tucker, M. A., Böhning-gaese, K., Fagan, W. F., Fryxell, J. M., Moorter, B. Van, Alberts, S. C., ... Rimmler, M. (2018). Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science*, **469**, 466–469.
- Valentine, L. E., Bretz, M., Ruthrof, K. X., Fisher, R., Hardy, G. E. S. J., & Fleming, P. A. (2017). Scratching beneath the surface: bandicoot bioturbation contributes to ecosystem processes. *Austral Ecology*, **42**, 265–276. doi: 10.1111/aec.12428
- Valentine, L. E., Ruthrof, K. X., Fisher, R., Hardy, G. E. S. J., Hobbs, R. J., & Fleming, P. A. (2018). Bioturbation by bandicoots facilitates seedling growth by altering soil properties. *Functional Ecology*, **32**, 2138–2148. doi: 10.1111/1365-2435.13179
- Van Dyck, S. M., & Strahan, R. (Eds.). (2008). *The Mammals of Australia* (3rd ed.). Sydney: Reed New Holland.
- Verdon, S. J., Gibb, H., & Leonard, S. W. J. (2016). Net effects of soil disturbance and herbivory on vegetation by a re-established digging mammal assemblage in arid zone Australia. *Journal of Arid Environments*, **133**, 29–36. doi: 10.1016/j.jaridenv.2016.05.008
- Wallach, A. D., Johnson, C. N., Ritchie, E. G., & O'Neill, A. J. (2010). Predator control promotes invasive dominated ecological states. *Ecology Letters*, **13**, 1008–1018. doi: 10.1111/j.1461-0248.2010.01492.x

- Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences*, **112**, 4531–4540. doi: 10.1073/pnas.1417301112
- Wootton, K. L. (2017). Omnivory and stability in freshwater habitats: Does theory match reality? *Freshwater Biology*, **62**, 821–832. doi: 10.1111/fwb.12908



## **Chapter 2: Rewilded mammal assemblages reveal the missing ecological functions of granivores**

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Deploying seed trays

Photo credit: Dimpu Dhar

## 2.1 Abstract

Rewilding is a strategy for ecological restoration that uses reintroductions of animals to re-establish the ecological functions of keystone species. Globally, rewilding efforts have focused primarily on reinstating the ecological functions of charismatic megafauna. In Australia, rewilding efforts have focused on restoring the ecological functions of herbivorous and omnivorous rodents and marsupials weighing between 30-5000g inside of predator-proof exclosures.

In many arid ecosystems, mammals are considered the dominant seed predators. In Australia, ants are considered to be the primary seed removers and mammals insignificant seed removers. However, most research on granivory in Australian deserts has occurred in areas where native mammals were rare or functionally extinct.

Here, we compare rates of seed removal by mammals and ants on shrub seeds and abundance of shrub seedlings in two rewilded desert ecosystems (Arid Recovery Reserve and Scotia Sanctuary) with adjacent areas possessing depauperate mammal faunas. We used foraging trays containing seeds of common native shrubs (*Acacia ligulata* and *Dodonaea viscosa*) to examine rates of seed removal by ants and mammals. We quantified the abundance of *A. ligulata* and *D. viscosa* seedlings inside and outside of rewilded areas along belt transects.

By excluding ants and mammals from foraging trays, we show that ants removed more seeds than mammals where mammal assemblages were depauperate, but mammals removed far more seeds than ants in rewilded areas. Shrub seedlings were more abundant in areas with depauperate mammal faunas than in rewilded areas.

Our study provides evidence that rewilding of an Australian desert mammal assemblage has restored the hitherto unappreciated ecological function of omnivorous rodents and bettongs as seed predators. We hypothesize that loss of omnivorous mammals across arid Australia may have facilitated shrub encroachment in arid Australia.

We contend that rewilding programs aimed at restoring ecological processes should not ignore consumers with relatively lower per capita consumptive effects. This is because consumers with low per capita consumptive effects often occur at high population densities or perform critical ecological functions and thus can have significant population level impacts that can be harnessed for ecological restoration programs.

## 2.2 Introduction

Rewilding is a strategy for ecological restoration that uses species reintroductions to re-establish the ecological functions of keystone species (Seddon et al. 2014).

Keystone species have disproportionately strong direct and indirect effects on ecological networks (Mouquet et al. 2013; Svenning et al. 2015) and include apex predators, ecosystem engineers and pollinators (Gordon et al. 2017; Anderson et al. 2011). Much of the focus of rewilding programs has been on returning large charismatic mammals, such as wolves, bears and bovids to ecosystems. Owing to the high metabolic demands of individuals these large animals have strong per capita effects as consumers and well documented ecological roles (Ripple & Beschta 2003; Seddon et al. 2014). In contrast, small mammals with low per capita metabolic demands but high population densities have largely been overlooked in rewilding efforts. However, there is growing evidence that the functional extinction of

granivores, pollinators and ecosystem engineers, such as small mammals and birds, can reshape ecosystems because they can be important drivers of ecosystem dynamics (Eldridge & James 2009; Anderson et al. 2011; Davidson, Detling & Brown 2012; Gordon & Letnic 2015).

Granivory by mammals, birds and ants can be an important driver of vegetation dynamics in desert ecosystems (Brown, Reichman & Davidson 1979b). Granivores can limit plant recruitment by depleting the seed bank and influence vegetation assemblages by preferencing certain seed species over others (Brown & Heske 1990; Vaz Ferreira, Bruna & Vasconcelos 2011). When released from seed predation, seed-limited plant species can experience large increases in abundance with concomitant shifts in the structure of plant assemblages (Brown, Davidson & Reichman 1979a; Brown et al. 1979b).

Around the world the major taxa responsible for post-dispersal granivory in arid ecosystems are mammals, ants and birds (Brown, Reichman & Davidson 1979). However, the dominant taxa responsible for seed predation varies between continents. In deserts of North America and Israel, mammals are the dominant granivores (Mares & Rosenzweig 1978; Brown et al. 1979b; Abramsky 1983), in Zimbabwe birds are the dominant seed predators (Linzey & Washok 2000), in South America the taxa involved in seed predation varies dramatically between sites (Mares & Rosenzweig 1978; Kelt, Meserve & Gutiérrez 2004) and in South Africa (Kerley 1991) ants are the dominant seed predators. In Australian deserts ants are generally regarded as the dominant seed predators, and mammals as insignificant predators (Brown et al. 1979b; Morton 1985). Similarly, ants are key post-dispersal

seed predators and mammals relatively unimportant seed predators in tropical (Andrew 1986) and temperate (Auld & Denham 1999) Australia.

The weak role played by mammals as seed predators in Australian desert ecosystems has been attributed to the absence of specialised granivores as most Australian desert rodents are omnivorous (Murray et al. 1999). However, an important and sometimes overlooked caveat of seed predation studies in arid regions of Australia is that many once common mammal species have become extinct or rare since European settlement due to predation by introduced predators, *Vulpes vulpes* (red fox) and *Felis catus* (feral cat) (Woinarski, Burbidge & Harrison 2015). Declines of medium sized mammals and native rodents preceded any understanding of their roles as granivores and drivers of vegetation dynamics.

In arid Australia, the endangerment and extinction of medium-sized marsupials and native rodents has coincided with an increase in density of unpalatable woody shrubs (Short & Smith 1994; Noble, Hik & Sinclair 2007). This shrub encroachment is typically viewed as an undesirable environmental change by pastoralists and conservation agencies (Eldridge & Soliveres 2015). Shrub encroachment is usually attributed to combined pressures of overgrazing by livestock, changed fire regimes and increasing CO<sub>2</sub> levels favouring the growth of shrubs over grasses (Archer, Schimel & Holland 1995). However, recent research shows that where native rodents persist, they are significant consumers of shrub seeds (Gordon & Letnic 2015). Hence it has been hypothesised that functional extinction of granivorous mammals and resulting lack of granivory by these consumers may have relaxed a recruitment bottleneck that once limited shrub populations (Noble et al. 2007; Gordon et al. 2017).

Rewilding efforts in arid Australia have focused on re-establishing populations of medium-sized marsupials and native rodents on predator-free islands or within reserves enclosed by predator-proof fences (Short & Smith 1994; Moseby, Hill & Read 2009). Many of the mammal species that have been repatriated to desert ecosystems such as *Bettongia* spp., *Macrotis lagotis*, and native rodents are omnivores that frequently dig to obtain food such as invertebrates, seeds, plants, fungi and roots (Murray & Dickman 1994; Gibson 2001; Robley, Short & Bradley 2001). The ecosystem engineering effects that rewilded omnivores have on ecosystems have been well documented (Eldridge & James 2009; Davidson et al. 2012; Fleming et al. 2014; Hayward et al. 2016); however, the consumptive impacts that rewilded omnivores have on the seedbank and vegetation have mostly been overlooked.

Rewilding programs provide opportunities to understand the role of rewilded mammals as seed predators and drivers of vegetation dynamics in arid Australia. In this study, we compare seed removal rates in rewilded desert ecosystems with those in adjacent ecosystems with depauperate native mammal fauna. We hypothesized that mammal species which are now largely missing from the arid zone once played a larger role in seed predation in arid Australia than is currently realised. Using a foraging tray experiment inside and outside of predator-proof reserves we expected to find that reintroduced omnivorous mammals would remove more seeds than ants. If the consumptive effects of reintroduced mammals resulted in reduced shrub recruitment, we expected to find fewer shrub seedlings in rewilded areas than adjacent areas with depauperate mammal fauna.

## 2.3 Methods

### 2.3.1 Study Sites

This research was conducted at Arid Recovery Reserve (latitude: -30.381155, longitude: 136.900283) and Scotia Wildlife Sanctuary (latitude: -33.211131, longitude: 141.166222) during August 2015 and March 2016 (Fig. 2.1). Arid Recovery Reserve and Scotia Wildlife Sanctuary provide rare opportunities to study mammal assemblages as they may have existed 200 years ago. Each reserve has predator-proof fences inside which locally extinct mammals have been rewilded after the eradication of introduced predators (Fig. 2.2). The difference in mammal communities between rewilded areas and adjacent areas outside the predator-proof fences allowed us to compare the ecological functions of “pre-European” mammal assemblages to “present day” assemblages. The reserves and surrounding areas are characterised by the same vegetation and landforms. To provide a buffer-zone which reduces external pressure on the predator-proof fences at Arid Recovery and Scotia, mammalian predators (i.e. *Felis catus*, *Vulpes vulpes* and *Canis dingo*) are subject to a lethal control program in the depauperate areas surrounding the reserves. Full lists of the mammal species present in the reserves are provided in Table S1 in Supporting Information.

Arid Recovery is situated near Roxby Downs in arid South Australia (mean annual rainfall 149.9 mm; Roxby Downs; Australian Bureau of Meteorology 2016).

Average daily minimum and maximum temperatures during the March survey period were 16 °C and 29.5 °C and during August 6.3 °C and 24 °C (Australian Bureau of Meteorology 2016). Dominant landforms at Arid Recovery include longitudinal sand dunes with clay swales. Vegetation in the exclosures and surrounding areas consists

of perennial shrubs with grass and forb understorey. The land encompassing Arid Recovery and its immediate surroundings (our “depauperate” study sites) is on a mining lease that has been destocked for over 20 years.

The fenced area at Arid Recovery Reserve encompasses a total area of 123 km<sup>2</sup>, split into six separate exclosures of varying dimensions. Of this, 60 km<sup>2</sup> is the main reintroduction area and is completely free of introduced mammals including *Vulpes vulpes*, *Felis catus* and *Oryctolagus cuniculus* (European rabbit). Four mammal species have been successfully rewilded to Arid Recovery and a number of others such as *Notomys alexis* have benefited from the exclusion of predators (Moseby et al. 2009).

Scotia Wildlife Sanctuary (Scotia) is operated by the not-for-profit organisation Australian Wildlife Conservancy in south-western New South Wales. Scotia is semi-arid with hot summers and cool winters (mean annual rainfall 286.5 mm; Wentworth; Australian Bureau of Meteorology 2016). Average daily minimum and maximum temperatures for March were 22 °C and 37 °C and for August 5.6 °C and 17 °C (Australian Bureau of Meteorology 2016). The dominant landforms of the fenced area and surrounding lands at Scotia Sanctuary are longitudinal sand dunes and loamy plains with an overstorey of basally sprouting *Eucalyptus* spp. (mallee) or *Casuarina pauper*, a midstorey of perennial shrubs and an understorey of *Triodia scariosa* or forbs.

Scotia covers 650 km<sup>2</sup>, of which 80 km<sup>2</sup> is arranged into two predator-proof exclosures. We conducted our experiment in one exclosure into which medium sized mammals (300 g – 6000 g) *Onychogalea fraenata*, *Bettongia lesueur*, *Macrotis lagotis* and *Myrmecobius fasciatus* have been rewilded. Local rodent fauna is



depauperate. Small mammals (body mass < 30 g) present are the insectivorous dasyurids *Ningaui yvonneai* and *Sminthopsis* spp., the uncommon rodent *Pseudomys bolami* and the introduced *Mus musculus*. Areas external to exclosures but within Scotia Sanctuary were “depauperate” sample sites and have the same land use history, excepting the rewilding program. All areas of Scotia including depauperate areas have been destocked since its establishment in 1994 as a wildlife sanctuary.

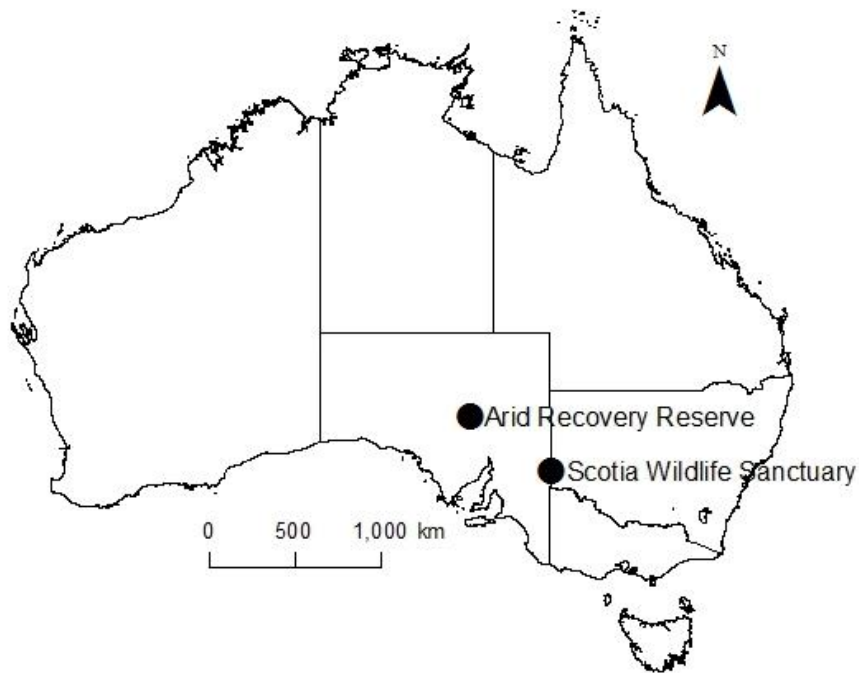


Figure 2.1 Location of Study Sites Arid Recovery and Scotia Wildlife Sanctuary within Australia

a) Arid Recovery



b) Scotia



Figure 2.2 Photographs of study sites along predator-proof fences: a) Arid Recovery Reserve and b) Scotia Wildlife Sanctuary. Right-hand side of each photo is the rewilded area. Photo credit: CM

### 2.3.2 Seed Species

We used seeds from two shrub species: *Dodonaea viscosa* subsp. *angustissima* (J.G. West) (mean seed weight 10.4 mg) and *Acacia ligulata* (A.Cunn. ex Benth) (mean seed weight 19.2 mg). *Dodonaea viscosa* is an encroaching species. The seed has a small aril, no eliasome, is dispersed by ants (Harrington & Driver 1995) and the plant is unpalatable to stock (Cunningham et al. 1992). *Dodonaea viscosa* has a short-lived soil seedbank (Semple & Koen 1997).

*Acacia ligulata* is not considered an encroaching species. The seed of *Acacia ligulata* has a large eliasome which is well known to attract ant and bird dispersers (Davidson & Morton 1984). It is of moderate palatability (Cunningham et al. 1992) and has a persistent seedbank (Davidson & Morton 1984).

We selected these species because they are widespread and occur in the same habitat. *Dodonaea viscosa* is locally abundant at both our study sites; however, *Acacia ligulata* is abundant at Arid Recovery and rare at Scotia. Anecdotal evidence suggests that *Bettongia lesueur* predates on the fruiting bodies of both species (Letnic pers. obs. 2016) but there is no evidence to suggest that they are dispersed or cached by mammals in the study areas. Seeds were sourced from a commercial supplier.

### 2.3.3 Spotlighting

To contrast the differences in the composition of mammal communities in rewilded and depauperate areas, we calculated relative mammal abundances along spotlight transects at Arid Recovery and Scotia. Mammals were counted using a 50 W spotlight from a vehicle travelling at 15 km per hour (Gordon & Letnic 2015). A

total of 20 km was surveyed in each treatment area in Scotia and at Arid Recovery 86 km was surveyed in the depauperate community and 80km in the rewilded community at Arid Recovery. The mean relative abundance of each mammal species observed (individuals sighted per km) was calculated by dividing the number of individuals per species by the total distance covered. Because detectability calculations depend on animal body size and because there are necessarily stark contrasts in mammal communities between rewilded and depauperate areas, we were unable to compare detection rates between depauperate and rewilded areas. To counter this, vegetation type and density on transects were kept consistent across depauperate and rewilded areas for each site. Surveys were conducted in August 2015 and March 2016.

#### 2.3.4 Seedling Density

To determine if there is evidence for a difference in shrub recruitment in rewilded areas compared to depauperate areas we measured shrub seedling density at Arid Recovery and Scotia along 100 m x 2 m belt transects. Surveys were conducted in May 2015 at Scotia and February 2013 at Arid Recovery. Shrub seedlings (<30cm height) for both *Dodonaea viscosa* and *Acacia ligulata* were counted along transects and density calculated as seedlings per metre squared. A minimum of 12 transects was conducted in both rewilded and depauperate areas at each reserve and vegetation and soils were consistent between transect locations within each reserve (Table S2). Using R version 3.3.1 (R Core Team 2016) we conducted a two sample Student's t-test to compare seedling abundances inside and outside rewilded areas at each reserve. To provide an overall test of seedling abundance inside and outside of rewilded areas for each shrub species we combined the probability values from the

two independent t-tests using Fisher's test for combining probabilities (Sokal & Rolf 1981).

### 2.3.5 Seed Removal Experiment

#### *2.3.5.1 Experimental Design*

A constraint of experiments such as this one that are designed around predator-proof enclosures is that the rewilded and depauperate treatments were by necessity spatially segregated and thus in a strictly statistical sense do not allow inferences concerning the effects of rewilded mammals (Hurlbert 1984). To overcome this, we have taken the following measures. First, we replicated our experiment by conducting the same experimental procedures inside and outside of fenced enclosures at two widely separated reserves to ask whether the trends in seed removal rates by different taxa were the same. Second, we conducted small-scale manipulative experiments that excluded mammals or ants to address our seed predation hypothesis (Oksanen 2001).

To assess seed removal by different taxa in rewilded and depauperate areas, we conducted a foraging tray experiment at both Arid Recovery and Scotia. Our experiment was conducted in August 2015 to represent a "winter" sample, when ant activity is low, and March 2016 to represent a "summer" sample, when ants are most active.

At each reserve, in rewilded areas and depauperate areas, we selected sites at least 400m apart. At each site, five foraging trays were placed in a line 20m apart. Each foraging tray consisted of a plastic tray (20cm diameter) placed flush with the ground, and filled with soil sifted to remove any existing seeds. For each

combination of fence treatment, season, and reserve, the number of sites sampled was between 10 and 29 (Table S2).

Foraging trays at each site were randomly assigned one of five treatments in a randomised block design. The five treatments consisted of: a mammal exclusion (caged enclosure), an ant exclusion (ring of insecticide powder), an ant exclusion procedural control (ring of bicarb soda, allowing full access for all taxa), a mammal exclusion procedural control (cage with no sides, allowing full access for all taxa), and a control (no cage or powder, full access) (Gordon & Letnic 2015).

In each foraging tray, 50 seeds of either *Dodonaea viscosa* subsp. *angustissima* or *Acacia ligulata* were placed in the soil. One seed species was used per site. Only unblemished seeds were used, determined by inspecting the seed for signs of predation, ensuring the eliasome was intact and ensuring the seed withstood a light force.

Trays were revisited after 48 hours and seeds counted. Seed removal was determined as the number of seeds removed from the foraging tray.

If mammals were significant seed predators we expected to find much higher seed removal in rewilded areas compared to depauperate areas for all treatments, except the mammal exclusion treatment which would be consistently low across both areas. If ants were the dominant seed predators and mammals insignificant seed predators we expected no difference in seed removal between rewilded areas and depauperate areas for all treatments, with the ant exclusion treatment experiencing consistently low seed removal. We deployed procedural controls for both the mammal exclusion treatment and the ant exclusion treatment to measure any effects of the exclusion structures on seed removal. If the exclusion structures had no influence, we expected

to find that seed removal from procedural controls would not differ from that at controls.

#### *2.3.5.2 Statistical Analysis*

A linear mixed-effects model using the Gaussian distribution was used to compare how season, predator-proof fence treatment (Fence) and experimental treatment affected seed removal using the lme4 version 1.1-12 (Bates et al. 2015) and car version 2.1-2 (Fox & Weisberg 2011) packages in R version 3.3.1 (R Core Team 2016). To reduce a left skew, the data were on log+1 transformed prior to analyses. To account for the split plot design experimental treatment block was incorporated into fence treatment as a random factor. Treatment, Season and Fence were fixed factors. Tukeys tests were used to undertake post hoc pairwise comparisons and determine where the differences lay.

#### *2.3.6 Visitation*

To determine which taxa (ants, birds, small mammals, medium mammals) were removing seeds, we swept the sandy substrate in a 50cm circumference around each tray and checked for the presence of tracks upon collection. Other spoor such as scats, presence of husks, soil disturbance in tray, removal of eliaosomes and direct observation of removal (ants) were also used to identify the seed removal culprits. Total visits by culprits was calculated as the number of trays at which their spoor was detected. If no tracks or other spoor were present ants were assumed to be the principle seed forager; however, because ants leave minimal trace we acknowledge that their rate of visitation will be underrepresented in this data.

To take into account tray visitations by multiple mammal species we used camera traps (Reconyx HC500) to cross-check our spoor interpretations. Camera traps were deployed simultaneously with trays and positioned 20cm high, one metre from the foraging tray. In summer, cameras were used at eight sites at Arid Recovery and 14 sites at Scotia, and in winter at 16 sites in Arid Recovery and 33 sites in Scotia.

Visitation using the camera trap technique was defined as an animal detected at the foraging tray and/or interacting with the experiment. Detections were calculated as the percentage of cameras on which each species appeared compared to total number of cameras deployed at the site across the survey period.

## 2.4 Results

### 2.4.1 Spotlighting

The mammal assemblages in rewilded areas were distinct from those in adjacent areas outside of the predator-proof exclosures (Fig. 2.3). Small (<100 g body mass) and medium sized (1000-3000g body mass) native omnivores were the most frequently sighted species in the rewilded areas but were absent outside of rewilded areas.

At Arid Recovery *Bettongia lesueur* and *Notomys alexis* were the species detected most often on spotlight transects inside the rewilded areas (Fig. 2.3a). At Arid Recovery, the mammal species observed in depauperate areas were *Macropus rufus* (red kangaroo, a large native herbivore), and introduced species *Oryctolagus cuniculus* (European rabbit), *Vulpes vulpes* (red fox) and *Felis catus* (feral cat).

At Scotia the omnivorous *Bettongia lesueur* was the most abundant mammal inside the rewilded areas (Fig. 2.3b), followed by the herbivorous *Onychogalea fraenata*.

Mammal species observed in the depauperate areas at Scotia were *Macropus rufus* and *Felis catus*.

#### 2.4.2 Seedling Density

Differences in seedling density between rewilded areas and areas depauperate of native mammals were dependent on species and site (Fig. 2.3c,d). T-tests showed that *Acacia ligulata* seedlings at Arid Recovery were more abundant outside of rewilded areas than inside ( $t_{24} = -3.53$ ,  $P < 0.01$ ), but the density of *Dodonaea viscosa* seedlings did not differ ( $t_{24} = -1.39$ ,  $P = 0.18$ ) (Fig. 2.3c). At Scotia, many more *Dodonaea viscosa* seedlings detected outside the rewilded areas ( $t_{60} = -2.54$ ,  $P < 0.05$ ), and there was no difference in density of *Acacia ligulata* ( $t_{60} = 1.8$ ,  $P = 0.86$ ), which occurred at very low densities in both rewilded and depauperate areas (Fig. 2.3d). Overall, the density of seedlings was greater in depauperate areas than rewilded areas for both species of shrub (Fisher's test of combined probabilities, *Acacia ligulata*:  $\chi^2 = 13.75$ , d.f. = 4,  $P < 0.01$ ; *Dodonaea viscosa*:  $\chi^2 = 12.04$ , d.f. = 4,  $P < 0.025$ ).



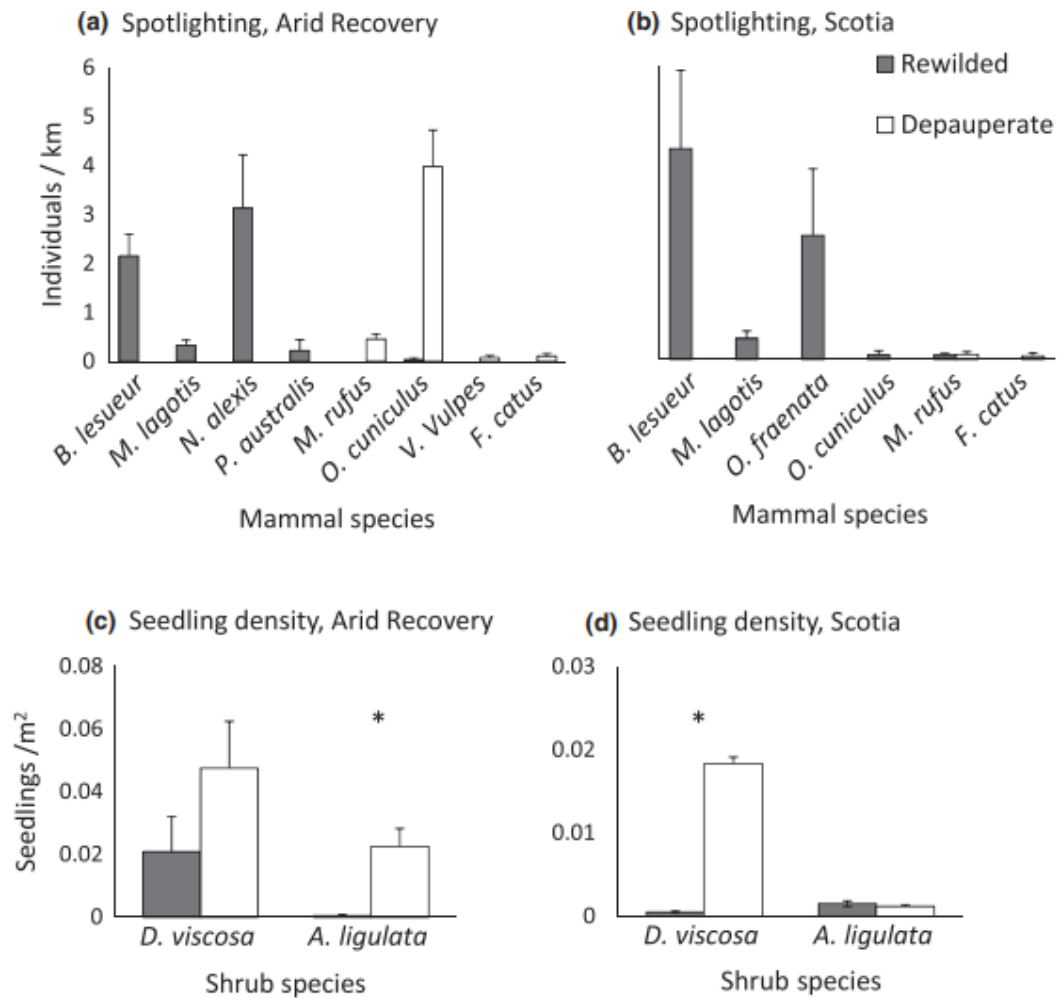


Figure 2.3 Spotlighting transects for a) Arid Recovery and b) Scotia mean number of animals/km for transects conducted in August 2015 and March 2016, +1 SEM. Seedling density per metre squared in c) Arid Recovery and d) Scotia. For c) and d), asterisks mark significant differences at  $P < 0.05$ .

### 2.4.3 Seed Removal Experiment

Seed removal was much higher in rewilded areas compared to adjacent areas outside predator-proof exclosures with the exception of the mammal exclusion treatment (Fig. 2.4; Table 2.1). Up to eight times more *Dodonaea viscosa* and up to three times as much *Acacia ligulata* seed were removed inside rewilded areas than outside the predator-proof exclosures. *Acacia ligulata* seeds had consistently higher removal rates than *Dodonaea viscosa* (Fig. 2.4) on both sides of predator-proof fences for all treatments and seed removal was higher in Arid Recovery than in Scotia. All pairwise comparisons reported below are within experimental treatments and between rewilded and depauperate areas, unless otherwise stated.

When compared within the same mammal community (i.e. rewilded or depauperate), procedural controls demonstrated no effect of treatments ( $P$  always  $> 0.05$ ) and were within one standard error of the mean for control treatments (Fig. 2.4) indicating that the physical presence of the experimental treatments had no unintended influence on seed removal.

At Arid Recovery seed removal was demonstrably higher in rewilded areas compared to areas depauperate of native mammals for both *Dodonaea viscosa* and *Acacia ligulata*, excepting the mammal exclusion treatment for which there was no difference in seed removal either side of the predator-proof fence. There was no difference between seasons (Fig. 2.4a; Table 2.1).

At Scotia, *Dodonaea viscosa* seed removal differed between seasons (Fig. 2.4b; Table 2.1). In winter, seed removal was dramatically different between the rewilded area and the adjacent areas depauperate of native mammals when comparing between treatments. This difference was significant for all treatments at  $P < 0.05$

except the mammal exclusion treatment which had very low seed removal in both rewilded and depauperate areas.

In summer, the seed removal trends for *Dodonaea viscosa* across treatments at Scotia were the same; however, only differences in seed removal from the ant exclusion treatment were statistically significant at  $P < 0.05$  ( $P = 0.019$ ). Seed removal from the ant exclusion treatment was much greater in rewilded areas than in depauperate areas, where neither mammals nor ants could access it. In rewilded areas the ant exclusion treatment had similar seed removal to all other treatments. There was no difference in seed removal from the mammal exclusion treatment either side of the fence ( $P = 1$ ), and although not statistically significant, the mammal exclusion treatment had the lowest seed removal rate inside the rewilded areas.

*Acacia ligulata* seeds were only deployed in summer at Scotia. At Scotia, seed removal for this species was consistently high across all combinations of mammal community and foraging tray treatment excepting the ant exclusion treatment outside the fence. Seed removal of *Acacia ligulata* from the ant exclusion treatment was much greater in rewilded areas where native mammals were abundant ( $P < 0.01$ ) (Fig. 2.4b; Table 2.1). Mammal exclusion treatments had the lowest seed removal of all treatments in the rewilded area but were not significantly different from other treatments.

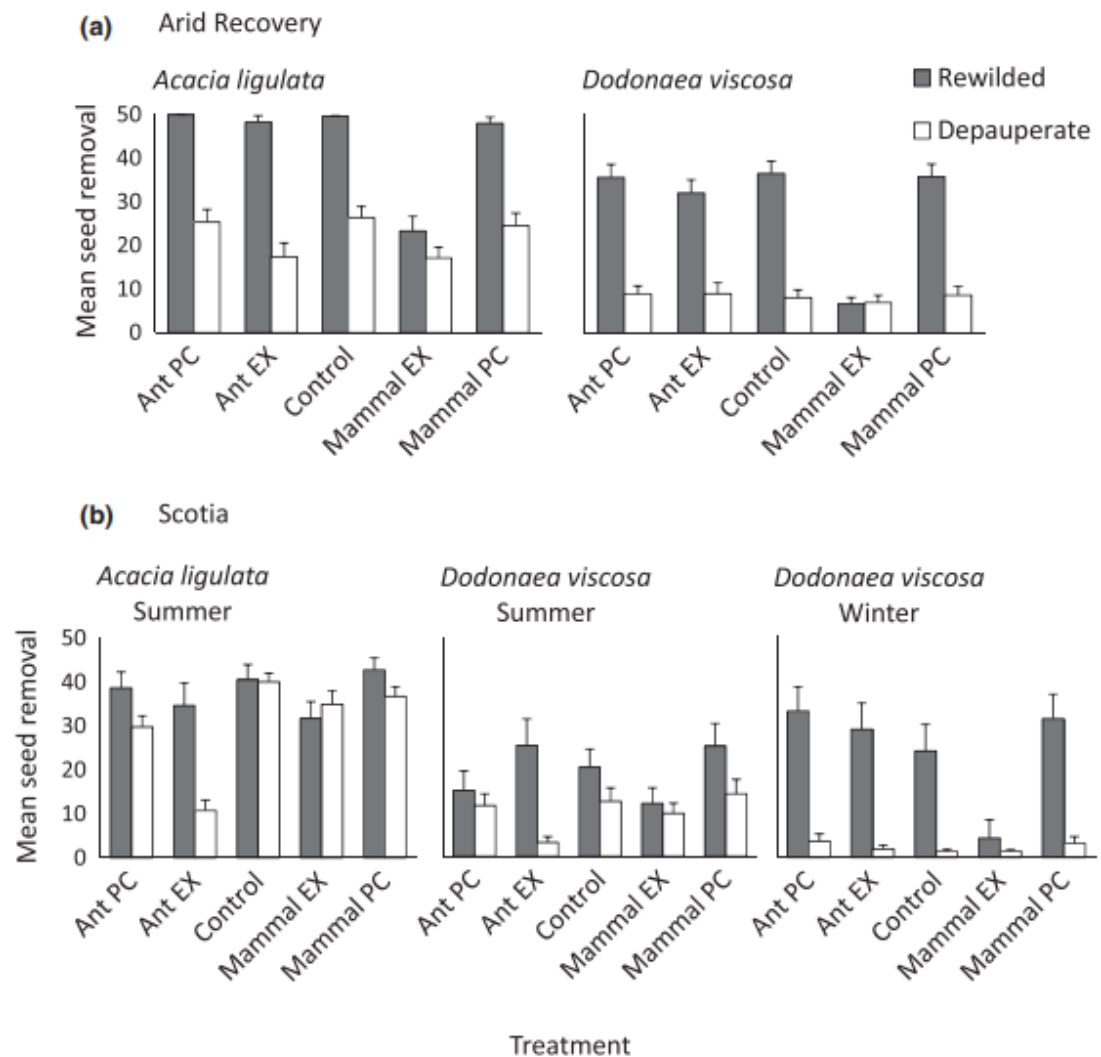


Figure 2.4 Average seed removal (after 48 hours) for each treatment, with +1 SEM for a) Arid Recovery and b) Scotia. Total possible seed removal is 50. Dark bars are inside predator-proof fences where rare mammals have been rewilded and light bars are outside

*Table 2.1* Results of generalised linear mixed-effects model comparing seed removal from experimental treatments across the fence treatment and both seasons (except *Acacia ligulata* at Scotia which was only tested in summer). Fence treatment is the comparison between rewilded and depauperate mammal communities.

a) <i>Acacia ligulata</i> at Arid Recovery		DF	ChiSq	p
Experimental Treatment	4	64.73	<0.001	
Fence Treatment	1	42.5	<0.001	
Season	1	0.17	0.68	
Experimental Treatment:Fence Treatment	4	37.28	<0.001	
Experimental Treatment:Season	4	4.4	0.35	
Fence Treatment:Season	1	0.41	0.52	
Experimental Treatment:Fence Treatment:Season	4	6.07	0.19	
b) <i>Dodonaea viscosa</i> at Arid Recovery				
Experimental Treatment	4	52.8	<0.001	
Fence Treatment	1	52.3	<0.001	
Season	1	1.32	0.25	
Experimental Treatment:Fence Treatment	4	42.51	<0.001	
Experimental Treatment:Season	4	6.03	0.2	
Fence Treatment:Season	1	2.38	0.12	
Experimental Treatment:Fence Treatment:Season	4	3.65	0.46	
c) <i>Acacia ligulata</i> at Scotia (summer only)				
Experimental Treatment	4	90.27	<0.001	
Fence Treatment	1	5.07	<0.05	
Experimental Treatment:Fence Treatment	4	30.25	<0.001	
d) <i>Dodonaea viscosa</i> at Scotia				
Experimental Treatment	4	19.25	<0.001	
Fence Treatment	1	54.14	<0.001	
Season	1	21.23	<0.001	
Experimental Treatment:Fence Treatment	4	28.73	<0.001	
Experimental Treatment:Season	4	15.54	<0.01	
Fence Treatment:Season	1	11.04	<0.001	
Experimental Treatment:Fence Treatment:Season	4	13.45	<0.01	

#### 2.4.4 Visitation

Spoor observations revealed that mammals were detected most often at foraging trays for both seed species at Arid Recovery and trays containing *Dodonaea viscosa* at Scotia, while ants had the most detections for trays containing *Acacia ligulata* seeds at Scotia. *Notomys alexis* and ants were the dominant removers in the depauperate area at Arid Recovery and ants only at Scotia. *Dodonaea viscosa* trays were visited mostly by *Bettongia lesueur* at both sites, while for *Acacia ligulata* trays the main visitors were *Notomys alexis* at Arid Recovery and ants at Scotia (Fig. 2.5). Birds were detected at <1% of all trays and were identified from camera observations as corvids. Camera observations aligned with spoor results with *Bettongia lesueur* most frequently detected (14% of cameras at Arid Recovery and 22% of cameras at Scotia), and *Notomys alexis* and other mammals detected at 9% of cameras at Arid Recovery and other mammals at 2% of cameras at Scotia. Seed husks at trays visited by *Notomys alexis* and photographs of *Bettongia lesueur* ingesting seeds provide evidence that mammals consumed seeds.

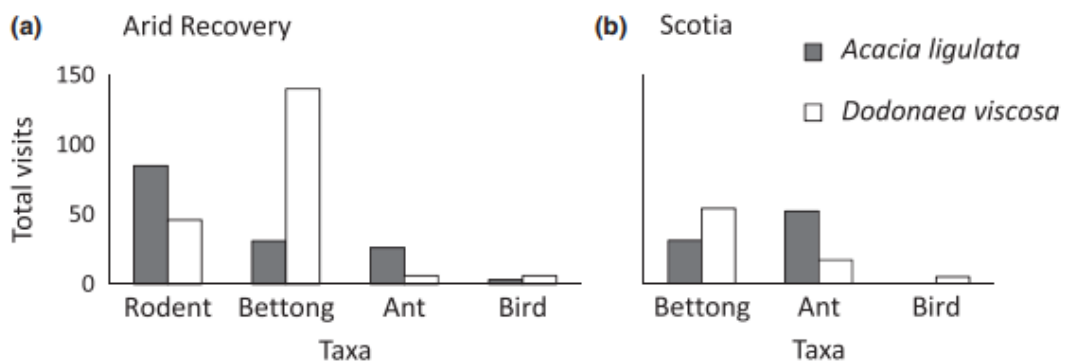


Figure 2.5 Total number of visits to foraging trays at (a) Arid Recovery, and (b) Scotia as observed in tracks, scats and other signs by taxa after 48 hours. Dark bars are *Dodonaea viscosa* and light bars are *Acacia ligulata*. Note at some trays spoor of more than one taxa was observed. Ants are underestimated as they often leave no trace.

## 2.5 Discussion

Our results provide evidence that rewilding of an Australian desert mammal assemblage has restored the hitherto unappreciated ecological function of omnivorous rodents and bettongs as seed predators. Using a foraging tray experiment we have shown that areas with rewilded mammal assemblages had higher rates of shrub-seed removal than adjacent areas with depauperate mammal assemblages at two rewilded sites in arid Australia. Our results suggest that mammals were once significant predators of seeds in arid Australia, at least equal to and in some places more important than ants. This finding highlights an important and overlooked consumptive role which native mammals once held in arid ecosystems.

That *Bettongia lesueur* and *Notomys alexis* are significant seed predators concurs with previous studies which have investigated seed predation by *Notomys fuscus* (Gordon & Letnic 2015) and with the known diets of these omnivores (Murray et al. 1999; Robley et al. 2001). Of particular note is the difference in magnitude of seed removal between the rewilded areas at the two sites. We suggest that the relatively higher rate of seed removal by mammals compared to ants at Arid Recovery was due to the presence of a less depauperate rodent assemblage there, with the rodent *Notomys alexis* removing a significant portion of seeds. In contrast, native rodents were not recorded at Scotia Sanctuary at the time of the study and *N. mitchelli*, a functionally similar species to *N. alexis*, is locally extinct (Menkhorst & Knight 2010).

Although ants were significant removers of seed at Scotia during summer, trays from which ants were excluded experienced seed removal by rewilded mammals that was similar to that at trays which both rewilded mammals and ants had access to. At the

same time, when rewilded mammals were excluded from trays, the quantity of seeds removed by ants was similar to that removed at trays where both ants and rewilded mammals had access. This compensatory seed removal exhibited by both ants and rewilded mammals when the other taxa was excluded may be the result of competition (Brown & Davidson 1977) between the two taxa and has been previously documented in the deserts of North America (Davidson, Inouye & Brown 1984).

An important caveat of our seed tray experiment is that seed removal does not necessarily equate to seed consumption and destruction (Vander Wall et al. 2005). Many granivorous mammals, especially rodents, perform seed-caching (Brown et al. 1979b; Hulme 1998a), although there is little empirical evidence that the mammals responsible for seed removal in our study cache seeds (though see Baker & Mutitjulu Community 1992). Comparatively, seeds removed by ants have a large range of possible fates, many of which do not lead to destruction of the seed (Auld & Denham 1999). Our observations of seed husks at the trays and photographic evidence of mammals ingesting seeds provides evidence that mammals consumed a large proportion of deployed seeds, and that they are important post-dispersal seed predators in rewilded assemblages.

Our finding that rewilded mammals were important removers of seeds is contrary to long held paradigms that ants are the dominant seed predators in arid Australia (Morton 1985). Instead, we have shown that native omnivores such as medium sized marsupials and native rodents likely played a significant role in seed predation prior to their declines in the 19<sup>th</sup> and early 20<sup>th</sup> centuries. Previous studies which attributed the weak role of mammalian seed predators in Australian deserts to the lack of



specialist granivores (Brown et al. 1979b; Morton & Baynes 1985) overlooked the role of omnivorous mammals as seed predators. This omission was likely because the functional extinction of many omnivorous mammals preceded any understanding of their role as seed predators (Morton 1985). Our contention that mammals were once the dominant seed predators in arid Australia prior to the introduction of red foxes and feral cats concords with desert systems such as in Israel and North America where mammals have primacy as seed predators (Mares & Rosenzweig 1978; Abramsky 1983).

By preferring larger seeds (Davidson et al. 1984; Hulme 1998a), digging for buried seed (Reichman 1979; Hulme 1998a; b) and consuming seeds unattractive to ants (Auld & Denham 1999), mammalian seed predators provide top-down pressure on seeds of plant species that may otherwise escape predation. Whether seed predation limits recruitment is a matter of some contention. Certainly, there are plant communities where seed predation is not a strong factor influencing recruitment (Andersen 1989; Pinto, Pearson & Maron 2014). However, when recruitment is seed-limited, granivorous mammals have been demonstrated to be an important driver of plant recruitment and community structure (Brown et al. 1979a; b; Inouye, Byers & Brown 1980; Davidson et al. 1984; Hulme 1998a). We suggest that if mammalian seed predators are removed, relaxation of predation pressure may lead to changes in the seed bank (Reichman 1979) and greater recruitment success for preferred plant species and thus be a driver of vegetation community structure (Brown et al. 1979a; b; Brown & Heske 1990; Gordon et al. 2017).

Our results showed that rewilded areas had lower densities of shrub seedlings than adjacent areas with depauperate mammal assemblages. This finding is consistent

with the notions that that small marsupial herbivores and rodents may once have played an important role in suppressing shrub abundance either as predators of shrub seeds or their seedlings and that the loss of these species has facilitated shrub encroachment (Noble et al. 2007; Gordon & Letnic 2015; Gordon & Letnic 2015b; Gordon et al. 2017). To further ascertain the relationship between shrub encroachment and functional extinction of mammalian seed predators, we suggest long-term studies tracking the fate of seedlings through time in areas with rewilded and depauperate mammal assemblages.

Another caveat of our study is that we do not know if the population densities of rewilded mammals within the fenced reserves reflect those that occurred prior to the introduction of foxes and cats. This is an important consideration because although historical observations of mammals and records of bounty payments suggest that species such as *Notomys* spp. (Sturt 1849) and *Bettongia* spp. (Short 1998) were once very abundant in some areas, the fenced reserves where we conducted our studies contained no mammalian predators. Similarly, due to the extinction debt incurred by introduced predators, the “present-day” mammal assemblages represented by the depauperate areas in our study are very species poor and provide no possible baseline for historical mammal densities. Thus, top-down regulation of rewilded mammal populations within the reserves was likely to be weak because they were only subject to predation by avian and reptilian predators. It is therefore possible that rewilded mammals within the fenced exclosures existed at higher population densities than they did prior to their extirpation when humans and native mammals would also have predated on them. However, because we do not know and likely can never know the densities at which these mammals once occurred we argue

that rewilded fenced exclosures provide important insights into how ecosystems functioned prior to the declines of small and medium sized mammals.

There is increasing awareness that extinctions can trigger ecological cascades that can theoretically be reversed by restoring the ecological functions of missing species through rewilding (Seddon et al. 2014; Svenning et al. 2015). Due to their strong per capita effects, much of the discussion on ecological restoration through rewilding has focused on re-establishing populations of large mammalian carnivores and herbivores which have high per capita metabolic demands and thus strong per capita effects on ecosystems (Ripple & Beschta 2003; Svenning et al. 2015). However, the results of our study provide evidence that the re-establishment of small mammals with comparatively low per capita consumptive effects can have potentially strong effects on ecosystems because they can occur at high population densities. Although the marked ecosystem effects that small mammals can have when they occur at high densities have been documented previously (Olofsson et al. 2004; Gordon & Letnic 2015), the ecosystem consequences of functional extinction of small mammals has been largely overlooked by rewilding programs. Indeed, in this vein we argue that rewilding should not be synonymous with the re-establishment of charismatic large fauna, but rather focus on re-establishing the critical ecological functions of missing fauna regardless of their size, taxon or ecological role.

## 2.6 References

- Abramsky, Z. (1983) Experiments on seed predation by rodents and ants in the Israeli desert. *Oecologia*, **57**, 328–332.
- Andersen, A.N. (1989) How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia*, **81**, 310–315.
- Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S. & Terry, J. (2011) Cascading

- effects of bird functional extinction reduce pollination and plant density. *Science*, **331**, 1068–1071.
- Andrew, M.H. (1986) Granivory of the annual grass *Sorghum intrans* by the harvester ant *Meranoplus* sp. in tropical Australia. *Biotropica*, **18**, 344–349.
- Archer, S., Schimel, D.S. & Holland, E.A. (1995) Mechanisms of shrubland expansion: land use, climate or CO<sub>2</sub>? *Climatic Change*, **29**, 91–99.
- Auld, T.D. & Denham, A.J. (1999) The role of ants and mammals in dispersal and post-dispersal seed predation of the shrubs *Grevillea* (Proteaceae). *Plant Ecology*, **144**, 201–213.
- Baker, L.M. & Mutitjulu Community (1992) Comparing two views of the landscape: Aboriginal traditional ecological knowledge and modern scientific knowledge. *Rangeland Journal*, **14**, 174–189.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.
- Brown, J.H. & Davidson, D.W. (1977) Competition between seed-eating rodents and ants in desert ecosystems. *Science*, **196**, 880–882.
- Brown, J.H., Davidson, D.W. & Reichman, O.J. (1979a) An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist*, **19**, 1129–1143.
- Brown, J.H. & Heske, E.J. (1990) Control of a desert-grassland transition by a keystone rodent guild. *Science*, **250**, 1705–1707.
- Brown, J.H., Reichman, O.J. & Davidson, D.W. (1979b) Granivory in desert ecosystems. *Annual Review of Ecology and Systematics*, **10**, 201–227.
- Cunningham, G.M., Mulham, W.E., Milthorpe, P.L. & Leigh, J.H. (1992) *Plants of western New South Wales*. CSIRO Publishing, Clayton South.
- Davidson, A.D., Detling, J.K. & Brown, J.H. (2012) Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment*, **10**, 477–486.

- Davidson, D.W., Inouye, R.S. & Brown, J.H. (1984) Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology*, **65**, 1780–1786.
- Davidson, D.W. & Morton, S.R. (1984) Dispersal Adaptations of Some Acacia Species in the Australian Arid Zone. *Ecology*, **65**, 1038–1051.
- Eldridge, D.J. & James, A.I. (2009) Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes. *Ecological Management and Restoration*, **10**, S27–S34.
- Eldridge, D.J. & Soliveres, S. (2015) Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia. *Australian Journal of Botany*, **62**, 594–608.
- Fleming, P.A., Anderson, H., Prendergast, A.S., Bretz, M.R., Valentine, L.E. & Hardy, G.E.S. (2014) Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Review*, **44**, 94–108.
- Fox, J. & Weisberg, S. (2011) *An {R} Companion to Applied Regression*, 2nd Ed. Sage, Thousand Oaks, California.
- Gibson, L.A. (2001) Seasonal changes in the diet, food availability and food preference of the greater bilby (*Macrotis lagotis*) in south-western Queensland. *Wildlife Research*, **28**, 121–134.
- Gordon, C.E., Eldridge, D.J., Ripple, W.J., Crowther, M.S., Moore, B.D. & Letnic, M. (2017) Shrub encroachment is linked to extirpation of an apex predator. *Journal of Animal Ecology*, **86**, 147–157.
- Gordon, C.E. & Letnic, M. (2015) Functional extinction of a desert rodent: implications for seed fate and vegetation dynamics. *Ecography*, **39**, 815–824.
- Harrington, G.N. & Driver, M.A. (1995) The effect of fire and ants on the seed-bank of a shrub in semi-arid grassland. *Australian Journal of Ecology*, **20**, 538–547.
- Hayward, M.W., Ward-Fear, G., L’Hotellier, F., Herman, K., Kabat, A.P. & Gibbons, J.P. (2016) Could biodiversity loss have increased Australia’s bushfire threat? *Animal Conservation*, **19**, 490–497.

- Hulme, P.E. (1998a) Post-dispersal seed predation: consequences for plant demography and evolution. *Perspectives in Plant Ecology, Evolution and Systematics*, **1**, 32–46.
- Hulme, P.E. (1998b) Post-dispersal seed predation and seed bank persistence. *Seed Science Research*, **8**, 513–519.
- Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.
- Inouye, R.S., Byers, G.S. & Brown, J.H. (1980) Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology*, **61**, 1344–1351.
- Kelt, D.A., Meserve, P.L. & Gutiérrez, J.R. (2004) Seed removal by small mammals, birds and ants in semi-arid Chile, and comparison with other systems. *Journal of Biogeography*, **31**, 931–942.
- Kerley, G.I.H. (1991) Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. *Journal of Arid Environments*, **20**, 63–69.
- Linzey, A. V. & Washok, K.A. (2000) Seed removal by ants, birds and rodents in a woodland savanna habitat in Zimbabwe. *African Zoology*, **35**, 295–299.
- Mares, M.A. & Rosenzweig, M.L. (1978) Granivory in North and South American deserts: rodents, birds, and ants. *Ecology*, **59**, 235–241.
- Menkhorst, P.W. & Knight, F. (2010) *A Field Guide to the Mammals of Australia*, 3rd ed. Oxford University Press, South Melbourne, Victoria.
- Morton, S.R. (1985) Granivory in arid regions: comparison of Australia with North and South America. *Ecology*, **66**, 1859–1866.
- Morton, S.R. & Baynes, A. (1985) Small mammal assemblages in arid Australia: a reappraisal. *Australian Mammalogy*, **8**, 159–169.
- Moseby, K.E., Hill, B.M. & Read, J.L. (2009) Arid Recovery - A comparison of reptile and small mammal populations inside and outside a large rabbit, cat and fox-proof enclosure in arid South Australia. *Austral Ecology*, **34**, 156–169.

- Mouquet, N., Gravel, D., Massol, F. & Calcagno, V. (2013) Extending the concept of keystone species to communities and ecosystems. *Ecology Letters*, **16**, 1–8.
- Murray, B.R. & Dickman, C.R. (1994) Granivory and microhabitat use in Australian desert rodents: are seeds important? *Oecologia*, **99**, 216–225.
- Murray, B.R., Dickman, C.R., Watts, C.H.S. & Morton, S.R. (1999) The dietary ecology of Australian desert rodents. *Wildlife Research*, **26**, 857–858.
- Noble, J.C., Hik, D.S. & Sinclair, A.R.E. (2007) Landscape ecology of the burrowing bettong: fire and marsupial biocontrol of shrubs in semi-arid Australia. *The Rangeland Journal*, **29**, 107–119.
- Oksanen, L. (2001) Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos*, **94**, 27–38.
- Olofsson, J., Hulme, P.E., Oksanen, L. & Suominen, O. (2004) Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos*, **106**, 324–334.
- Pinto, S.M., Pearson, D.E. & Maron, J.L. (2014) Seed dispersal is more limiting to native grassland diversity than competition or seed predation. *Journal of Ecology*, **102**, 1258–1265.
- R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reichman, O.J. (1979) Desert granivore foraging and its impact on seed densities and distributions. *Ecology*, **60**, 1085–1092.
- Ripple, W.J. & Beschta, R.L. (2003) Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*, **184**, 299–313.
- Robley, A.J., Short, J. & Bradley, S. (2001) Dietary overlap between the burrowing bettong (*Bettongia lesueur*) and the European rabbit (*Oryctolagus cuniculus*) in semi-arid coastal Western Australia. *Wildlife Research*, **28**, 341–349.
- Seddon, P.J., Griffiths, C.J., Soorae, P.S. & Armstrong, D.P. (2014) Reversing

- defaunation: restoring species in a changing world. *Science*, **345**, 406–412.
- Semple, W.S. & Koen, T.B. (1997) Effect of seedbed on emergence and establishment from surface sown and direct drilled seed of *Eucalyptus* spp. and *Dodonaea viscosa*. *The Rangeland Journal*, **19**, 80–94.
- Short, J. & Smith, A. (1994) Mammal decline and recovery in Australia. *Journal of Mammalogy*, **75**, 288–297.
- Short, J. (1998) The extinction of rat-kangaroos (Marsupialia:Potoroidae) in New South Wales, Australia, **86**, 365–377.
- Sokal, R.R. & Rolf, F.J. (1981) *Biometry*. New York, USA: Freeman and Company.
- Sturt, C. (1849) Narrative of an expedition into Central Australia, performed under the authority of Her Majesty's government, during the years 1844, 5, and 6: together with a notice of the province of South Australia in 1847 / by Charles Sturt. T. and W. Boone.
- Svenning, J.-C., Pedersen, P.B.M., Donlan, J., Ejrnaes, R., Faurby, S., Galetti, M., ... Vera, F.W.M. (2015) Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences*, **113**, 898–906.
- Vaz Ferreira, A., Bruna, E.M. & Vasconcelos, H.L. (2011) Seed predators limit plant recruitment in Neotropical savannas. *Oikos*, **120**, 1013–1022.
- Vander Wall, S.B., Kuhn, K.M., Beck, M.J. & Eck, M.A.J.B. (2005) Seed removal, seed predation, and secondary dispersal. *Ecology*, **86**, 801–806.
- Woinarski, J.C.Z., Burbidge, A.A. & Harrison, P.L. (2015) Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences*, **112**, 4531–4540.



## 2.7 Supplementary Material

*Table S2.1* Species of terrestrial mammals present inside and outside predator proof fences at Arid Recovery (since 1997) and Scotia (since 2014), their diet and body mass. Body mass values taken from *A Field Guide to the Mammals of Australia*, Menkhorst and Knight (2010).

Key: R = Successfully reintroduced, I=non-native, E=existing/self-introduced

Species	Scientific Name	Diet	Body Mass (g)	Scotia		ARR	
				INSIDE	OUTSIDE	INSIDE	OUTSIDE
Bolam's mouse	<i>Pseudomys bolami</i>	Omnivorous	10-21	E	E	E	E
Bridled Nail Tail Wallaby	<i>Onychogalea fraenata</i>	Herbivorous	3000-6000	R	-	-	-
Burrowing Bettong	<i>Bettongia lesueur</i>	Omnivorous	900-1600	R	-	R	-
Cat	<i>Felis catus</i>	Carnivorous	2500-6500	-	E	-	E
Desert Mouse	<i>Pseudomys desertor</i>	Herbivorous	15-30	-	-	E	E
Dingo	<i>Canus lupus dingo</i>	Carnivorous	12000-24000	-	E	-	E
Dunnart (various)	<i>Sminthopsis spp.</i>	Insectivorous	12-28	E	E	E	E
Eastern Grey Kangaroo	<i>Macropus giganteus</i>	Herbivorous	37000-66000	-	E	-	-
Euro	<i>Macropus robustus</i>	Herbivorous	25000-55000	-	E	-	-
European Rabbit	<i>Oryctolagus cuniculus</i>	Herbivorous	1000-2400	-	I	-	I, E
Forrest's mouse	<i>Leggadina forresti</i>	Omnivorous	15-25	-	-	E	E
Fox	<i>Vulpes vulpes</i>	Carnivorous	3500-8000	-	E	-	E
Giles' Planigale	<i>Planigale gilesi</i>	Insectivorous	6-15	-	-	E	E
Greater Bilby	<i>Macrotis lagotis</i>	Omnivorous	800-2400	R	-	R	-
Greater Stick-Nest Rat	<i>Leporillus conditor</i>	Herbivorous	190-450	-	-	R	-
House mouse	<i>Mus musculus</i>	Omnivorous	10-20	I, E	E	I, E	I, E
Numbat	<i>Myrmecobius fasciatus</i>	Myrmecophagous	300-715	R	-	-	-
Plains Mouse	<i>Pseudomys australis</i>	Herbivorous	40-75	E	E	E	E

Red Kangaroo	<i>Macropus rufus</i>	Herbivorous	35000-85000	-	E	E	E
Sandy Inland Mouse	<i>Pseudomys hermannsburgensis</i>	Omnivorous	9-17	E	E	E	E
Short-beaked Echidna	<i>Tachyglossus aculeatus</i>	Myrmecophagous	2000-7000	E	E	E	E
Southern Ningai Spinifex Hopping Mouse	<i>Ningai yvonneae</i>	Insectivorous	5-10	E	E	-	-
Western Barred Bandicoot	<i>Peremeles bougainville</i>	Omnivorous	27-45	-	-	E	E
Western Grey Kangaroo	<i>Macropus fulliginosus</i>	Insectivorous	170-285	-	-	R	-
		Herbivorous	28000-54000	-	E	E	E

*Table S2.2* Sample sizes for Spotlighting Transects (sampled in August 2015 and March 2016 at both sites), Seedling Transects (sampled in May 2015 at Scotia and February 2013 at Arid Recovery) and Seed Removal Experiment (sampled in August 2015 (winter) and March 2016 (summer)) at both sites

**a) Spotlighting Transects**

Site	Fence	<i>n</i>
Arid Recovery	Rewilded	10
Arid Recovery	Depauperate	8
Scotia	Rewilded	4
Scotia	Depauperate	3

**b) Seedling Transects**

Site	Fence	<i>n</i>
Arid Recovery	Rewilded	12
Arid Recovery	Depauperate	14
Scotia	Rewilded	20
Scotia	Depauperate	42

**c) Arid Recovery Seed Removal experiment**

***Acacia ligulata* at Arid Recovery (Summer)**

Experimental Treatment	Fence Treatment	<i>n</i>
Ant Exclusion PC	Rewilded	21
Control	Rewilded	21
Ant Exclusion	Rewilded	21
Mammal Exclusion	Rewilded	20
Mammal Exclusion PC	Rewilded	20
Ant Exclusion PC	Depauperate	29

Control	Depauperate	29
Ant Exclusion	Depauperate	28
Mammal Exclusion	Depauperate	29
Mammal Exclusion PC	Depauperate	29

***Acacia ligulata* at Arid Recovery (Winter)**

<b>Experimental Treatment</b>	<b>Fence Treatment</b>	<b><i>n</i></b>
Ant Exclusion PC	Rewilded	11
Control	Rewilded	11
Ant Exclusion	Rewilded	11
Mammal Exclusion	Rewilded	10
Mammal Exclusion PC	Rewilded	11
Ant Exclusion PC	Depauperate	13
Control	Depauperate	14
Ant Exclusion	Depauperate	14
Mammal Exclusion	Depauperate	13
Mammal Exclusion PC	Depauperate	14

***Dodonaea viscosa* at Arid Recovery (Summer)**

<b>Experimental Treatment</b>	<b>Fence Treatment</b>	<b><i>n</i></b>
Ant Exclusion PC	Rewilded	21
Control	Rewilded	21
Ant Exclusion	Rewilded	21
Mammal Exclusion	Rewilded	21
Mammal Exclusion PC	Rewilded	22
Ant Exclusion PC	Depauperate	29
Control	Depauperate	29
Ant Exclusion	Depauperate	29
Mammal Exclusion	Depauperate	29
Mammal Exclusion PC	Depauperate	29

***Dodonaea viscosa* at Arid Recovery (Winter)**

<b>Experimental Treatment</b>	<b>Fence Treatment</b>	<b><i>n</i></b>
Ant Exclusion PC	Rewilded	27
Control	Rewilded	27
Ant Exclusion	Rewilded	28
Mammal Exclusion	Rewilded	25
Mammal Exclusion PC	Rewilded	28
Ant Exclusion PC	Depauperate	18
Control	Depauperate	18
Ant Exclusion	Depauperate	18
Mammal Exclusion	Depauperate	18
Mammal Exclusion PC	Depauperate	18

**d) Scotia Seed Removal experiment**

***Acacia ligulata* at Scotia (Summer)**

<b>Experimental Treatment</b>	<b>Fence Treatment</b>	<b><i>n</i></b>
Ant Exclusion PC	Rewilded	16
Control	Rewilded	16
Ant Exclusion	Rewilded	16
Mammal Exclusion	Rewilded	16
Mammal Exclusion PC	Rewilded	16
Ant Exclusion PC	Depauperate	21
Control	Depauperate	20
Ant Exclusion	Depauperate	19
Mammal Exclusion	Depauperate	20
Mammal Exclusion PC	Depauperate	20

***Dodonaea viscosa* at Scotia (Summer)**

<b>Experimental Treatment</b>	<b>Fence Treatment</b>	<b><i>n</i></b>
Ant Exclusion PC	Rewilded	16
Control	Rewilded	16
Ant Exclusion	Rewilded	16
Mammal Exclusion	Rewilded	16
Mammal Exclusion PC	Rewilded	16
Ant Exclusion PC	Depauperate	20
Control	Depauperate	20
Ant Exclusion	Depauperate	20
Mammal Exclusion	Depauperate	20
Mammal Exclusion PC	Depauperate	20

***Dodonaea viscosa* at Scotia (Winter)**

<b>Experimental Treatment</b>	<b>Fence Treatment</b>	<b><i>n</i></b>
Ant Exclusion PC	Rewilded	15
Control	Rewilded	15
Ant Exclusion	Rewilded	15
Mammal Exclusion	Rewilded	12
Mammal Exclusion PC	Rewilded	15
Ant Exclusion PC	Depauperate	32
Control	Depauperate	32
Ant Exclusion	Depauperate	32
Mammal Exclusion	Depauperate	32
Mammal Exclusion PC	Depauperate	32

### **Chapter 3: Reversing functional extinction of mammals prompts a rethink of paradigms about seed fate in arid Australia**

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Contributions: C.M. conducted 80% of the total work. Both authors conceived the study. C.M. collected and analysed data and led the writing of the manuscript.



Desert dunes and mallee as far as the eye can see

### 3.1 Abstract

Functional extinction of once abundant species has frequently preceded understanding of their ecological roles. Consequently, our understanding of ecosystems is prone to shifting baselines because it often relies on observations made on depauperate species assemblages. In Australian deserts, current paradigms are that ants are the dominant granivores, mammals are unimportant seed predators and that myrmecochory in many Australian shrubs is an adaptation to increase dispersal distance and direct seeds to favourable germination sites. Here, we ask whether these paradigms could be artefacts of mammal extinction. We take advantage of a predator-proof reserve within which locally extinct native mammals have been reintroduced to compare seed removal by ants and mammals. Using foraging trays that selectively excluded mammals and ants we show that a reintroduced mammal, the woylie (*Bettongia penicillata*) was at least as important as ants in the removal of seeds of two shrub species (*Dodonaea viscosa* and *Acacia ligulata*). Our results provide evidence that the dominance of ants as granivores and current understanding of the adaptive benefit of myrmecochory in arid Australia may be artefacts of the functional extinction of mammals. Our study shows how reversing functional extinction can provide the opportunity to rethink contemporary understanding of ecological processes.

### 3.2 Introduction

Population declines of historically abundant species have often preceded understanding of their ecological roles (Jackson et al., 2001). Consequently, changes in ecosystem processes resulting from the loss of species that are now rare or extinct may go unappreciated (Gordon et al., 2017). In Australia, around 30 endemic

marsupial and rodent species have become extinct in the last 200 years. Many more have undergone range declines and become rare due primarily to predation by introduced predators (Woinarski, Burbidge, & Harrison, 2015). For many of these mammals it has not been possible to identify shifts in ecosystem processes triggered by their functional extinction. This is because such effects can be difficult, if not impossible, to isolate if there is no opportunity to contrast comparable ecosystems where now rare or extinct mammals are present or absent.

In many of the world's deserts, mammals are key predators and dispersers of seeds (Brown, Reichman, & Davidson, 1979) and therefore important drivers of vegetation dynamics (Inouye, Byers, & Brown, 1980). In contrast, the paradigm in Australian deserts is that ants are the dominant dispersers and predators of seeds and that mammals are unimportant predators and dispersers of seeds (Brown et al., 1979; Morton, 1985). In addition, many Australian arid zone shrubs have well-recognised mutualisms with ants as seed dispersers (Davidson & Morton, 1984). Hypothesized adaptive benefits of myrmecochory for arid Australian shrubs are that ants increase dispersal distance and direct seeds to sites favourable for germination, but unlike other continents myrmecochory is thought to accrue little benefit as an adaptation to avoid seed predation (Davidson & Morton, 1984; Giladi, 2006; Harrington & Driver, 1995). However, as noted by Morton (1985) most studies examining the primacy of ants and mammals as seed predators and adaptive benefits of myrmecochory in Australian deserts were undertaken in ecosystems in which the native mammal communities had been greatly diminished (Morton, 1985; Woinarski et al., 2015). Rewilding efforts in arid Australia have focused on re-establishing populations of medium-sized marsupials within predator-proof fenced reserves and provide a rare

opportunity to study mammal assemblages as they may have existed 200 years ago (Verdon, Gibb, & Leonard, 2016). In a previous study (Mills, Gordon, & Letnic, 2015; Chapter 2) we found that native mammals within predator-proof exclosures at Arid Recovery (the burrowing bettong, *Bettongia lesueur* and spinifex hopping mouse, *Notomys alexis*) and Scotia Sanctuary (the burrowing bettong, *Bettongia lesueur*) were more significant predators of shrub seeds than ants and that their loss is a likely driver of vegetation changes such as shrub encroachment. In this study we further the idea that rewilded mammals are significant seed predators by conducting an experiment in a different exclosure to that investigated by Mills et al. (2018) at Scotia Sanctuary and examining the role of another rewilded mammal, the brush-tailed bettong (*Bettongia pencillata*) as a seed predator. Specifically, we ask if the paradigm that mammals are unimportant seed predators in Australian deserts is an artefact of their historical decline and hence functional extinction. To determine if ants or reintroduced mammals were the dominant seed predators we conducted a foraging tray experiment with treatments that selectively excluded ants or mammals.

### 3.3 Methods

#### 3.3.1 Study Site

This research was conducted at Scotia Wildlife Sanctuary (Scotia; -33.20 °S, 141.16 °E), a conservation reserve run by the Australian Wildlife Conservancy in south-west New South Wales, Australia. Scotia is semi-arid with hot summers and cool winters (mean annual rainfall 286 mm; Australian Bureau of Meteorology, 2017). Scotia boasts two independent 40km<sup>2</sup> predator-proof exclosures into which locally extinct marsupials have been reintroduced (Stage 1 and Stage 2). The bridled nail-



tailed wallaby (*Onychogalea fraenata*, body mass 3 – 6 kg); numbat (*Myrmecobius fasciatus*, 0.3 – 0.7 kg) and greater bilby (*Macrotis lagotis*, 0.8 – 2.4 kg) are present in both Stage 1 and Stage 2. Of the two species of bettong reintroduced at Scotia, the burrowing bettong (*Bettongia lesueur*, 0.9 – 1.6 kg) is only present in Stage 1 while the woylie is only present in Stage 2 (*Bettongia penicillata ogilbyi*, 1- 1.6 kg). We conducted our experiment within Stage 2 of Scotia. Mammal populations in the two exclosures are separated by a fence which they cannot traverse and thus the populations in the two exclosures are independent.

### 3.3.2 Seed Removal Experiment

To compare seed removal rates by ants and mammals we conducted foraging tray experiments in August 2015 (“winter”) and March 2016 (“summer”) using seeds of two shrub species that occur locally: *Acacia ligulata* and *Dodonaea viscosa* subsp. *angustissima*. The seed of *A. ligulata* (seed weight: 19 mg) has a large eliasome which attracts ant and bird dispersers (Davidson & Morton, 1984). The seed of *D. viscosa* (seed weight: 10mg) has a small aril, no eliasome and is dispersed by ants (Harrington & Driver, 1995). Seeds were sourced from a commercial supplier.

At sites spaced 1km apart we placed five foraging trays along a transect at 20 m intervals. Each foraging tray consisted of a plastic-tray (20 cm diameter) buried flush with the ground and filled with sifted soil. Trays were designed to mimic natural deposits of seed that occur under shrubs during fruiting. In summer we deployed 16 sites for each seed species and in winter we deployed 15 sites for *D. viscosa* and 10 sites for *A. ligulata*.

Foraging trays at each site were randomly assigned one of five treatments: Mammal Exclusion (caged exclosure), Ant Exclusion (ring of Coopex® insecticide powder), Ant Exclusion Procedural Control (ring of bicarb soda, allowing full access for all taxa), Mammal Exclusion Procedural Control (cage with no sides, allowing full access for all taxa), and Control (no cage or powder, full access) (Gordon & Letnic, 2015). The Mammal Exclusion treatment also excluded birds; however, during a pilot study we found that birds did not visit the foraging trays. In each tray we placed 50 unblemished seeds of *D. viscosa* or *A. ligulata*. One seed species was used per site. To identify the taxa removing seeds we swept the substrate in a 50cm circumference around each tray and at collection recorded presence of spoor and if any ants were in the tray. After 48 hours, trays were revisited and seeds sifted from sand and counted to determine the number of seeds removed. Visitation was calculated as the percentage of trays at which spoor of taxa (woylie, ant, bird) was detected and the respective taxon had access.

If mammals were significant seed predators and ants insignificant seed predators, we expected to find no difference in seed removal between Ant Exclusion treatments and Control treatments, but lower seed removal from Mammal Exclusion treatments. If mammals and ants are equally significant seed predators, we expected that seed removal from Mammal Exclusion treatments and Ant Exclusion treatments would be equal. If ants were the dominant seed predators and mammals insignificant seed predators we expected no difference in seed removal from Mammal Exclusion treatments and Control treatments, but lower seed removal from Ant Exclusion treatments. We deployed Procedural Controls for both Exclusion treatments to measure any effects of the exclusion structures on seed removal. If the exclusion

structures had no influence on results, we expected to find that seed removal from Procedural Controls would not differ from Controls.

### 3.3.3 Statistical Analysis

To compare the effects of season, treatment and their interaction on seed removal we used a generalised linear mixed-effects model with a Gaussian distribution and site as a random factor. We used Tukey's HSD tests to perform post hoc pairwise comparisons. Analyses were conducted in R version 3.3.2 (R Core Team, 2016) using lme4 version 1.1.12.

### 3.4 Results

Woylies were the only mammalian predator of seeds. Woylie spoor was detected at 45% of foraged trays containing *D. viscosa* seeds and 34% of foraged trays containing *A. ligulata* seeds. Ants were detected in 15% of *A. ligulata* foraged trays and 2% of *D. viscosa* foraged trays. Bird spoor was not detected at any of the trays.

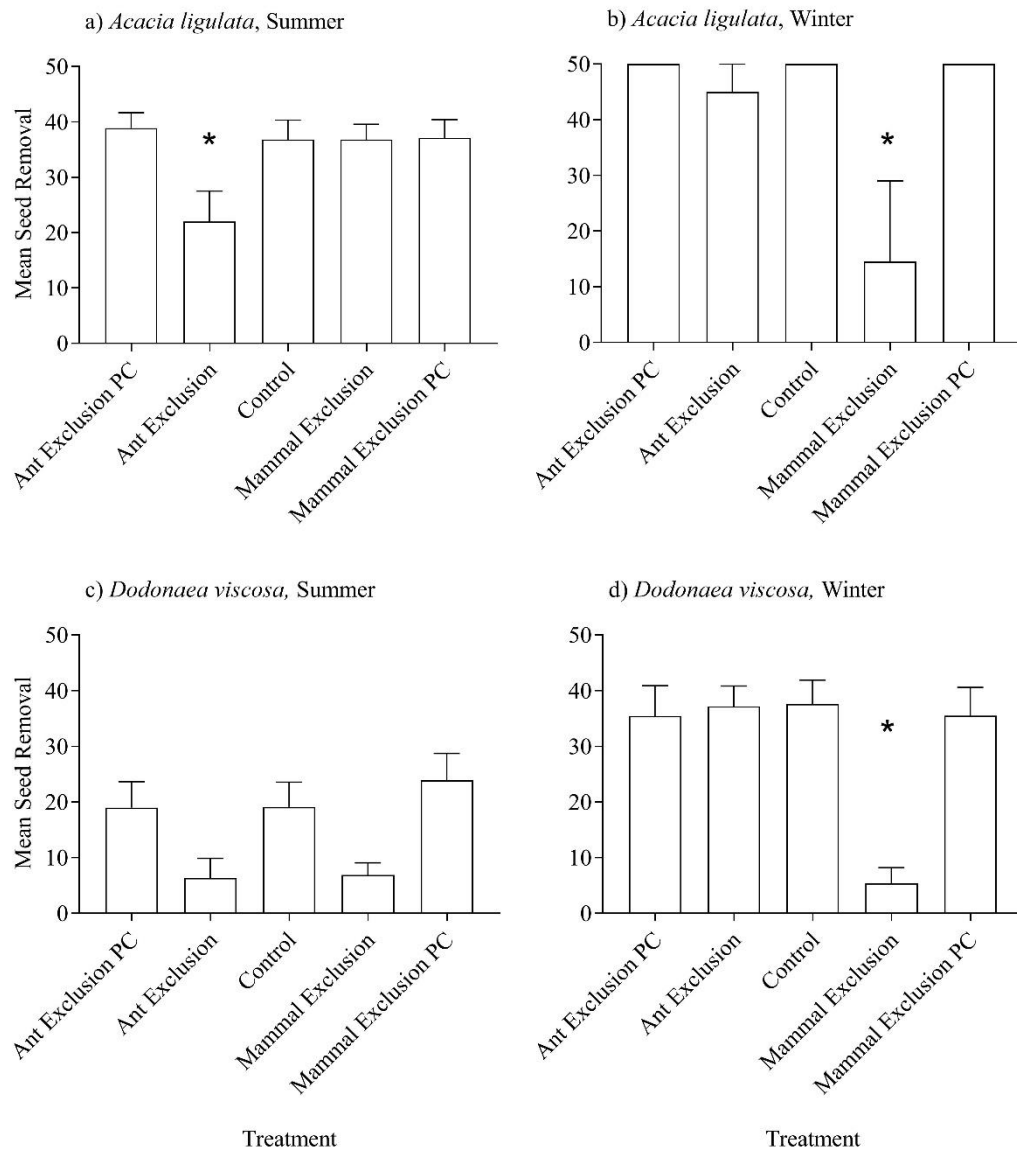
There was an effect of treatment for both *Acacia ligulata* ( $F = 5.66$ ,  $df = 4$ ,  $112$ ,  $P < 0.001$ ) and *Dodonaea viscosa* ( $F = 10.05$ ,  $df = 4$ ,  $143$ ,  $P < 0.001$ ). There was an effect of season for both *A. ligulata* ( $F = 27.09$ ,  $df = 1$ ,  $112$ ,  $P < 0.001$ ) and *D. viscosa* ( $F = 33.43$ ,  $df = 1$ ,  $143$ ,  $P < 0.001$ ) and there was an interaction between treatment and season for *A. ligulata* ( $F = 4.81$ ,  $df = 1$ ,  $112$ ,  $P < 0.001$ ) and for *D. viscosa* ( $F = 3.76$ ,  $df = 4$ ,  $143$ ,  $P < 0.01$ ).

Post-hoc pairwise tests revealed that during winter there was less seed removal from Mammal Exclusion treatments compared to Control treatments for *A. ligulata* ( $P < 0.05$ ) (Fig. 3.1b) and compared to all other treatments for *D. viscosa* ( $P < 0.001$ ) (Fig. 3.1d), but no difference for other pair combinations ( $P > 0.05$ ). In summer,

there was a difference between the Ant Exclusion and Control for *A. ligulata* ( $P < 0.01$ ) (Fig. 3.1a), but there was no difference between treatments in summer for *D. viscosa* ( $P > 0.05$ ) (Fig. 3.1c). *A. ligulata* seeds had consistently higher removal rates than *D. viscosa*. Overall, seed removal was higher in winter than in summer (Fig. 3.1). Procedural Controls for both species were not significantly different from Controls for summer or winter ( $P > 0.1$ ) (Fig. 3.1), indicating that the physical presence of the experimental treatments had no unintended influence on seed removal.

### 3.5 Discussion

Our results imply that the dominance of ants as granivores in arid Australia (Morton, 1985) may be an artefact of the decline and hence functional extinction of native mammals (Woinarski et al., 2015). The foraging tray experiment revealed that reintroduced woylies were at least as important as ants in the removal of seeds of two shrub species. Moreover, high rates of seed predation from the Ant Exclusion treatments in winter and for *A. ligulata* in summer suggest that woylies predate on seeds year-round whereas ants primarily removed seeds during summer and took very few seeds during winter. Our experiment provides evidence that woylies are significant seed predators, although it is important to note that the mammal assemblage at Scotia had a depauperate native rodent assemblage with just one species of native rodent present in low density. Because many native rodents are granivorous (Gordon & Letnic, 2016, Mills et al., 2018, Seddon, Griffiths, Soorae, & Armstrong, 2014; Chapter 2) it is likely that restoration of native rodent assemblages would increase the overall rate of seed predation by mammals.



*Figure 3.1* Mean seed removal (+1 SEM) for each treatment for both seed species in both seasons. Total possible seed removal is 50. Asterisks denote significant differences from the Control treatment at  $P < 0.05$ .

Our study highlights how reversing functional extinction can allow us to rethink contemporary ecological processes (Seddon et al., 2015). In many cases population declines of once abundant species occurred prior to understanding of the roles they fulfilled within ecosystems (Jackson et al., 2001; Mills et al., 2018; Gordon &

Letnic, 2016; Valentine et al., 2017; Chapter 2). Consequently, contemporary understanding of ecosystem processes may be prone to shifting baselines because we simply do not know how species that are now rare or extinct shaped ecosystems in the past (Gordon et al. 2017; Mills et al., 2018; Gordon & Letnic, 2016; Chapter 2).

Taken together with previous studies showing that the burrowing bettong (*Bettongia lesueur*) (Mills et al., 2018; Chapter 2), spinifex hopping mouse (*Notomys alexis*) (Mills et al., 2018; Chapter 2), and dusky hopping mouse (*Notomys fuscus*) (Gordon & Letnic, 2016) are significant consumers of seeds, our results contribute to a growing body of work demonstrating that where small and medium sized mammals persist or have been reintroduced they can be significant seed predators. These findings suggest that granivorous mammals may once have been the dominant consumers and removers of seeds across the vast areas of arid Australia where they are now rare or extinct and that their presence or absence may have far-reaching ramifications for seed fate. This is because mammals frequently destroy seeds while consuming them whereas many of the seeds removed by ants are not consumed but simply have their eliasome removed before they are discarded (Davidson & Morton, 1984).

Our findings add a new dimension to current thinking about the adaptive benefits that myrmecochory has for arid Australian plants (Davidson & Morton, 1984; Giladi, 2006; Harrington & Driver, 1995). Globally, myrmecochory is thought to provide benefits for plants by dispersing seeds away from sites where they will be vulnerable to predation by granivores, particularly mammals, increasing dispersal distance and directing seeds to microsites suitable for germination (Auld & Denham, 1999; Giladi, 2006). However, in arid Australia myrmecochory is thought to accrue little

benefit as an adaptation to avoid seed predation (Davidson & Morton, 1984; Harrington & Driver, 1995). This may be because seed predation by mammals had little influence on the fate of seeds in studies that were conducted where granivorous mammals were rare or extinct (Morton, 1985). By showing that rewilded mammals are significant predators of shrub seeds our study provides support for the idea that myrmecochory in Australian arid zone shrubs may also be an adaptation to escape predation by mammals (Giladi, 2006; Paulsen et al., 2013).

### 3.6 References

Australian Bureau of Meteorology. (2017) Retrieved from <http://www.bom.gov.au/> (Accessed 4 May 2017).

Auld, T.D. & Denham, A.J. (1999) The role of ants and mammals in dispersal and post-dispersal seed predation of the shrubs *Grevillea* (Proteaceae). *Plant Ecology*, **144**, 201–213.

Brown, J.H., Reichman, O.J. & Davidson, D.W. (1979) Granivory in desert ecosystems. *Annual Review of Ecology and Systematics*, **10**, 201–227.

Davidson, D.W. & Morton, S.R. (1984) Dispersal adaptations of some *Acacia* species in the Australian arid zone. *Ecology*, **65**, 1038–1051.

Giladi, I. (2006) Choosing benefits or partners: A review of the evidence for the evolution of myrmecochory. *Oikos*, **112**, 481–492.

Gordon, C.E., Eldridge, D.J., Ripple, W.J., Crowther, M.S., Moore, B.D. & Letnic, M. (2017) Shrub encroachment is linked to extirpation of an apex predator. *Journal of Animal Ecology*, **86**, 147–157.

Gordon, C.E. & Letnic, M. (2016) Functional extinction of a desert rodent: implications for seed fate and vegetation dynamics. *Ecography*, **39**, 815–824.

Harrington, G.N. & Driver, M.A. (1995) The effect of fire and ants on the seed-bank of a shrub in semi-arid grassland. *Australian Journal of Ecology*, **20**, 538–547.

Inouye, R.S., Byers, G.S. & Brown, J.H. (1980) Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology*, **61**, 1344–1351.

Jackson, JBC, Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. ... Warner, R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–637.

Mills C.H., Gordon C.E., & Letnic M. (2017) Rewilded mammal assemblages reveal the missing ecological functions of granivores. *Functional Ecology* **32**, 475–485.

Mills CH, Letnic M. (2018) Data from: Rewilding reveals functional extinction of a granivorous mammal in arid Australia. Dryad Digital Repository.

Morton, S.R. (1985) Granivory in arid regions: comparison of Australia with North and South America. *Ecology*, **66**, 1859–1866.

Murray, B.R., Dickman, C.R., Watts, C.H.S. & Morton, S.R. (1999) The dietary ecology of Australian desert rodents. *Wildlife Research*, **26**, 857–858.

Paulsen, T.R., Colville, L., Kranner, I., Daws, M.I., Högstedt, G., Vandvik, V., & Thompson, K. (2013) Physical dormancy in seeds: a game of hide and seek? *New Phytologist* **198**, 496–503.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Seddon, P.J., Griffiths, C.J., Soorae, P.S. & Armstrong, D.P. (2014) Reversing defaunation: restoring species in a changing world. *Science*, **345**, 406–412

Valentine, L.E., Bretz, M., Ruthrof, K.X., Fisher, R., StJ Hardy, G.E., & Fleming, P.A. (2017) Scratching beneath the surface: bandicoot bioturbation contributes to ecosystem processes. *Austral Ecology* **42**, 265–276.

Verdon, S.J., Gibb, H., & Leonard, S.W.J. (2016) Net effects of soil disturbance and herbivory on vegetation by a re-established digging mammal assemblage in arid zone Australia. *Journal of Arid Environments* **133**, 29–36.

Woinarski, J.C.Z., Burbidge, A.A. & Harrison, P.L. (2015) Ongoing unraveling of a



continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences*, **112**, 4531–4540.

## **Chapter 4: The Rewilding-Jigsaw Dilemma: a rewilded mammal assemblage shapes a desert ecosystem in unexpected ways**

Author List: Mills, C. H., Ooi, M., Tuft, K. D., & Letnic, M.

Contributions: C.M. conducted 80% of the total work. C.M. and M.L conceived the study and conducted statistical analyses. C.M. and M.O. collected the data. C.M. led the writing of the manuscript with input from all authors.



A drone's eye view of experimental exclosures

#### 4.1 Abstract

Rewilding is the deliberate reintroduction of species to restore missing ecosystem processes and often refers to the reintroduction of a single, charismatic species and its top-down ecological function. Increasingly, the goal of rewilding is to reassemble an ecosystem by restoring the ecological functions of multiple species. However, because the extinction of rewilded species has often preceded an understanding of their ecological functions, and other co-occurring species have become extinct while new ones introduced, rewilding is in many ways analogous to reassembling an incomplete jigsaw puzzle. Consequently, rewilding can be fraught with guesswork because from the perspective of contemporary knowledge the outcome of rewilding may be the formation of a novel ecosystem.

Two important groups of mammals that are functionally extinct across Australia are digging marsupials and native rodents. Globally, digging mammals and rodents are recognised as being keystone guilds; however, in Australia knowledge of their functional roles is limited to the effects of their diggings.

Here, we investigate the effects that restoring populations of the digging marsupial *Bettongia lesueur lesueur* and rodents *Notomys alexis* and *Pseudomys australis* have on above ground vegetation and the seed bank using selective exclosure experiments in arid Australia.

We found that interactions between mammals and vegetation were more complicated than predicted from prior knowledge of these species' functional roles. Mammal activity drove a shift in the architecture and composition of the vegetation community from standing vegetation cover and longer-lived plants to increased litter

and grass cover. Native rodents and bettongs also reduced the abundance of two forb species and were pre-dispersal seed predators.

Our results highlight a key dilemma facing rewilding, primarily that there may be considerable uncertainty in predicting the outcome of ecosystem reassembly. This is because, in many instances, we have insufficient information about species' ecosystem functions in their rewilded contexts to set goals. As a potential solution to the rewilding-jigsaw dilemma, we suggest detailed monitoring that allows for partitioning the effects of different consumers. Having such information at hand will enable informed decisions to be made about how to manage the novel ecosystems created through rewilding.

## 4.2 Introduction

Rewilding, the reintroduction of species to restore ecosystem processes, is growing in popularity around the world as a means to restore wild places in an otherwise human dominated landscape (Fernández, Navarro, & Pereira, 2017; Svenning et al., 2015; Sweeney et al., 2019). The term rewilding is often used to describe the reintroduction of a single species and the top-down ecological function it provides (Ripple & Beschta, 2003; Seddon, Griffiths, Soorae, & Armstrong, 2014).

Many rewilding projects have focused on reintroducing large-bodied, charismatic animals to ecosystems. In particular, large mammals such as wolves, bears and ungulates have high per capita metabolic demand and therefore strong per capita effects as consumers and well-documented ecological roles (Ripple & Beschta, 2003; Seddon et al., 2014). In contrast, small mammals, birds and reptiles with low per capita metabolic demands but high population density have often been overlooked in rewilding programs. However, their roles as keystone species,

ecosystem engineers, granivores, and pollinators with the potential to drive ecosystem dynamics has been highlighted in some ecosystems, such as via the functional extinction of small bodied mammals and birds and the reintroduction of tortoises to Mauritius (Anderson, Kelly, Ladley, Molloy, & Terry, 2011; Davidson, Detling, & Brown, 2012; Delibes-Mateos, Smith, Slobodchikoff, & Swenson, 2011; Gordon & Letnic, 2016; Griffiths et al., 2010).

Extinction has often preceded understanding of species' ecological functions, and in many regions of the Earth more than one species has become extinct and new species have been introduced. Thus, rewilding an ecosystem is in many ways analogous to assembling an incomplete jigsaw puzzle, where the box showing the solution to the puzzle was lost some generations ago, the number of missing pieces is unknown, and other puzzle pieces have been thrown in (Hunter, Britz, Jones, & Letnic, 2015). The rewilding jigsaw dilemma is particularly pertinent in cases where the historical ranges and abundances of locally extinct species are poorly understood, or where introduced species have become established and exert strong interactions within the remnant ecosystem (Estes et al., 2011; Legge et al., 2018). Consequently, rewilding can be fraught with guesswork and unintended consequences because the outcome may, from the perspective of contemporary knowledge, be the formation of a novel ecosystem (Hobbs et al., 2014).

Australia has an appalling record of mammal extinctions. In the last 200 years around 30 mammals have become extinct and many more have undergone dramatic range declines (Woinarski, Burbidge, & Harrison, 2015). Australia's mammal declines have been most severe in arid regions, where numerous species of marsupials and native rodents, weighing between 35 - 5,500g, have become rare or

extinct since European arrival, partly due to the introduction of novel predators, the red fox (*Vulpes vulpes*) and cat (*Felis catus*) (Burbidge & McKenzie, 1989; Woinarski et al., 2015). The flow-on effects that mammal declines have had on the functioning of Australia's vast arid ecosystems are largely unknown, but there is speculation that now rare or extinct mammals were once keystone species whose activities were essential for maintaining healthy ecosystems (Gordon & Letnic, 2016; James, Eldridge, & Hill, 2009; Mills, Gordon, & Letnic, 2018; Mills & Letnic, 2018; Chapter 2, 3).

Two potentially important groups of mammals that have become functionally extinct across much of the Australian arid zone are digging marsupials and native rodents (Fleming et al., 2014; Woinarski et al., 2015). Rodents and digging mammals are recognised globally as keystone species (Davidson et al., 2012; Delibes-Mateos et al., 2011; Prugh & Brashares, 2012) for their role as herbivores, prey, and as ecosystem engineers (Davidson et al., 2012; Delibes-Mateos et al., 2011). Indeed, there is a considerable body of evidence showing that the diggings created by many Australian marsupials function as fertile pits that accumulate seeds and nutrients, thereby stimulating germination (Decker, Eldridge, & Gibb, 2019; Hayward et al., 2016; James et al., 2009; Valentine et al., 2018). However, very little is known about how digging marsupials and native rodents can shape vegetation communities through their roles as consumers (Gordon & Letnic, 2016; Lyons, Mills, Gordon, & Letnic, 2018). Similarly, little is known regarding how their functional roles as consumers and diggers interact (Verdon, Gibb, & Leonard, 2016).

Rewilding efforts in Australia have largely focused on restoring the ecological functions of small bodied, digging marsupials, while native rodents are

underrepresented in rewilding programs (Legge et al., 2018; Mills et al., 2018; Chapter 2). At the Arid Recovery Reserve in South Australia, locally extinct mammals have been introduced into a 123 km<sup>2</sup> mammalian predator-free enclosure with the vision to reassemble the ecosystem which existed prior to the invasion of introduced predators and European rabbits (*Oryctolagus cuniculus*; Moseby, Lollback, & Lynch, 2018). The removal of introduced animals from the fenced area has facilitated increased abundances of rodents that existed in the area (Moseby, Hill, & Read, 2009).

Here we investigate the effects that the three most abundant mammals within Arid Recovery, the digging marsupial burrowing bettongs (*Bettongia lesueur lesueur*) and two rodents (*Notomys alexis* and *Pseudomys australis*), have on the architecture and composition of vegetation and seed bank on sand dunes using exclosures. Based on previous knowledge of the foraging ecology of digging marsupials and rodents we expected that:

- 1) litter cover will be greater in plots where bettongs have access because litter accumulates in the foraging pits they create (Hayward et al., 2016; James et al., 2009);
- 2) plants would be shorter where bettongs and rodents have access as omnivorous mammals often selectively consume the reproductive parts of plants (Murray, Dickman, Watts, & Morton, 1999; Weltzin, Archer, & Heitschmidt, 1997);
- 3) woody plant cover would be greater in plots which excluded mammals because omnivorous mammals preferentially consume their seeds (Gordon & Letnic, 2016; Mills et al., 2018; Chapter 2) and vegetative parts (Gordon et al., 2017; Moseby et al., 2018);

4) overall vegetation cover and plant species richness would be greater where bettongs have access due to the accumulation of seeds, nutrients and moisture in the pits they create (Davidson et al., 2012; James et al., 2009; Valentine et al., 2018);

5) finally, we predicted that the seed bank would largely reflect the above-ground vegetation, with fewer seeds of woody plants which are selectively consumed by rodents (Gordon & Letnic, 2016; Mills et al., 2018; Chapter 2) but greater seed abundance overall due to the accumulation of seeds in pits created by bettongs (James et al., 2009).

### 4.3 Methods

#### 4.3.1 Study Site and Study Species

Arid Recovery (Latitude -30.381155° S, Longitude 136.900283° E) is situated in the Moondipitchnie Dunefield near Roxby Downs in arid South Australia and has a mean annual rainfall of 148 mm (Australian Bureau of Meteorology 2018). The landscape at Arid Recovery is characterized by east-west longitudinal sand dunes spaced approximately 200 -1000 m apart with clay swales between the dunes. Vegetation on the dunes consists of perennial trees and shrubs (*Acacia aneura*, *Dodonaea viscosa*, *Callitris glaucophylla*) with an understorey of grasses and forbs. Dune-top sand in this area is highly mobile (Lyons et al., 2018).

Five mammal species have been reintroduced to Arid Recovery, and of them, burrowing bettongs (body mass 1200 g) are most numerous (Mills et al., 2018; Moseby et al., 2018; Chapter 2). Burrowing bettongs are omnivores that frequently dig when foraging to obtain roots, seeds and fungi but also consume herbage (Robley, Short, & Bradley, 2001). Populations of the omnivorous rodents *Notomys*



*alexis* (body mass 30 g) and *Pseudomys australis* (body mass 45 g) have increased dramatically since introduced predators were removed from the reserve (Mills et al., 2018; Moseby et al., 2009; Chapter 2). Other rodents present in the reserve include *Pseudomys bolami* (body mass 15 g), and the introduced *Mus musculus* (body mass 15 g).

#### 4.3.2 Rainfall

To provide an index of rainfall during our study period, we obtained monthly rainfall data from January 2016 until May 2018. To assess if rainfall conditions for our study period were below average, average, or above average, we compared monthly rainfall against percentiles of the distribution of historic records for the same months. We defined below-average conditions as when monthly rainfall totals were below the 50<sup>th</sup> percentile (median) of the historic record, average conditions as between the median and the 75<sup>th</sup> percentile of the historic record and above average conditions as above the 75<sup>th</sup> percentile of the historic record. Rainfall data for the years 1931 – 1997 came from Roxby Downs Station (21 km from study site). Rainfall data for the years 1998 – 2018 came from Roxby Downs, Olympic Dam Aerodrome (9 km from study site) and when there were missing data, from Andamooka (35 km from study site; Figs 4.1-4.2; Australian Bureau of Meteorology, 2018).

Monthly rainfall totals during the study period are clearly separated into two rainfall periods, a wet period and a dry period (Fig. 4.1). The period between March 2016 and April 2017 was a period of wet climatic conditions. This was evidenced by 7/14 months receiving rainfalls above the 75<sup>th</sup> percentile. The period from May 2017 to May 2018 was a period of dry climatic conditions, as evidenced by 10/13 months receiving rainfall below the median and only three months above (Fig. 4.1).

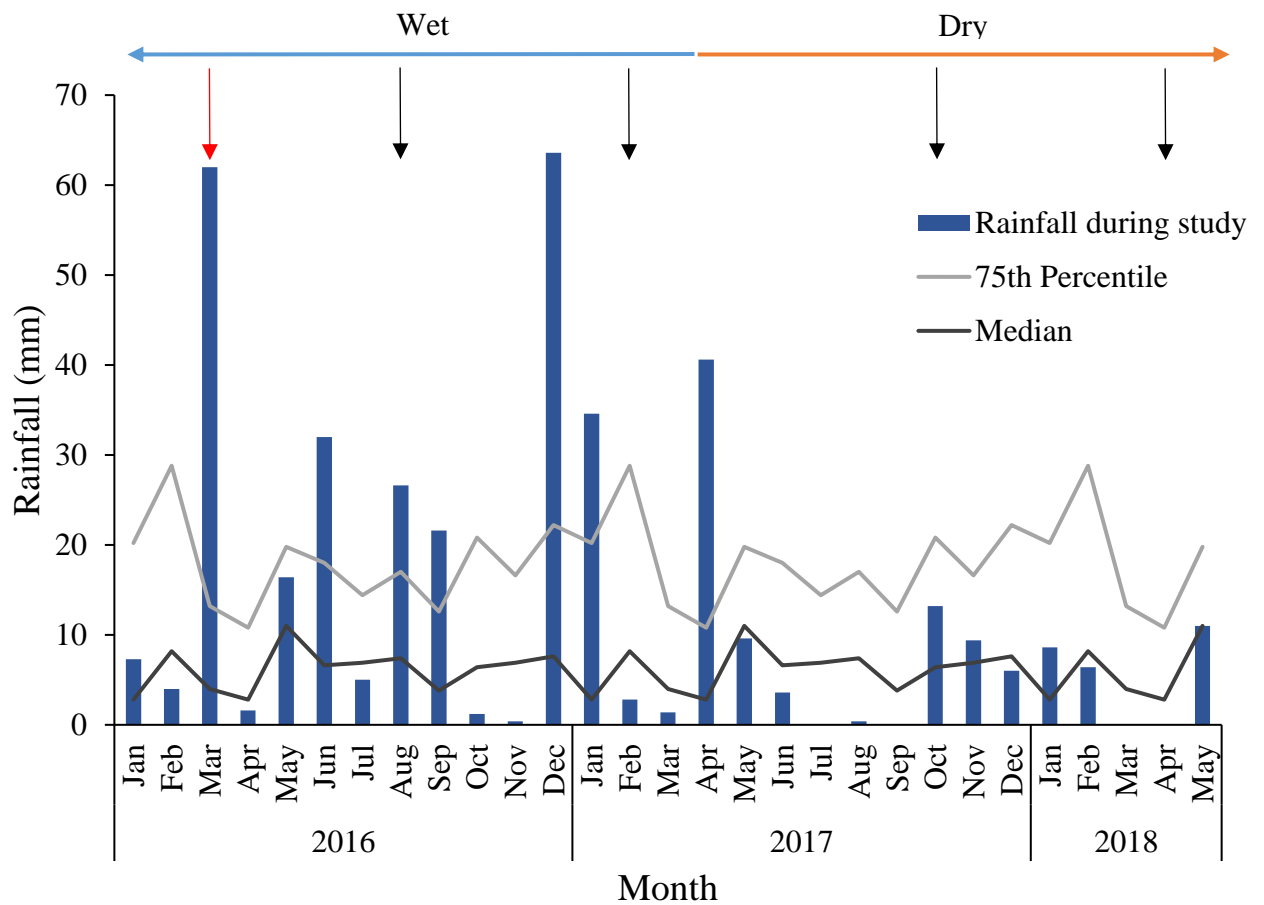


Figure 4.1 Rainfall for our study period (blue bars), with long-term median and 75<sup>th</sup> percentile overlaid. Red arrow indicates when fences were constructed, black arrows are sampling occasions. Rainfall between the median and 75<sup>th</sup> quantiles is average, rainfall above the 75<sup>th</sup> quantile is above average (wet periods) and rainfall below the median is below average (dry periods).

#### 4.3.3 Exclusion Experiment

In April 2016 we established five randomised blocks of exclosures on the crests of sand-dunes within Arid Recovery (Fig. 4.2). Exclosure treatments were each 11 m x 11 m with a 0.5 m buffer zone to account for fence effects and allowed access to kangaroos (*Macropus* spp.) which are large herbivores present at low density in Arid Recovery (Moseby et al., 2009). We established blocks on dune-tops because these are the primary habitats for the most abundant mammal species in the reserve; burrowing bettongs, *Notomys alexis* and *Pseudomys australis*.

Each enclosure block consisted of five treatments:

- Exclude All: Aviary netting (13 mm aperture) 0.9 m high with 0.5 m floppy top and 0.5 m foot netting.
- Exclude bettongs but not rodents (referred to as “Exclude Bettongs”): 30 mm aperture netting with 0.5 m floppy top and 0.5 m foot netting.
- Exclude Rodents: Aviary netting (13 mm aperture) 0.3 m high with 0.5 m foot netting.
- Control: posts marking corners of plot with full access and no sides.
- Procedural Control: Aviary netting (13 mm aperture) 0.3 m high with 0.5 m foot netting with gaps.

a) Exclusion; wet



b) Exclusion; dry



c) Control; wet



d) Control; dry



*Figure 4.2* Experimental exclusion fences (a, b) and controls (c, d) in Arid Recovery Reserve, during a wet period in the August 2016 sampling trip (a, c) and during a dry period in the April 2018 sampling trip (b, d).

#### 4.3.4 Mammal Activity

To provide an index of general visitation to the dune top study area and to identify the efficacy of our exclusion fencing treatments, we placed motion-sensing camera traps (Reconyx Hyperfire HC500) along the fences of all treatments from April 2016 – August 2016 for a total of 1,928 trap nights. Cameras were set to take five photos in a “Rapidfire” burst with no delay. To assess the efficacy of exclusion treatments we identified how many visits were recorded inside each treatment for a total of between 243 - 459 trap nights per treatment. We identified the animals in the photos and scored unique visits as images of a species that were separated by more than 30 minutes. The number of unique visits was then divided by trap nights for the site or the treatment as appropriate to calculate number of visits per 100 trap nights.

#### 4.3.5 Vegetation Composition and Architecture

We conducted vegetation surveys within experimental exclosures over a two-year period, with survey trips occurring in spring and autumn of each year (August 2016, February 2017, October 2017 and April 2018). Within each exclosure treatment we randomly selected and marked out ten 1 x 1 m quadrats. We excluded quadrats which contained adult shrubs to avoid nurse effects (Howard, Eldridge, & Soliveres, 2012) and quadrats which were located in bare windswept patches where vegetation cannot grow. Within each quadrat we estimated percent cover of live vegetation, total standing vegetation (including dead and alive vegetation), sand and litter.

To detect any architectural impacts of herbivory, we measured the individual plants in each plot to represent the maximum and mode for grass and forb functional groups.

We used Generalised Linear Mixed-effects Models (GLMMs) with a Gaussian distribution to test for effects of experimental treatment and sampling trip on above ground vegetation variables including total vegetation and litter cover, cover of functional groups (shrub, grass, forb), cover of dominant species, and maximum and mode heights of grasses and forbs. We log+1 transformed litter cover and total vegetation cover to account for a left skew in the dataset. Dominant grass and forb species were identified as those which occurred in all experimental blocks during the August 2016 sampling trip, when vegetation cover was greatest, and which were subsequently detected on one or more sampling occasions. These were *Aristida contorta* (Poaceae; grass), *Brassica tournefortii* (Brassicaceae; annual forb), *Crotalaria eremaea* (Fabaceae; perennial forb), *Gnephosis eriocarpa* (Asteraceae; annual forb), *Paractaenum novae-hollandiae* (Poaceae; grass), *Rhodanthe moschata* (Asteraceae; annual forb), *Salsola australis* (Chenopodiaceae; biennial forb) and *Sida ammophila* (Malvaceae; subshrub). For taxonomic nomenclature of all plant species in this article see Council of Heads of Australasian Herbaria (2019).

All GLMMs were performed using the statistical platform R, version 3.5.2 (R Core Team, 2016) and the lme4 version 1.1 (Bates, Maechler, Bolker, & Walker, 2015) and lmerTest version 3.1 (Kuznetsova, Brockhoff, & Christensen, 2017) packages, using sampling trip and treatment as fixed factors. We included treatment block as a random factor and quadrat as a random factor nested in treatment block to account for repeated measurements. We used Tukey's tests for post-hoc pairwise comparisons where a significant effect was found in the main model.

Richness was calculated by counting the total number of species within each treatment, excluding shrubs, over all sampling times. We compared species richness

across treatments using a GLMM with a Gaussian distribution, with treatment as a fixed factor and block as a random factor.

#### 4.3.6 Soil Seed Bank

To measure diversity and abundance of seeds in the soil seed bank in each exclusion treatment, we collected soil in October 2017 by randomly selecting nine locations within each enclosure and removing soil samples of dimensions 10 cm x 10 cm and 5 cm depth. Any litter present on the soil surface of the sample area was stored separately. We used stratified random sampling, where samples were within 30 cm of forbs or grasses but not in open areas, areas under adult shrubs or in fresh animal digs. All samples for each plot were combined prior to transport.

A 1.9 L subsample from the original bulked sample for each plot was then used for seed bank analysis. In a glasshouse in Sydney, Australia, soil samples were placed in trays 30 cm x 20 cm lined with geotextile fabric. Trays were randomly arranged on glasshouse benches. The entire litter sample (between 1 g and 16 g) was placed separately in a 10 cm x 20 cm tray on a bed of soil from the study site which had been heated in an oven at 180 °C overnight to sterilise any viable seeds. We established three trays of sterilised sand as glasshouse controls. No plants emerged from the sterilized sand demonstrating that the sterilisation treatment was effective.

On the 18<sup>th</sup> January 2018, during the Southern Hemisphere summer all trays were flooded with water to mimic a large rainfall event. We provided excess water each day until germination was observed and then watering was reduced to 2 minutes at 9 am and 3 pm daily using overhead sprinklers. Tray order was rearranged randomly at four weeks. Seedlings were identified and removed weekly for two months, by

which time no new seedlings appeared. Trays were dried and any large seeds (specifically *Acacia ligulata* (Fabaceae; perennial shrub), *Crotalaria eremaea* (Fabaceae; perennial forb) and *Dodonaea viscosa* subsp. *angustissima* (Sapindaceae; perennial shrub)) were sieved out with a 2 mm sieve and counted. We sieved specifically for this group because they are hard seeded, physically dormant species which are unlikely to germinate under the glasshouse conditions. We combined the total seedlings from the litter and the soil with the counts of sieved seeds for analysis.

To determine if there was a difference between treatments in the soil seed bank, we used a GLMM with a Gaussian distribution, including treatment as a fixed factor and experimental block and mass of litter in the sample as random factors. Our response variables included the total number of emergent seedlings and the number of seedlings from each functional group (forbs and grasses). We ran separate analyses for the common species (top 30 %): *Brassica tournefortii* (Brassicaceae; annual forb), *Crotalaria eremaea* (Fabaceae; perennial forb), *Rhodanthe moschata* (Asteraceae; annual forb), *Euphorbia porcata* (Euphorbiaceae; annual forb), *Phyllanthus lacunellus* (Phyllanthaceae; perennial forb).

## 4.4 Results

### 4.4.1 Mammal Activity

Bettongs, *Notomys alexis*, and *Pseudomys australis* were the most frequent visitors to the study area. Bettongs visited six times more frequently than any other

marsupial digging mammal and *Notomys alexis* and *Pseudomys australis* visited at least four times as frequently as any other rodent (Fig. 4.3a).

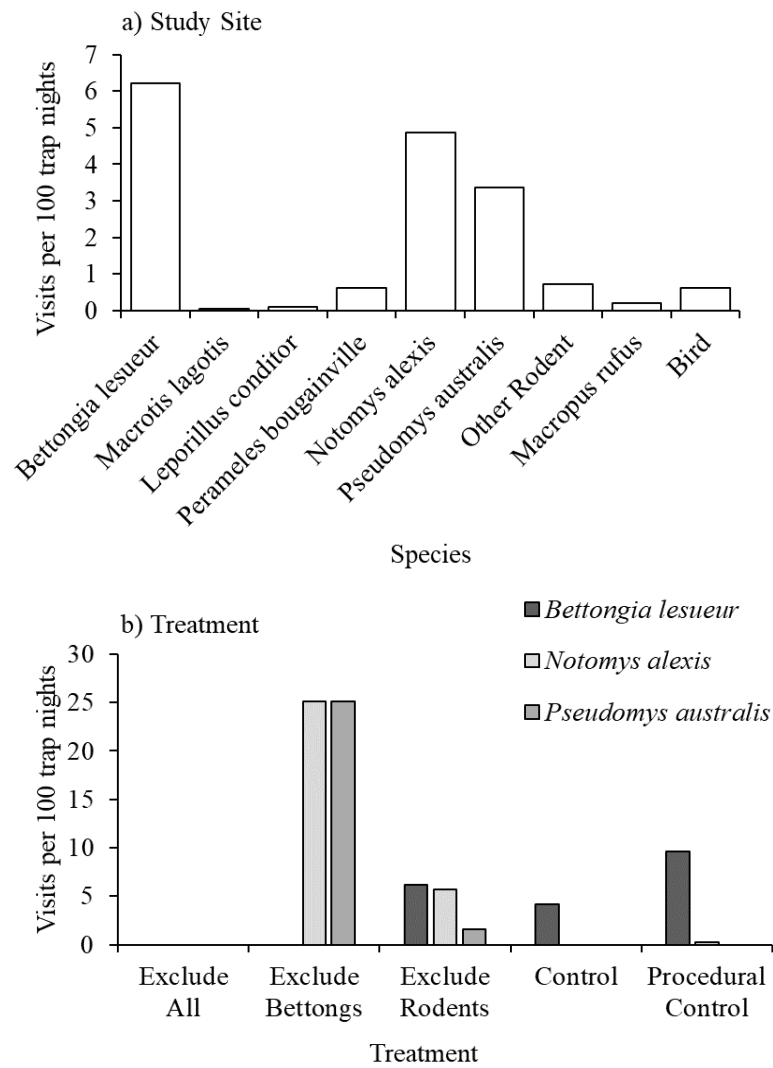
Bettongs visited the Exclude Rodents, Control and Procedural Control treatments almost equally (Fig. 4.3b). *Notomys alexis* and *Pseudomys australis* visited the Exclude Bettong treatment most often and did not visit the Exclude All or the Control treatments. *Notomys alexis* visited the Exclude Rodents treatment less than 20 % as many times as the Exclude Bettongs treatment and visited the Procedural Control once (Fig. 4.3b). *Pseudomys australis* visited the Exclude Rodents treatment on 2% of trap nights and did not visit the Procedural Control treatment.

*Macrotis lagotis*, *Perameles bougainville* and other rodent species together made up less than 9 % of all visits. The Exclude All treatment was only visited by *Macropus rufus* (red kangaroo) and birds.

#### 4.4.2 Vegetation Composition and Architecture

There were varied responses of vegetation cover and architecture to mammal exclusion or access (Fig. 4.4). Overall, litter cover was lower and total vegetation cover was higher in Exclude All, Exclude Bettongs and Exclude Rodents treatments compared to the Control treatment; however, during the wet conditions that prevailed prior to the August 2016 sampling trip there was a flush of vegetation growth and little detectable difference between the treatments. Differences between treatments became apparent during the dry climatic conditions that prevailed after the August 2016 sampling trip. By the October 2017 and April 2018 sampling periods, many plant species were present only within the exclusion fences (Exclude All, Exclude Bettongs, Exclude Rodents) and not within the Controls (Figs 4.4-4.5).





*Figure 4.3* Number of unique visits per 100 trap nights by species for a) all species at whole study site and b) each treatment for the three most common species.

Vegetation cover decreased after the August 2016 sampling period, resulting in significant differences between sampling trips for all cover and height variables except for woody perennials including the shrub functional group and the chenopod *Salsola australis* (Table 1). There was no interaction between sampling trip and mammal exclusion treatment except for *Sida ammophila*. All Procedural Controls were within one standard error of Controls unless otherwise stated, demonstrating that fence structure had little unintentional effect on our results.

There was more total vegetation cover where mammals were excluded (Table 4.1a; Fig. 4.4a), with significantly less vegetation cover in the control treatment compared to the Exclude All ( $P < 0.01$ ) and Exclude Rodents ( $P < 0.01$ ) treatments and no difference between the other treatments.

Mammals did not affect the cover of forb and shrub functional groups ( $P > 0.05$ ; Table 4.1d,e); however, there was a difference in the cover of the grass functional group between the Exclude Rodents and the Exclude All treatments ( $P < 0.05$ ; Table 4.1c, Fig. 4.4b). By October 2017 when conditions were dry, the grass species *Paractaenum novae-hollandiae* showed a trend towards greater cover in Control and Procedural Control treatments compared to Exclude All, Exclude Bettongs and Exclude Rodents treatments; however, this effect was not significant at the  $P = 0.05$  threshold (Table 4.1j).

Cover of *Crotalaria eremaea* was greater in the Exclude Bettongs compared to the Exclude Rodents ( $P < 0.05$ ; Fig. 4.4c; Table 4.1h) with no other detectable differences between treatments. By April 2018 when conditions were extremely dry (Fig. 4.1- 4.2) *Crotalaria eremaea* was only present in the Exclude Bettongs treatment.

During the February 2017 sampling trip when conditions were wet, cover of *Sida ammophila* was much greater in the Procedural Control compared to all other treatments (all  $P < 0.01$ ). However, during the dry period after April 2017 cover persisted in exclusion treatments but was reduced in control treatments, and by April 2018 *Sida ammophila* was only present in the Exclude Bettongs treatment, leading to a significant interaction between sampling trip and treatment (Fig. 4.4d). Mammal access did not affect cover of *Brassica tournefortii*, *Rhodanthe moschata*, *Gnephosis eriocarpa*, *Salsola australis*, *Sida ammophila*, nor *Aristida contorta*.

There was more litter where mammals had access (Fig. 4.5a), with the least litter in the Exclude All (Table 4.1b). Both the Exclude Bettongs ( $P < 0.01$ ) and the Control ( $P < 0.001$ ) treatments had more litter cover than the Exclude All, and there was no difference in litter cover between the Exclude Bettongs and the Control. Mammals did not influence the maximum heights of grasses and forbs (Table 4.1n-q).

However, forbs were shorter on average in the Exclude All treatment compared to the Exclude Bettongs ( $P = 0.01$ ; Table 4.1o) and the Exclude Rodents ( $P < 0.05$ ).

Overall plant species richness did not differ between mammal access treatments ( $F = 0.69$ ,  $df\ 4/20$ ;  $P > 0.5$ ).

#### 4.4.3 Soil Seed Bank

There was no effect of mammal activity on the total number of seeds in the soil seed bank ( $F = 0.49$ ,  $df = 4/18$ ,  $P = 0.74$ ; Fig. 4.6a); however, mammal activity did impact individual species (Fig. 4.6). Specifically, more *Rhodanthe moschata* seedlings emerged ( $F = 4.02$ ,  $df = 4/18$ ,  $P = 0.02$ ) in the Exclude All compared to the Exclude Rodents ( $P = 0.001$ , Fig. 4.6b) and there were more seedlings in the Exclude All

compared to the Control and the Procedural Control although not at a statistically significant level ( $P > 0.05$ ).

Mammals reduced the number of *Crotalaria eremaea* seeds in the soil seed bank ( $F = 3.57$ ,  $df = 4/12$ ,  $P = 0.04$ ), with more seeds detected in the Exclude All compared to all other treatments ( $P < 0.05$ ; Fig. 4.6c). There was no difference between treatments in the number of Poaceae ( $F = 0.8$ ,  $df = 4/25$ ,  $P = 0.54$ ), forb ( $F = 0.25$ ,  $df = 4/17$ ,  $P = 0.9$ ), *Brassica tournefortii* ( $F = 0.59$ ,  $df = 4/17$ ,  $P = 0.68$ ), *Euphorbia porcata* ( $F = 2.7$ ,  $df = 4/24$ ,  $P = 0.055$ ) or *Phyllanthus lacunellus* ( $F = 1.28$ ,  $df = 4/20$ ,  $P = 0.31$ ) seedlings.

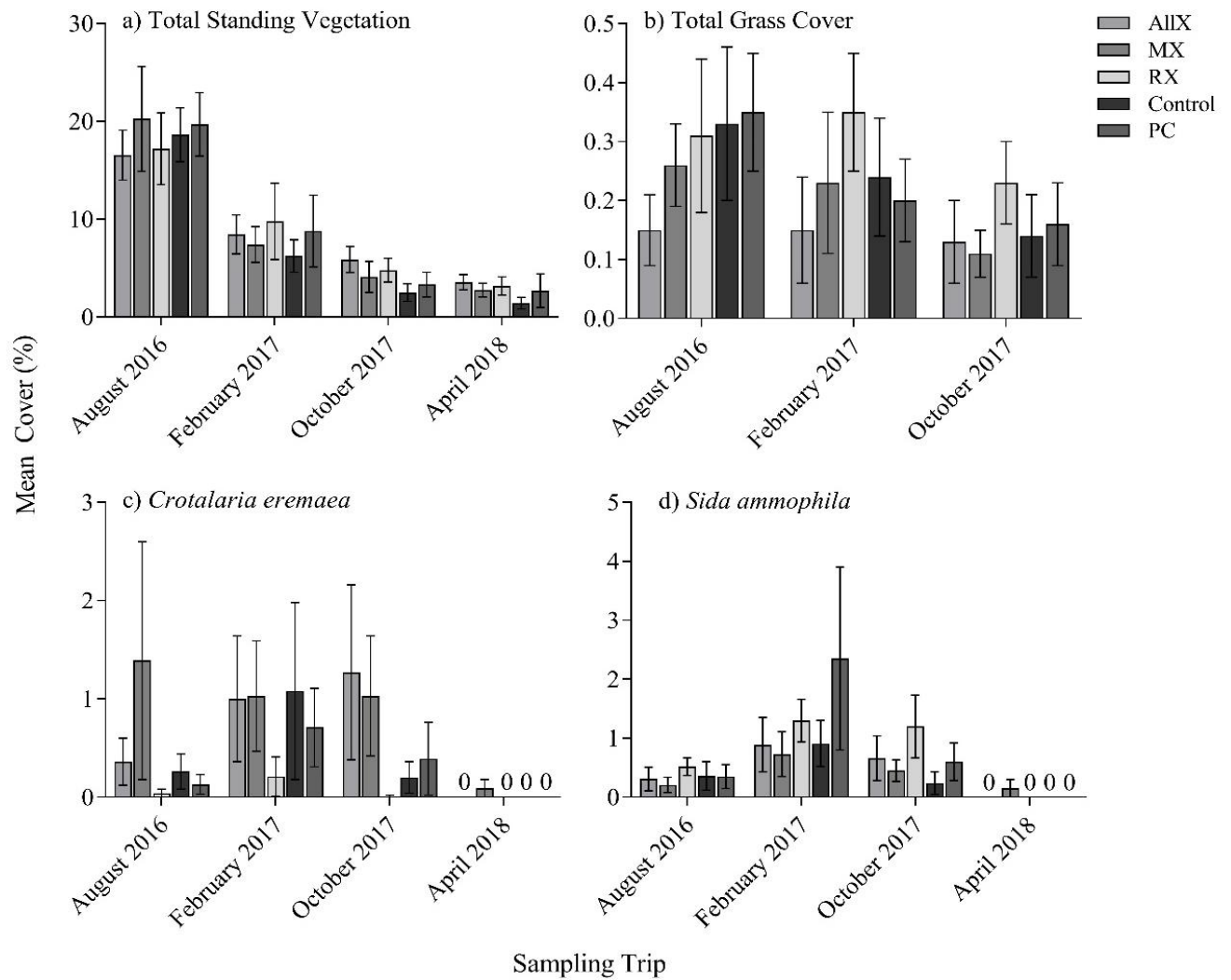
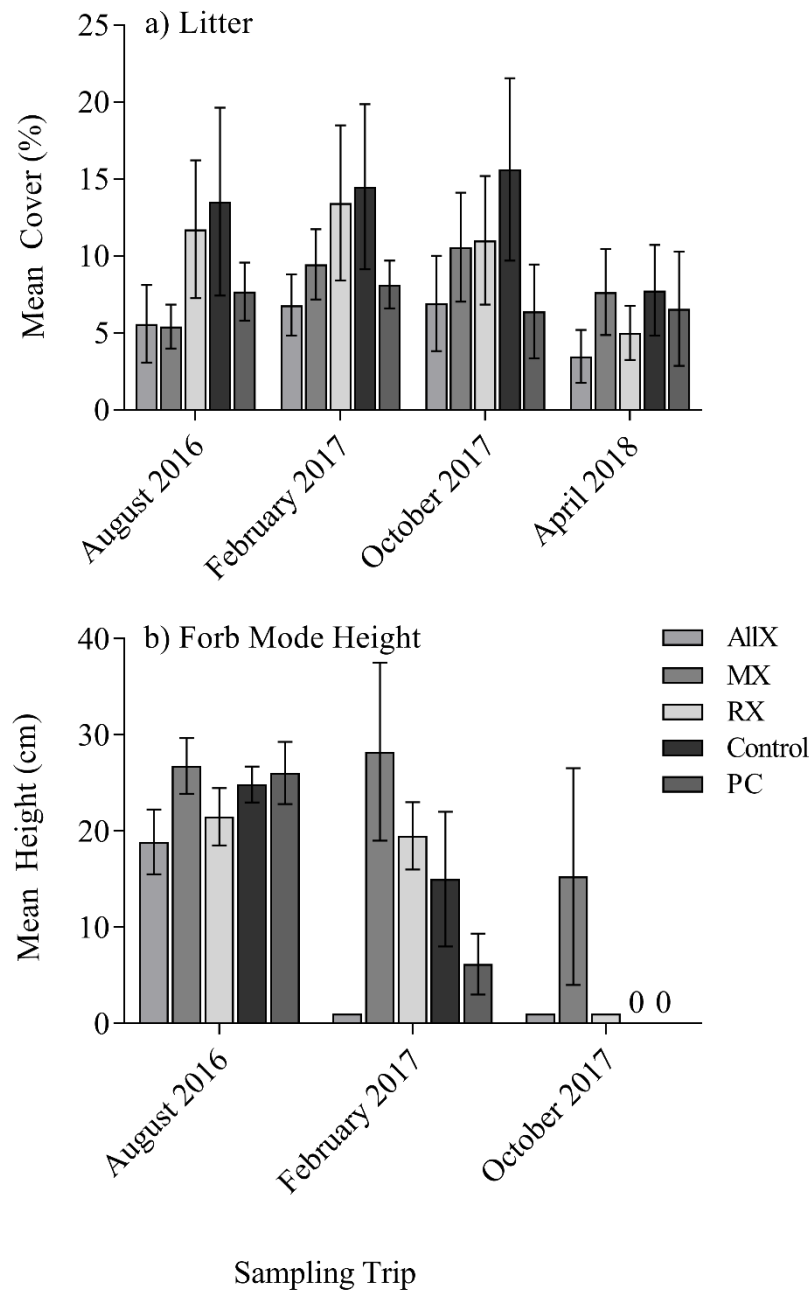


Figure 4.4 Mean cover ( $\pm 1$  SE) by treatment and sampling trip for functional variables a) Total Standing Vegetation, b) Total Grass Cover, and two perennial forb species c) *Crotalaria eremaea* and d) *Sida ammophila*. In b) only sampling trips when grass cover was detected are shown.



*Figure 4.5* Mean cover and height ( $\pm 1$  SE) by treatment and sampling trip for structural variables a) Litter and b) Forb Mode Height. There were no forb mode heights observed in the April 2018 sampling trip.

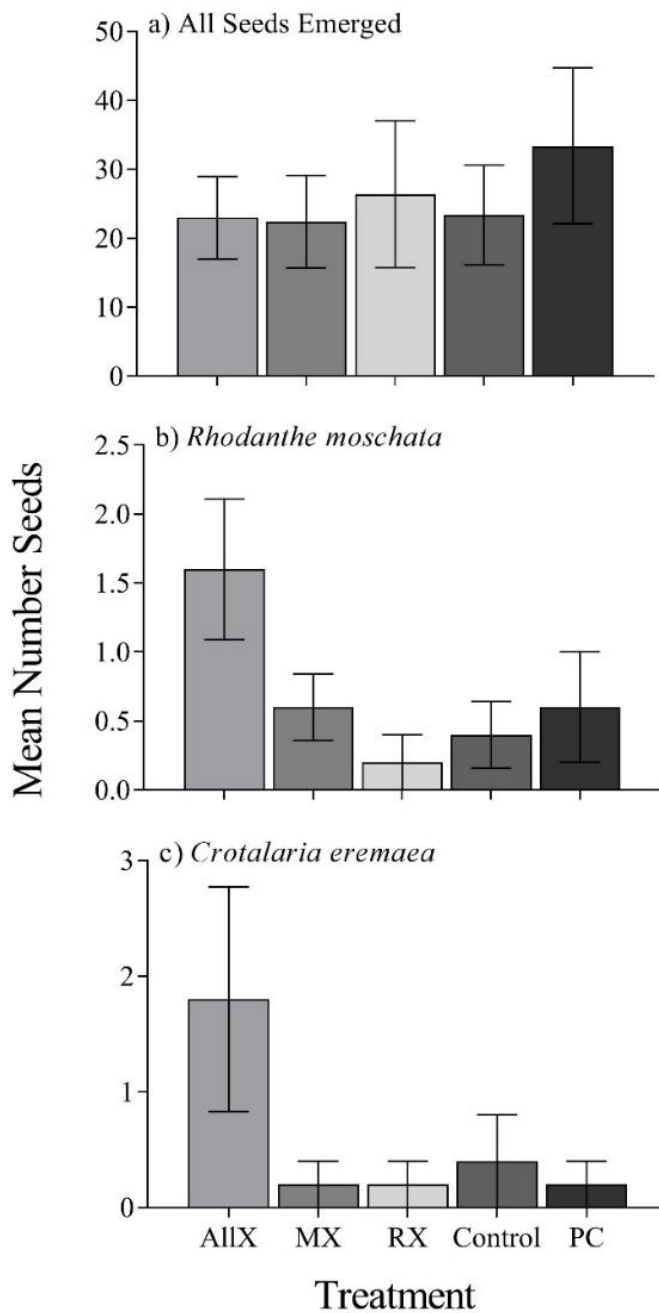


Figure 4.6 Mean seeds/seedlings ( $\pm 1$ SE) by treatment for a) Total Seeds, b) *Rhodanthe moschata* and c) *Crotalaria eremaea* grown and sieved from soil seedbank samples.

*Table 4.1* Results of generalised linear mixed-effects models comparing vegetation cover and heights across treatments and sampling trips, with quadrat nested in block as a random factor.

MODEL	df (n)	df (d)	F	P
<b>a) Total Standing Vegetation Cover (log+1 transformed)</b>				
Experimental Treatment	4	820	4.21	<b>&lt;0.01</b>
Sampling Trip	3	745	217.83	<b>&lt;0.0001</b>
Sampling Trip* Experimental Treatment	12	745	1.39	0.16
<b>b) Litter Cover (log+1 transformed)</b>				
Experimental Treatment	4	829	5.64	<b>&lt;0.001</b>
Sampling Trip	3	741	11.14	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	741	1.43	0.15
<b>c) Grass Functional Group</b>				
Experimental Treatment	4	786	2.38	<b>0.049</b>
Sampling Trip	3	745	35.47	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	746	0.96	0.49
<b>d) Shrub Functional Group</b>				
Experimental Treatment	4	753	1.45	0.22
Sampling Trip	3	775	2.37	0.07
Sampling Trip: Experimental Treatment	12	775	0.43	0.95
<b>e) Forb Functional Group</b>				
Experimental Treatment	4	833	1.33	0.26
Sampling Trip	3	833	257	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	833	1.11	0.35
<b>f) <i>Aristida contorta</i></b>				
Experimental Treatment	4	809	0.95	0.43
Sampling Trip	3	749	24.84	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	750	0.79	0.66
<b>g) <i>Brassica tournefortii</i></b>				
Experimental Treatment	4	834	1.65	0.16
Sampling Trip	3	833	92.53	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	833	1.6	0.09
<b>h) <i>Crotalaria eremaea</i></b>				
Experimental Treatment	4	757	2.67	<b>0.03</b>
Sampling Trip	3	773	4.39	<b>&lt;0.01</b>
Sampling Trip: Experimental Treatment	12	773	0.92	0.52
<b>i) <i>Gnephosis eriocarpa</i></b>				
Experimental Treatment	4	833	0.7	0.59
Sampling Trip	3	833	71.32	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	833	0.92	0.52



j) <i>Paractaenum novae-hollandiae</i>				
Experimental Treatment	4	835	1.97	0.097
Sampling Trip	3	833	14.61	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	833	1.25	0.24
k) <i>Rhodanthe moschata</i>				
Experimental Treatment	4	834	0.77	0.54
Sampling Trip	3	832	25.6	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	832	1.57	0.095
l) <i>Salsola australis</i>				
Experimental Treatment	4	685	1.31	0.27
Sampling Trip	3	723	1.76	0.15
Sampling Trip: Experimental Treatment	12	723	0.77	0.69
m) <i>Sida ammophila</i>				
Experimental Treatment	4	722	3.07	<b>0.02</b>
Sampling Trip	3	755	20.9	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	755	2.21	<b>0.01</b>
n) Forb Height Maximum				
Experimental Treatment	4	370	1.62	0.17
Sampling Trip	2	371	23.52	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	8	370	1.29	0.25
o) Forb Height Mode				
Experimental Treatment	4	270	5.09	<b>&lt;0.001</b>
Sampling Trip	2	273	12.93	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	6	270	2.14	<b>0.049</b>
p) Grass Height Maximum				
Experimental Treatment	4	332	1.94	0.1
Sampling Trip	2	302	220	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	8	305	1.22	0.28
q) Grass Height Mode				
Experimental Treatment	4	216	1.47	0.21
Sampling Trip	2	208	287	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	8	205	1.12	0.35



*Figure 4.7* Pre-dispersal seed predation by *Notomys alexis* captured by motion sensing cameras in control plots of exclusion experiment.

#### 4.5 Discussion

Our results show that a rewilded mammal assemblage shapes the architecture and composition of above ground vegetation and the composition of the seed bank in sand dune communities. However, the effects we observed did not conform with our predictions. We expected that the accumulation of litter, seeds, nutrients and moisture observed in foraging pits (James et al., 2009; Valentine et al., 2018) would lead to greater vegetation cover and litter in our control plots, with some reduction in the height of vegetation and woody shrub cover from selective herbivory and granivory (Gordon & Letnic, 2016; Mills et al., 2018; Murray et al., 1999; Chapter 2). Instead, we found that mammal activity reduced standing vegetation cover and led to a shift in the composition and architecture of above-ground vegetation from longer-lived plants to increased litter and grass. Native rodent activity led to changes

in the seed bank composition, reducing the number of seeds of key plant species.

Overall, we found that the combined effect of foraging pit creation and consumption by digging marsupials and native rodents had a more complicated effect on the vegetation community and the seed bank than we initially predicted.

Visitation records for each treatment indicate that the Rodent Exclusion treatment was only partially effective as a barrier to rodents but do suggest that rodents avoid bettongs when foraging. Rodents were not detected in the Control and Procedural Control where bettongs had access but were detected most frequently in the Exclude Bettongs treatment. While similar effects found in analogous systems have been attributed to dietary niche overlap and competition for limited resources (Davidson & Lightfoot, 2006), behavioural observations of rodent-bettong interactions from our study site (M. Letnic unpubl. data) demonstrate that rodents actively avoid bettongs and that bettongs monopolise food resources. This finding highlights the nuances involved with disentangling species interactions, as species may exclude one another and therefore observed effects on ecosystem processes may not necessarily be the direct additive effect of multiple species.

Our survey trips encompassed two extremes of the highly variable rainfall characteristic of the Australian arid zone (Morton et al., 2011). Following the flush of growth from above average rainfall in early survey trips, the landscape dried out and differences between treatments became apparent as the pressure from foraging mammals was concentrated on fewer plants. The two perennial forb species *Crotalaria eremaea* and *Sida ammophila* which were impacted by mammal species reduced in cover in all treatments following the wet period. However, cover had greater proportional reductions between sampling trips for control plots compared to

exclusion plots due to the pressure from foraging mammals. By the April 2018 sampling trip *Crotalaria eremaea* and *Sida ammophila* only remained in the Exclude Bettong treatment.

We found no treatment effect on ephemeral forbs despite their rapid response to rainfall events and the activity of digging mammals (Davidson & Lightfoot, 2006; Eldridge & Simpson, 2002; Hobbs & Mooney, 1985). Ephemeral forbs quickly senesce, so we suspect that more targeted sampling trips would be required to detect any changes in the cover of this functional group.

Our exclusion experiment showed that both native rodents and digging marsupials reduced abundance of seeds from two dominant forb species. The reduction in the numbers of forb seeds where mammals were active reflected shifts in the above-ground vegetation and is consistent with other studies which show that granivory and disturbance by mammals is associated with greater abundance of annual plant species (Davidson & Lightfoot, 2006; Eldridge & Simpson, 2002). While post-dispersal seed predation is an established driver of seed bank dynamics (Brown & Heske, 1990; Gordon & Letnic, 2016), we suggest that pre-dispersal seed predation by mammals, was the driver of the reduction in forb abundance that we report. This hypothesis is supported by incidental camera trap footage (Fig. 4.7) which shows that both rodents and bettongs engaged in pre-dispersal seed predation, consuming the seed pods and flowers of a range of forb species.

In addition to observed shifts in plant community composition, we found that mammals drove changes in the architecture of above ground vegetation. As predicted, mammal activity led to greater litter cover. Although we expected increases in litter cover to result from litter capture in foraging pits (James et al.

2009), we suggest that this litter accumulation is primarily due to mammals breaking up standing plants whilst they foraged. This is because we have photographs which show mammals breaking up standing plants while they foraged (Fig. 4.7) and because pits dug in the highly mobile sand of dune-tops are short-lived (James et al., 2009). Our prediction that plant height would be higher in the absence of mammals was supported. However, we found that this was primarily driven by an absence of standing plants in areas where bettongs and rodents had access, further supporting our finding that mammal activity, especially foraging, contributes to an architectural shift on dune-top habitats from standing vegetation to litter.

While our results show that rewilded mammals can shape the vegetation and seed bank it is important to note that some of the effects we report are more complex and not in line with our a priori predictions. Bettong density was particularly high at the time of our study (Moseby et al., 2018) which may have contributed to the contrast between our predictions which were built on prior research conducted at lower bettong densities (James et al., 2009), and our results. Our results highlight a key dilemma facing rewilding, which is that there may be considerable uncertainty in predicting the outcome of rewilding initiatives. This is particularly the case for species that became functionally extinct before we understood their ecological functions, or where rewilding efforts involve the re-establishment of multiple species into novel contexts (Fernández *et al.* 2017). These uncertainties also raise questions about how we should define baselines and targets for ecosystem restoration. We suggest that the possible solution to this rewilding-jigsaw dilemma is to have detailed monitoring programs and experiments that partition the effects of different consumers. Having such information at hand will enable informed decisions to be

made about how to manage the novel ecosystems created through rewilding (Hobbs et al., 2014; Schweiger, Boulangeat, Conradi, Davis, & Svenning, 2019).

#### 4.6 References

- Anderson, S. H., Kelly, D., Ladley, J. J., Molloy, S., & Terry, J. (2011). Cascading effects of bird functional extinction reduce pollination and plant density. *Science*, **331**, 1068–1071. doi: 10.1126/science.1199092
- Australian Bureau of Meteorology (2018). Retrieved from <http://www.bom.gov.au/> (Accessed 20 June 2018).
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**, 1–48. doi: 10.18637/jss.v067.i01
- Brown, J. H., & Heske, E. J. (1990). Control of a desert-grassland transition by a keystone rodent guild. *Science*, **250**, 1705–1707. doi: 10.1126/science.250.4988.1705
- Burbidge, A. A., & McKenzie, N. L. (1989). Patterns in the modern decline of western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation*, **50**, 143–198. doi: 10.1016/0006-3207(89)90009-8
- Council of Heads of Australasian Herbaria. (2019). Australian Plant Census, IBIS database. Centre for Australian National Biodiversity Research. Retrieved from <http://www.chah.gov.au/apc/index.htm> (Accessed 29/7/2019).
- Davidson, A. D., Detling, J. K., & Brown, J. H. (2012). Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment*, **10**, 477–486. doi: 10.1890/110054
- Davidson, A. D., & Lightfoot, D. C. (2006). Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography*, **29**, 755–765.
- Decker, O., Eldridge, D. J., & Gibb, H. (2019). Restoration potential of threatened

ecosystem engineers increases with aridity: broad scale effects on soil nutrients and function. *Ecography*, **42**, 1–13. doi: 10.1111/ecog.04259

Delibes-Mateos, M., Smith, A. T., Slobodchikoff, C. N., & Swenson, J. E. (2011).

The paradox of keystone species persecuted as pests: A call for the conservation of abundant small mammals in their native range. *Biological Conservation*, **144**, 1335–1346. doi: 10.1016/j.biocon.2011.02.012

Eldridge, D. J., & Simpson, R. (2002). Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. *Basic and Applied Ecology*, **3**, 19–29. doi: 10.1078/1439-1791-00078

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, **333**, 301–306. doi: 10.1126/science.1205106

Fernández, N., Navarro, L. M., & Pereira, H. M. (2017). Rewilding: a call for boosting ecological complexity in conservation. *Conservation Letters*, **10**, 276–278. doi: 10.1111/conl.12374

Fleming, P. A., Anderson, H., Prendergast, A. S., Bretz, M. R., Valentine, L. E., & Hardy, G. E. S. (2014). Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Review*, **44**, 94–108. doi: 10.1111/mam.12014

Gordon, C. E., Eldridge, D. J., Ripple, W. J., Crowther, M. S., Moore, B. D., & Letnic, M. (2017). Shrub encroachment is linked to extirpation of an apex predator. *Journal of Animal Ecology*, **86**, 147–157. doi: 10.1111/1365-2656.12607

Gordon, C. E., & Letnic, M. (2016). Functional extinction of a desert rodent: implications for seed fate and vegetation dynamics. *Ecography*, **39**, 815–824. doi: 10.1111/ecog.01648

Griffiths, C. J., Jones, C. G., Hansen, D. M., Puttoo, M., Tatayah, R. V., Muller, C. B., & Harris, S. (2010). The use of extant non-indigenous tortoises as a restoration tool to replace extinct ecosystem engineers. *Restoration Ecology*, **18**,

1–9. doi: 10.1111/j.1526-100X.2009.00612.x

- Hayward, M. W., Ward-Fear, G., L’Hotellier, F., Herman, K., Kabat, A. P., & Gibbons, J. P. (2016). Could biodiversity loss have increased Australia’s bushfire threat? *Animal Conservation*, **19**, 490–497. doi: 10.1111/acv.12269
- Hobbs, R. J., Higgs, E., Hall, C. M., Bridgewater, P., Chapin, F. S., Ellis, E. C., ... Yung, L. (2014). Managing the whole landscape: historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment*, **12**, 557–564. doi: 10.1890/130300
- Hobbs, R. J., & Mooney, H. A. (1985). Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia*, **67**, 342–351.
- Howard, K. S. C., Eldridge, D. J., & Soliveres, S. (2012). Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland. *Basic and Applied Ecology*, **13**, 159–168. doi: 10.1016/j.baae.2012.02.008
- Hunter, D. O., Britz, T., Jones, M., & Letnic, M. (2015). Reintroduction of Tasmanian devils to mainland Australia can restore top-down control in ecosystems where dingoes have been extirpated. *Biological Conservation*, **191**, 428–435. doi: 10.1016/j.biocon.2015.07.030
- James, A. I., Eldridge, D. J., & Hill, B. M. (2009). Foraging animals create fertile patches in an Australian desert shrubland. *Ecography*, **32**, 723–732. doi: 10.1111/j.1600-0587.2009.05450.x
- Kuznetsova, A., Brockhoff, P., & Christensen, R. (2017). lmerTest Package: tests in linear mixed effects models. *Journal of Statistical Software*, **82**, 1–26.
- Legge, S., Woinarski, J. C. Z., Burbidge, A. A., Palmer, R., Ringma, J., Radford, J. Q., ... Tuft, K. D. (2018). Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. *Wildlife Research*, **45**, 627–644. doi: 10.1071/WR17172



- Lyons, M. B., Mills, C. H., Gordon, C. E., & Letnic, M. (2018). Linking trophic cascades to changes in desert dune geomorphology using high-resolution drone data. *Journal of the Royal Society Interface*, **15**, 20180327. doi: 10.1098/rsif.2018.0327
- Mills, C. H., Gordon, C. E., & Letnic, M. (2018). Rewilded mammal assemblages reveal the missing ecological functions of granivores. *Functional Ecology*, **32**, 475–485. doi: 10.1111/1365-2435.12950
- Mills, C. H., & Letnic, M. (2018). Reversing functional extinction of mammals prompts a rethink of paradigms about seed fate in arid Australia. *Royal Society Open Science*, **5**, 171977. doi: 10.1098/rsos.171977
- Morton, S. R., Stafford Smith, D. M., Dickman, C. R., Dunkerley, D. L., Friedel, M. H., McAllister, R. R. J., ... Westoby, M. (2011). A fresh framework for the ecology of arid Australia. *Journal of Arid Environments*, **75**, 313–329. doi: 10.1016/j.jaridenv.2010.11.001
- Moseby, K. E., Hill, B. M., & Read, J. L. (2009). Arid Recovery - a comparison of reptile and small mammal populations inside and outside a large rabbit, cat and fox-proof enclosure in arid South Australia. *Austral Ecology*, **34**, 156–169. doi: 10.1111/j.1442-9993.2008.01916.x
- Moseby, K. E., Lollback, G. W., & Lynch, C. E. (2018). Too much of a good thing; successful reintroduction leads to overpopulation in a threatened mammal. *Biological Conservation*, **219**, 78–88. doi: 10.1016/j.biocon.2018.01.006
- Murray, B. R., Dickman, C. R., Watts, C. H. S., & Morton, S. R. (1999). The dietary ecology of Australian desert rodents. *Wildlife Research*, **26**, 857–858. doi: 10.1071/WR97046\_CO
- Prugh, L. R., & Brashares, J. S. (2012). Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. *Journal of Animal Ecology*, **81**, 667–678. doi: 10.1111/j.1365-2656.2011.01930.x
- R Core Team. (2016). *R: A language and environment for statistical computing*.

Vienna: R Foundation for Statistical Computing.

- Ripple, W. J., & Beschta, R. L. (2003). Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*, **184**, 299–313. doi: 10.1016/S0378-1127(03)00154-3
- Robley, A. J., Short, J., & Bradley, S. (2001). Dietary overlap between the burrowing bettong (*Bettongia lesueur*) and the European rabbit (*Oryctolagus cuniculus*) in semi-arid coastal Western Australia. *Wildlife Research*, **28**, 341–349. doi: 10.1071/WR00060
- Schweiger, A. H., Boulangeat, I., Conradi, T., Davis, M., & Svenning, J. C. (2019). The importance of ecological memory for trophic rewilding as an ecosystem restoration approach. *Biological Reviews*, **94**, 1–15. doi: 10.1111/brv.12432
- Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: restoring species in a changing world. *Science*, **345**, 406–412. doi: 10.1126/science.1251818
- Svenning, J.-C., Pedersen, P. B. M., Donlan, J., Ejrnaes, R., Faurby, S., Galetti, M., ... Vera, F. W. M. (2015). Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences*, **113**, 898–906. doi: 10.1073/pnas.1502556112
- Sweeney, O. F., Turnbull, J., Jones, M., Letnic, M., Newsome, T. M., & Sharp, A. (2019). An Australian perspective on rewilding. *Conservation Biology*, **33**, 812–820. doi: 10.1111/cobi.13280
- Valentine, L. E., Ruthrof, K. X., Fisher, R., Hardy, G. E. S. J., Hobbs, R. J., & Fleming, P. A. (2018). Bioturbation by bandicoots facilitates seedling growth by altering soil properties. *Functional Ecology*, **32**, 2138–2148. doi: 10.1111/1365-2435.13179
- Verdon, S. J., Gibb, H., & Leonard, S. W. J. (2016). Net effects of soil disturbance and herbivory on vegetation by a re-established digging mammal assemblage in arid zone Australia. *Journal of Arid Environments*, **133**, 29–36. doi: 10.1016/j.jaridenv.2016.05.008

- Weltzin, J. F., Archer, S., & Heitschmidt, R. K. (1997). Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology*, **78**, 751–763.
- Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences*, **112**, 4531–4540. doi: 10.1073/pnas.1417301112

## **Chapter 5: An omnivorous rodent has strong effects on resources in a pulsed desert environment**

Author List: Mills, C.H., Contos, P., Ooi, M. & Letnic, M.

Contributions: C.M. conducted 80% of the total work. CM, PC & ML designed the experiments, CM, PC & ML conducted the fieldwork, CM conducted the seed bank germination experiment with guidance from MO, CM conducted data analysis and led the writing of the manuscript with input from all authors.



A hopping-mouse highway

Photo credit: Hailey Durham

## 5.1 Abstract

Omnivores are species that feed across multiple trophic levels, consuming a variety of both low-quality and high-quality food resources. Theoretical models predict that the strength of interactions between omnivores and their food resources directly impacts ecosystem stability. Therefore, knowing whether omnivores have strong or weak effects on their resources is fundamental to understanding the role of omnivores within ecosystems.

Broad scale declines of many species have preceded an understanding of the strength of their trophic interactions, and the effects that the loss of omnivores has on ecosystems are poorly understood. In arid Australia, many native omnivorous rodent species are now absent from their former ranges but we know little about the strength of their interactions with their food resources.

We used foraging tray and exclosure experiments to investigate the strength of effects that an omnivorous rodent, *Notomys fuscus* had on the composition of the seed bank, the composition of above ground vegetation, and the abundance of invertebrates in arid Australia. In all of our experiments, we hypothesised that protein content would drive the strength of interactions between *N. fuscus* and its food resources. We also tested the macronutrient preferences of *N. fuscus* using a choice experiment.

*Notomys fuscus* persisted in high population densities throughout our study period.

We found that *N. fuscus* preferred food resources with a high protein content but had strong effects on both protein-rich and protein-poor dietary items including grass, flowers and invertebrates. *Notomys fuscus* had no detectable effect on seeds or forbs,

and effects on grass were strongest in treatments which provided *N. fuscus* with refuge from predators.

Our study demonstrates that omnivores can have strong, focal effects on many food resources as they become available in unpredictable environments. We propose that an omnivorous feeding strategy enables *N. fuscus* to maintain high population densities in an ecosystem with highly pulsed nutrient and resource availability. By demonstrating that omnivores have strong effects on multiple resources, our study adds to a growing case that the functional extinction of omnivores is an under-appreciated driver of environmental change.

## 5.2 Introduction

Omnivores are species that feed across multiple trophic levels (Pimm & Lawton, 1978; Polis & Strong, 1996) and by doing so maintain macronutrient balance by supplementing highly abundant but poor nutritional quality food items with sporadically available but high nutritional quality food items (Denno & Fagan, 2003; Raubenheimer & Simpson, 1997). Because the consumptive effects of omnivory are spread across many food sources and a species may switch feeding strategies between life stages (Kratina, LeCraw, Ingram, & Anholt, 2012; Vadas Jr, 1990), omnivores can have strong or weak effects on the species they consume (McCann & Hastings, 1997; Thompson, Hemberg, Starzomski, & Shurin, 2007).

The strength of interactions between omnivores and the resources they consume is fundamental to understanding the role of omnivores within ecosystems (McCann & Hastings, 1997; Thompson et al., 2007; Wootton, 2017). Theory predicts that strong effects between an omnivorous species and its food resources can destabilise ecosystems, while the presence of an omnivore with weak effects on many resources

will create stability in an ecosystem (Vandermeer, 2006; Wootton, 2017). However, it is challenging to study diffuse ecological interactions such as omnivory, and as a result, most research on the implications of omnivory on food resources is largely theoretical (McCann & Hastings, 1997; Wootton, 2017).

The world's mammals are in peril (Davis, Faurby, & Svenning, 2018), and broad scale declines of many species have preceded an understanding of their ecological roles and the strength of their trophic interactions (Mills, Gordon, & Letnic, 2018; Chapter 2). The functional extinction of consumers with specialised roles such as herbivores (Griffiths et al., 2010), and carnivores (Ripple et al., 2014) has revealed their ecological roles as keystone species. In contrast, the effects that loss of omnivores has on ecosystems are poorly understood. One reason for this may be that omnivores only have weak effects because they feed on many species, another explanation is that omnivores' effects are seldom studied because they feed on many species and regularly switch their diets and thus it is difficult to conduct targeted studies of their consumptive effects (Kratina et al., 2012).

In arid areas, rapid pulses of primary productivity are driven by irregular and unpredictable rainfall events which stimulate vegetation growth from a reserve of seeds and nutrients (Letnic & Dickman, 2010; Morton et al., 2011). The unpredictability of food resources in desert environments is a factor that could favour the flexible dietary strategy of omnivores. Indeed, omnivorous rodents and marsupials were once a conspicuous element of Australia's arid mammal fauna (Van Dyck & Strahan, 2008). However, omnivores are now poorly represented in the contemporary fauna because many species have become extinct or endangered due to the introduction of novel predators (Woinarski, Burbidge, & Harrison, 2015).

Nonetheless, there is evidence that functional extinction of omnivorous mammals may be a driver of vegetation change in Australia's arid zone ecosystems (Gordon & Letnic, 2016; Mills et al., 2018; Mills, Ooi, Tuft, & Letnic, 2019; Chapter 2, 4).

The flow-on effects that declines of omnivorous rodents have had on the functioning of Australia's vast arid ecosystems are largely unknown. This is because relatively few studies have investigated the roles they fulfil as consumers, seed dispersers or as prey (Gordon & Letnic, 2016; Morton & Baynes, 1985; Murray & Dickman, 1994b). Here, we examine the strength of interactions between a gregarious, desert-dwelling native rodent, *Notomys fuscus*, and its food resources. *Notomys fuscus* is an opportunistic omnivore with seed and herbage comprising the main part of its diet but invertebrates also making up a significant portion (Murray, Dickman, Watts, & Morton, 1999). We used foraging tray and exclosure experiments to investigate the effects that *N. fuscus* had on the composition of the seed bank, the composition of above ground vegetation, and the abundance of invertebrates. Furthermore, field observations we made during the study showed that *N. fuscus* consumed other resources when they became available. Consequently, we conducted opportunistic surveys on ephemeral forbs within our experimental exclosures to further test the strength of interactions between *N. fuscus* and its dietary items.

We expected that *N. fuscus* would have strong effects on high quality food resources, such as seeds and invertebrates, and weak effects on low quality foods such as herbage and flowers. Because seeds are a large component of *N. fuscus*' diet (Murray et al., 1999) and because granivorous rodents preferentially consume large seeds (J. H. Brown & Heske, 1990) we expected that plots which excluded *N. fuscus* would have more large-sized seeds and that *N. fuscus* would remove greater numbers of larger seeds than smaller seeds from foraging trays. We expected that *N. fuscus*



exclusion treatments would have weak effects on the proportion of forbs flowering, vegetation cover and plant species richness, as herbage is a low-quality food source compared to foods such as seeds or invertebrates (Murray & Dickman, 1994a). Because invertebrates are a high quality food resource for omnivores (Denno & Fagan, 2003) and omnivorous rodents preferentially consume invertebrates over other food sources (Murray & Dickman, 1994a), we expected that fewer experimentally provisioned mealworms would be removed and more Lycosid spider burrows would be present in plots which excluded *N. fuscus*.

In all of the experiments, we hypothesised that the main driver of food choice would be the macronutrient composition of different food resources, namely that protein, as both a limiting resource for omnivores (Denno & Fagan, 2003) and a limited resource in the Australian arid zone (Morton et al., 2011) would drive the strength of interactions between *N. fuscus* and its food. However, protein requires high levels of metabolic water to digest relative to other macronutrients, and in the water-limited arid zone food choice by rodents has been correlated with water content (Murray & Dickman, 1994a). Therefore, we conducted a macronutrient preference experiment (Simpson & Raubenheimer, 2001) to test our hypothesis that protein, not water, drives the strength of observed interactions between *N. fuscus* and its food resources.

## 5.3 Methods

### 5.3.1 Study Site and Study Species

Our study sites were located on the cattle stations Lindon (29.127069° S, 140.901921° E) and Quinyambie (29.670592° S, 140.528015° E) in the Simpson-Strzelecki Dunefield in north-east South Australia. The paddocks in which we

conducted our research were used for grazing cattle at low densities (0.1-2.85 cattle per km<sup>2</sup>). The mean annual maximum and minimum temperatures at the closest weather station (Tibooburra Airport, 29.43° S, 142.01° E) are 28 °C and 15 °C respectively (Australian Bureau of Meteorology 2019).

The most abundant small mammal species present at the study sites is *Notomys fuscus* (body mass 35 g), occurring at abundances 20 – 70 times higher than any other small mammal species (Rees, Rees, Kingsford, & Letnic, 2019). Other small mammals that occur in the study sites include the native rodents *Pseudomys australis*, *Pseudomys hermannsbergensis*, *Pseudomys desertor* and *Rattus villosissimus*, the marsupial Dasyurids *Sminthopsis crassicaudata*, *Sminthopsis macroura* and *Dasyercus cristicauda*, and the introduced rodent *Mus musculus*. The introduced herbivore the European rabbit (*Oryctolagus cuniculus*) is also present.

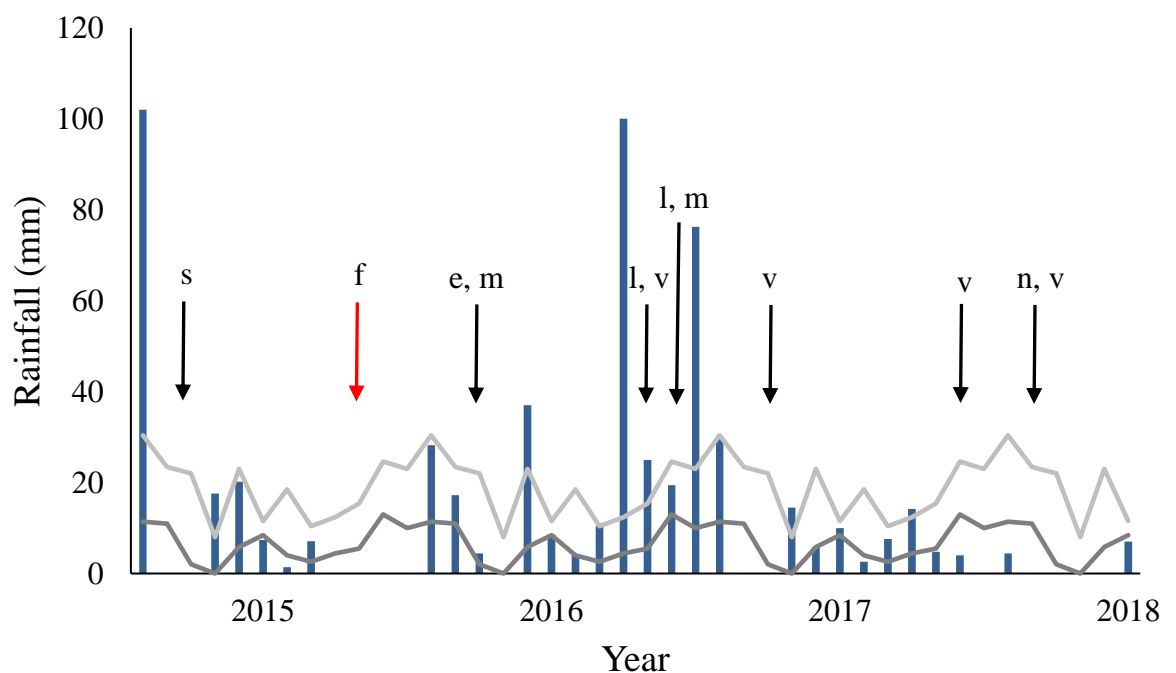
As sand dunes are the preferred habitats for *N. fuscus*, we conducted both our exclusion fence experiment and foraging tray experiments on the crests of sand dunes. All surveys were conducted between March 2015 and November 2018.

### 5.3.2 Rainfall

To provide an index of rainfall during our study period against which we could compare the cover of vegetation and abundances of rodents we obtained monthly rainfall data from July 2015 to June 2018 from the Lindon weather station (29.126972° S, 140.901988° E) (Australia Bureau of Meteorology 2019). To assess if rainfall conditions for our study period were dry, average, or wet, we compared monthly rainfall against percentiles of the distribution of all records (1988 – 2018) for the same months. We defined dry conditions as when monthly rainfall totals were

below the 50<sup>th</sup> percentile (median) of the historic record, average conditions as between the median and the 75<sup>th</sup> percentile of the historic record and wet conditions as above the 75<sup>th</sup> percentile of the historic record.

Monthly rainfall totals show our study period began during a period of dry conditions (Fig. 5.1). Between January 2016 and January 2017 was a period of wet conditions with two months each receiving over 70 mm of rainfall and all months receiving rainfall at or above the median. After February 2017 and until June 2018 our study site became dry with 12 out of 17 monthly rainfall totals falling below the long-term median.



*Figure 5.1* Monthly rainfall during study period with long-term median and 75<sup>th</sup> percentile overlaid. Red arrow (f) indicates when exclusion fences were constructed on Lindon Station, black arrows are sampling times for (s = seed take, e = ephemeral forbs, m = mealworms, l = Lycosid burrows, v = vegetation composition surveys, n = nutritional preferences). Rainfall between the median and 75<sup>th</sup> quantiles is average, rainfall above the 75<sup>th</sup> quantile is a wet period and rainfall below the median is a dry period.

### 5.3.3 Mammal Abundances

We surveyed *N. fuscus* and rabbit abundance on 11 sampling trips between 2015 – 2018, surveying the same area each trip. We recorded the number of *N. fuscus* and rabbits sighted by an observer spotlighting from the roof of a vehicle travelling on transects at a constant speed of 15 km/h, at night (Rees et al., 2019). Total transect length each trip was 25-30 km. For each individual encountered we determined the perpendicular distance from the transect at first sighting using a rangefinder.

We determined the effective strip width for each species by truncating the top 5% of all observations (Supplementary Fig. S5.1). We divided the number of individuals observed by the total area surveyed (length of transect x strip width) to obtain a density of each species.

### 5.3.4 Exclusion Fences

We used exclosure fences to determine the effects that *N. fuscus* had on the proportion of forbs in flower, vegetation cover, seed bank composition, Lycosid abundance and consumption of mealworms. We used a randomised block design to establish five fenced exclosures on five dunetops on Lindon Station. Fences were constructed in November 2015. Each exclosure consisted of five treatments measuring 11 m x 11 m within which 0.5 m on each side is considered buffer zone to exclude fence effects. Fenced treatments were built using aviary netting (13 mm aperture). All plots allowed access to large herbivores such as cattle and kangaroos (*Macropus* spp.) which were present at low densities in the area. Because rabbits were only present in low numbers during the study period, we expected that rabbits, an herbivore, would have minimal effects on vegetation. To ensure we could

distinguish between the effects of *N. fuscus* and rabbits on vegetation and the seedbank we used a selective exclusion design. The treatments were:

- Exclude all small mammals: 0.9 m high fence with 0.5 m foot netting.
- Exclude medium sized mammals but not rodents (“Exclude Rabbits”): 90 cm fence with small “doors” cut in for small mammals to pass through.
- Exclude Rodents: 0.3 m high fence with 0.5 m foot netting.
- Control: unrestricted access with posts demarcating corners of plot.
- Procedural Control: non-functioning fence up to 30 cm high with gaps to test for fence effects.

#### 5.3.5 Granivory

##### 5.3.5.1 Soil Seed Bank

To measure the abundance and composition of seeds in the soil seed bank within our experimental exclosures, we collected soil seed bank samples in November 2017, two years after the fences were established. We randomly selected nine locations within each exclosure treatment and removed soil samples of dimensions 10 cm x 10 cm and 5 cm depth, combining the nine samples for each exclosure treatment prior to transport. Any litter present on the soil surface of the sample area was stored separately from the soil seed bank sample (see Mills et al. 2019; Chapter 4). We used stratified random sampling, where samples were within 30 cm of forbs or grasses but not in open areas, areas under adult shrubs or in fresh animal digs. A 1.9 L subsample of soil and the entire litter sample (between 1 g and 27 g) were placed in separate trays and germinated in a glasshouse in Sydney, Australia, in the Southern Hemisphere summer, 2018. Every week for two months, seedlings were identified and removed. After two months, samples were dried and large seeds (specifically

*Acacia ligulata* (Fabaceae; perennial shrub), and *Crotalaria eremaea* (Fabaceae; perennial forb)) were removed from the soil with a 2 mm sieve and counted. We sieved specifically for this group because they are hard seeded, physically dormant species which are unlikely to germinate under glasshouse conditions. For analyses, we combined the total seedlings from the litter and the soil with counts of sieved seeds.

To identify if there was an effect of rodent exclusion on the abundance of seeds of different sizes, functional groups and taxonomic family we analysed the seed abundance data and traits (trait details available in Supplementary Table S5.3) using the fourth-corner modelling approach `traitglm` in the package `mvabund` version 4.0.1 (A. M. Brown et al., 2014; Wang, Naumann, Wright, & Warton, 2012) in the statistical software R version 3.5.2 (R Core Team, 2016). We used a negative binomial distribution to model our data for fourth-corner analysis.

#### 5.3.5.2 Seed Take

To test if *N. fuscus* preferred to forage larger seeds we placed foraging trays 20 m apart on the crests of five dunes at both Quinyambie and Lindon stations for one night in March 2015. For each species, five plastic bowls (15 cm diameter, 5 cm depth) filled with sand were buried flush with the ground. On each dune we used five foraging trays for each of four seed species from locally abundant plants: *D. viscosa angustissima* (Sapindaceae; seed mass 4.90 mg; small aril present, no elaiosome); *C. eremaea* (Fabaceae; seed mass 13.10 mg; no aril nor elaiosome); *Senna artemisioides artemisioides* (Fabaceae; seed mass 11.43 mg, no aril nor elaiosome); and *Acacia ligulata* (Fabaceae; seed mass 27.60 mg including large elaiosome of 9mg). As elaiosomes are a rich source of energy and attract seed predators (Auld &

Denham, 1999), we also included seed of *A. ligulata* with and without the elaiosome present in separate trays. Seeds were obtained from a commercial supplier. Each tray contained 50 seeds and after 24 hours we returned and counted the number of seeds remaining. To identify which vertebrate granivores were consuming seeds, we swept the sand 30 cm around each tray and identified the tracks of visitors to the foraging trays (Gordon et al., 2017). We used a ring of insecticide powder around each tray to exclude ants (Mills et al., 2018; Chapter 2).

For analyses, we calculated the number of seeds taken for each shrub species on each dune as an average from the five trays and used linear models to test for an association between the number of seeds removed and seed mass.

### 5.3.6 Herbivory

#### 5.3.6.1 Vegetation Composition

To assess the effect of *N. fuscus* exclusion on vegetation composition, we conducted vegetation surveys within our experimental exclosures over four sampling trips.

Sampling trips were conducted in October 2016, March 2017, November 2017 and March 2018. Within each exclosure treatment we randomly selected and marked out ten 1 x 1 m quadrats. We excluded quadrats which contained adult shrubs to avoid nurse effects (Howard, Eldridge, & Soliveres, 2012) and quadrats which were located in bare windswept patches where vegetation cannot grow. Within each quadrat we estimated percent cover total standing vegetation (including dead and alive vegetation), litter, sand, and all live vegetation to species.

We used Generalised Linear Mixed-effects Models (GLMMs) with a Gaussian distribution to test for effects of experimental treatment and sampling trip on above ground variables including total vegetation and litter cover and cover of grasses and

forbs. We used Tukey's tests for post-hoc pairwise comparisons where a significant effect was found in the main model. We log+1 transformed total vegetation cover and litter cover to account for a left skew in the dataset.

We calculated species richness for each treatment by counting the total number of species within each treatment, over all sampling times. We compared species richness across treatments using a GLMM with a Gaussian distribution, with treatment as a fixed factor and block as a random factor.

#### 5.3.6.2 *Ephemeral Forbs*

We conducted surveys of flowering and non-flowering forbs using the point intercept method (Letnic, 2004) in June 2016 when there was an abundance of ephemeral forbs and multiple forb species were in flower. Point intercept surveys consisted of 10, 10 m transects which covered the whole area within each enclosure treatment. At every metre we recorded the presence or absence of ephemeral forbs, and if an ephemeral forb was present, we classified the individual plant as reproductive (flowers or fruit present) or non-reproductive. We then calculated the percent cover and proportion in flower for each ephemeral forb species.

We used Generalised Linear Mixed-effects Models with a Gaussian distribution (GLMM) to test for effects of experimental treatment on forb cover and proportion of forbs with flowers for all forb species and for the two most abundant ephemeral forb species: *Blennodia pterosperma* (Brassicaceae; annual forb) and *Senecio gregorii* (Asteraceae; annual forb). When analysing the treatment effect for the proportional data we included a weighting factor for the total number of individuals present. We used Tukey's tests for post-hoc pairwise comparisons where a significant effect was found in the main model.



### 5.3.7 Insectivory

#### 5.3.7.1 Mealworm Removal

To index insectivory by *Notomys fuscus* we deployed feeding trays inside our experimental exclosures for three nights in June 2016 and November 2016. Each treatment contained one tray (30 cm x 15 cm x 5 cm depth) buried flush with the ground into which a known number of mealworms (*Tenebrio molitor*) were mixed through a 1 L matrix of sand. We did not deploy trays in the Exclude Rodents treatment because we did not have sufficient mealworms available in the field to deploy foraging trays in each exclosure. We chose mealworms as they are commonly used in food choice experiments (Murray & Dickman, 1994a). Each morning we recorded the number of mealworms remaining. To identify which vertebrates were consuming mealworms, we cleared the sand 30 cm around each tray and identified the tracks present each day.

We calculated the percentage of mealworms removed and used the mean from all three nights for analysis. To identify if more mealworms were taken from the treatments to which rodents had access compared to the Exclude All treatment, we conducted a GLMM using experimental treatment, sampling trip and their interaction as fixed factors and exclosure block as a random factor. We used Tukey's tests for post-hoc pairwise comparisons where a significant effect was found in the main model. All GLMMs were performed using the statistical platform R, version 3.5.3 (Team, 2016) and the package lme4 version 1.1 (Bates, Maechler, Bolker, & Walker, 2015).

#### 5.3.7.2 *Lycosid Burrow Surveys*

To determine if *N. fuscus* affects Lycosid spider abundance (Order: Araneae, Family: Lycosidae) we conducted a systematic count of spider burrows in each enclosure treatment in October 2016 and November 2016. We restricted our counts to the same plots as those used to deploy mealworm trays. We counted Lycosids because they are a common at our study sites (Contos & Letnic, 2019) and produce distinctive burrows which can be readily counted. To determine if there were significantly more Lycosid burrows within treatments to which rodents had access compared to the Exclude All treatment we conducted a GLMM using factors as detailed for the mealworm removal experiment.

#### 5.3.8 Nutritional Preferences

To determine if water availability or macronutrients were the drivers of *N. fuscus* foraging behaviour we used a foraging choice experiment where we offered three commercial native animal foods with manipulated ratios of protein and carbohydrate content and equal energy value (between 8.1-9.4 MJ/kg; recipes in Supplementary Table S5.4). We presented one tray (20 cm diameter) of 120 g of each of three foods with different protein : carbohydrate ratios (7:35, 21:21, 35:7; Simpson & Raubenheimer 2001) in a block with a fourth tray containing water or sand. All four trays were within two metres of each other. Four blocks were installed on the crests of eight dunes at Lindon Station and six dunes at Quinyambie Station, each dune separated by 1 km, and water supplementation treatments (present/absent) were alternated by dune. Each morning for three mornings we measured the amount of food removed from the tray and replenished food in the evening. As pilot tests indicated that ants were attracted to the high carbohydrate food, we sprinkled a ring

of insecticide powder around each tray to prevent ants from accessing the food. To identify which species visited macronutrient trays, we cleared the sand 30 cm around each tray and recorded tracks.

To test for effects of macronutrient content and water availability on the amount of food removed, we used a GLMM where the response variable was the amount of food removed, and fixed factors were food type, water (present or absent) and site (Quinyambie or Lindon) and the interactions between the fixed factors. Dune was included as a random factor and block was a random factor nested in dune. Only blocks which were discovered (*N. fuscus* tracks observed within 30cm of at least one food tray in the block) were included in analysis. We used a mean of food taken across all three nights for analysis.

## 5.4 Results

### 5.4.1 Mammal Abundances

The effective strip width was 3 m each side of the transect for *N. fuscus* and 50 m each side of the transect for rabbits (Supplementary Fig. S5.1). *Notomys fuscus* were more abundant than rabbits on all spotlight surveys at both sites (Fig. 5.2), with mean densities at 600 individuals per km<sup>2</sup> for *N. fuscus* and 15 individuals per km<sup>2</sup> for rabbits. At Quinyambie both rabbits and *N. fuscus* density fluctuated between survey trips, and rabbit abundance was typically higher at Quinyambie than at Lindon. At Lindon, rabbit populations were very low for the entirety of our study period. From 2016 onwards *N. fuscus* populations steadily rose at both locations and *N. fuscus* density peaked in 2017 at 2100 individuals per km<sup>2</sup> and 1400 individuals

per km<sup>2</sup> for Lindon and Quinyambie respectively, after which *N. fuscus* density fell rapidly in density at both sites.

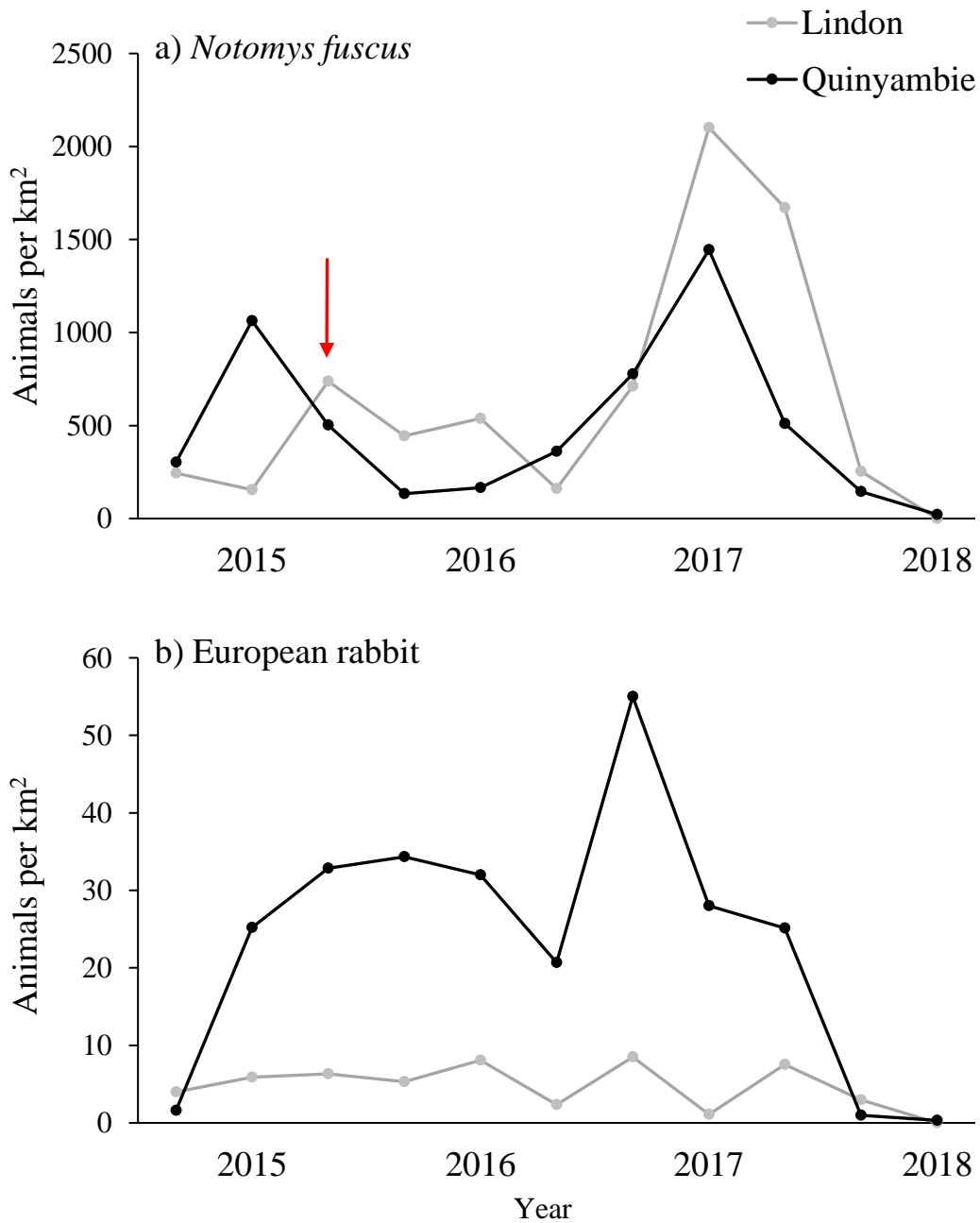


Figure 5.2 a) *Notomys fuscus* and b) European rabbit (*Oryctolagus cuniculus*) density per square kilometre counted on spotlighting surveys at Lindon Station and Quinyambie Station. Red arrow indicates when exclusion fences were constructed on Lindon Station.

## 5.4.2 Granivory

### 5.4.2.1 Soil Seed Bank

There was no difference between treatments for seeds in the soil seed bank in relation to seed mass (LRT = 1.843,  $P > 0.2$ ), functional group (LRT = 0.001,  $P > 0.9$ ), or family (LRT = 1.734,  $P > 0.2$ ).

### 5.4.2.2 Seed Take

Seed removal from foraging trays was not correlated with seed mass ( $R^2 = 0.055$ ,  $F_{1,54} = 2.72$ ,  $P = 0.11$ ,  $y = 0.22x + 0.25$ ). Seed take was highest for *Acacia ligulata* with elaiosome, followed by *Dodonaea viscosa angustissima*, *Acacia ligulata* with no elaiosome, *Crotalaria eremaea* and *Senna artemisioides artemisioides* (Fig. 5.3). *Notomys fuscus* tracks were recorded at 87% of trays, bird tracks were recorded at 2% of trays and no other vertebrate granivores were recorded.

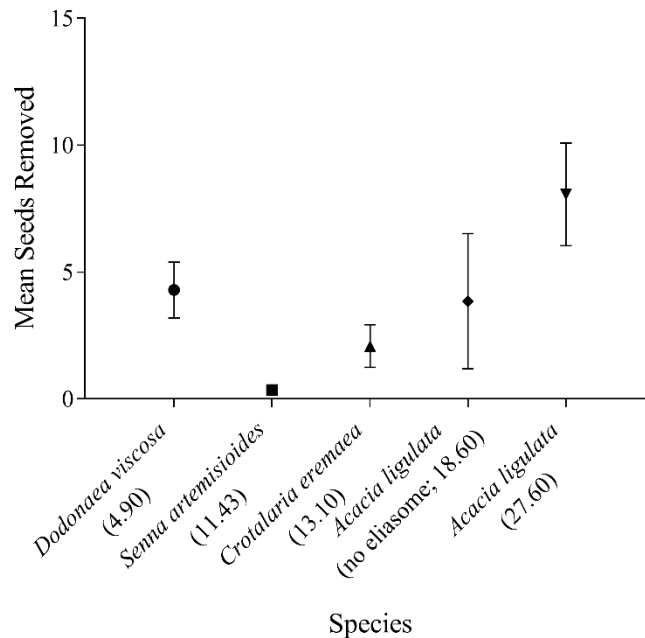


Figure 5.3 Mean number of seeds removed  $\pm 1$  SE for seed species, pooled across sites, ordered from left to right in order of seed mass (mg).

### 5.4.3 Herbivory

#### 5.4.3.1 *Vegetation Composition*

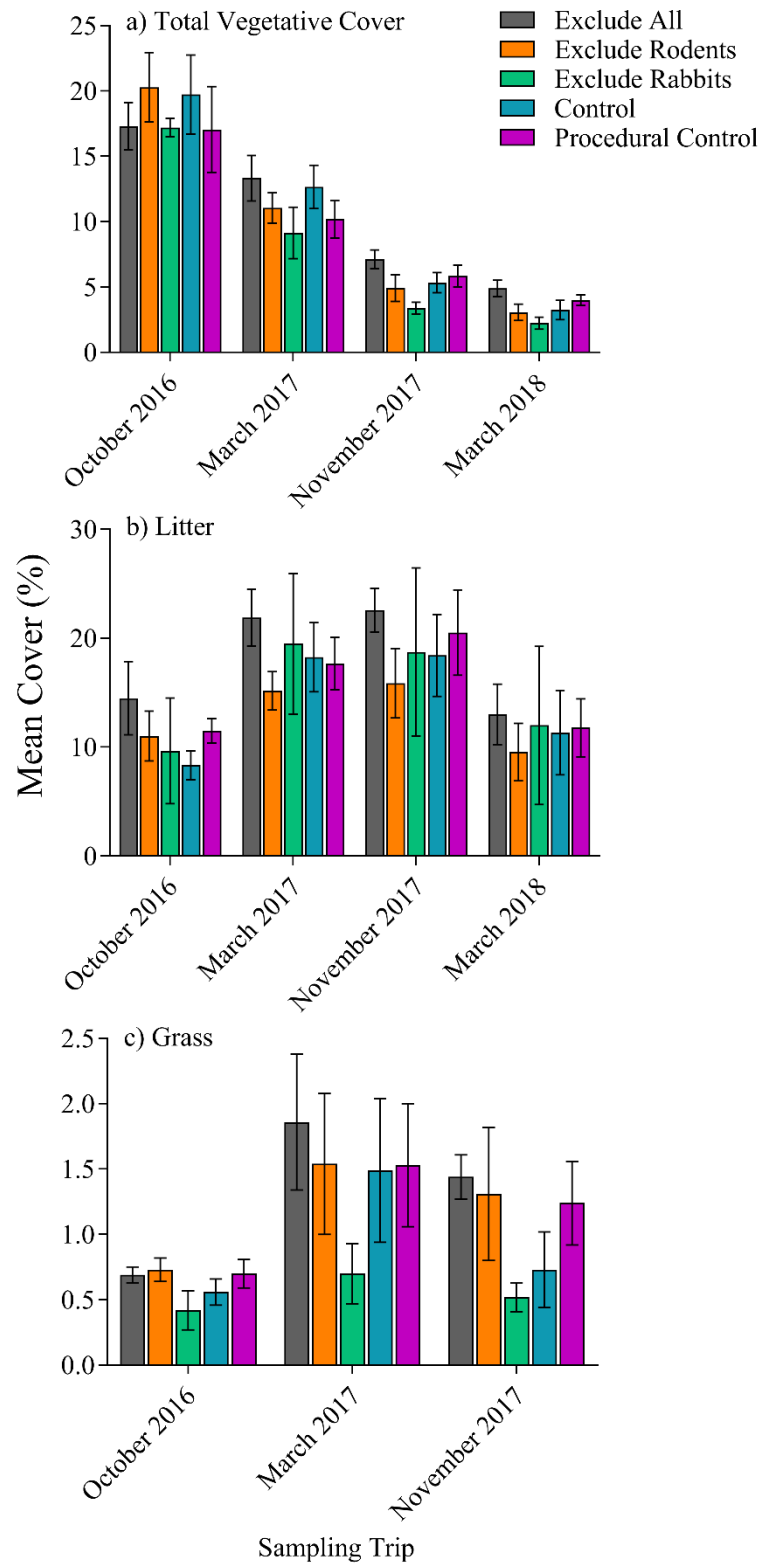
Overall, there was more total vegetation cover in the Exclude All ( $P < 0.001$ ), Exclude Rodents ( $P < 0.05$ ) and Control ( $P = 0.01$ ) treatments compared to the Exclude Rabbits treatment (Fig. 5.4a; Table 5.1a) and greater grass cover in all treatments compared to the Exclude Rabbits treatment, especially during the March 2017 sampling trip (Exclude All  $P < 0.001$ ; all others  $P < 0.02$ ; Fig. 5.4c; Table 5.1c). By March 2018 there was no grass remaining in any experimental plots. There was a significant effect for treatment on litter cover, and although there were no differences between treatments in our post-hoc test, inspection of the graph revealed that there was less litter cover in the Exclude Rodents treatment compared to the Exclude All treatment in March and November 2017 (Fig. 5.4b; Table 5.1b). There was no effect of rodent exclusion treatment on forb cover (Table 5.1d). All Procedural Controls were within one standard error of Controls unless otherwise stated, demonstrating that fence structure had little unintentional effect on our results.

During the wet conditions that prevailed until January 2017 there was a flush of vegetation growth (Fig. 5.4) and little detectable differences between treatments. As the landscape began to dry after January 2017 vegetation cover decreased across all treatments. During this period of dry conditions there were significant differences between sampling trips for all cover variables and differences between treatments became apparent, leading to the significant interaction effects between sampling trip and treatment for grass cover (Fig. 5.4; Table 5.1).

Overall plant species richness did not differ between mammal access treatments ( $F_{4,20} = 1.70$ ,  $P > 0.2$ ).

*Table 5.1* Results of generalised linear mixed-effects models comparing ground cover across treatments and sampling trips.

MODEL	df (n)	df (d)	F	P
<b>a) Total Standing Vegetation (log+1 transformed)</b>				
Experimental Treatment	4	949	15.81	<b>&lt;0.0001</b>
Sampling Trip	3	893	271.42	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	893	1.73	0.056
<b>b) Litter (log+1 transformed)</b>				
Experimental Treatment	4	970	7.81	<b>&lt;0.0001</b>
Sampling Trip	3	880	35.49	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	880	0.51	0.91
<b>c) Grass</b>				
Experimental Treatment	4	929	8.06	<b>&lt;0.0001</b>
Sampling Trip	3	860	87.4	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	860	2.02	<b>&lt;0.01</b>
<b>d) Forb</b>				
Experimental Treatment	4	975	0.75	0.56
Sampling Trip	3	975	465	<b>&lt;0.0001</b>
Sampling Trip: Experimental Treatment	12	975	0.94	0.5



*Figure 5.4* Mean cover for ground cover variables  $\pm 1$  SE by exclusion treatment across sampling trips: a) total standing vegetative cover, b) litter cover and c) grass cover.



#### 5.4.3.2 Ephemeral Forbs

There was an effect of *N. fuscus* exclusion on total forb cover ( $F_{4, 20} = 2.85$ ,  $P = 0.05$ ), with greater cover in the Exclude All treatment compared to the Exclude Rodents and Procedural Control ( $P < 0.05$ ). There was no difference between exclusion treatments in the proportion of forbs with flowers ( $F_{4, 20} = 2.65$ ,  $P = 0.64$ ). There was an effect of *N. fuscus* exclusion on the proportion of *B. pterosperma* with flowers ( $F_{4, 24} = 6.86$ ,  $P < 0.001$ ; Fig. 5.5), with more *B. pterosperma* flowers within the Exclude All treatment compared to Exclude Rabbits, Control, Procedural Control (all  $P < 0.001$ ) and the Exclude Rodents treatment ( $P = 0.04$ ; Fig. 5.5), and no difference between treatments in the total cover of *B. pterosperma* ( $F_{4, 20} = 1.25$ ,  $P = 0.32$ ; Fig. 5.5). There was no difference in the proportion of plants flowering nor in overall cover for *S. gregorii* (flowers:  $F_{4, 19} = 1.32$ ,  $P = 0.30$ ; all:  $F_{4, 20} = 1.22$ ,  $P = 0.33$ ).

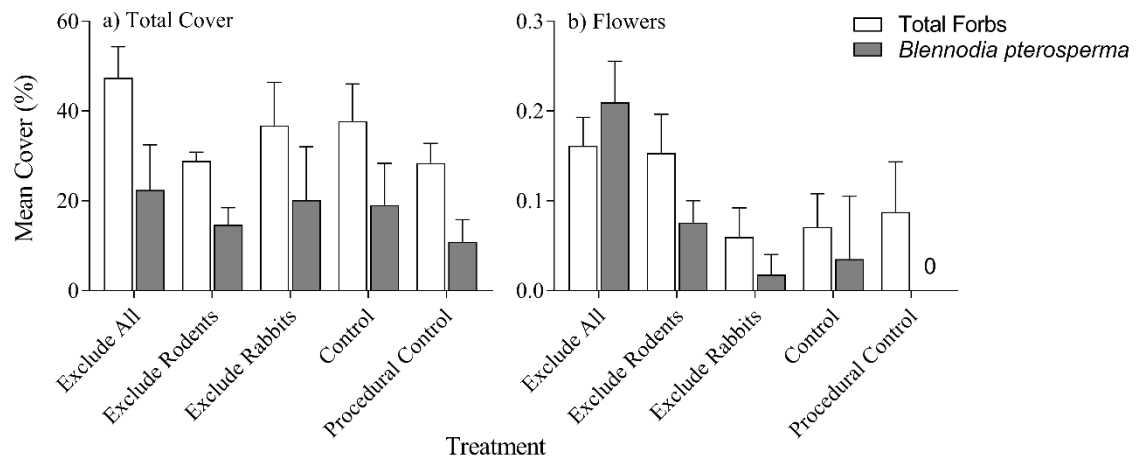


Figure 5.5 Mean cover of a) mean total cover for forbs and *Blennodia pterosperma* + 1 SE and b) all forbs and *Blennodia pterosperma* in flower as a proportion of mean total cover + 1 SE, weighted by the total cover.

#### 5.4.4 Insectivory

##### 5.4.4.1 Mealworm Removal

*Notomys fuscus* tracks were recorded at none of the trays within Exclude All treatments, and at 56% of trays within other treatments. The percentage of mealworms removed differed between treatments ( $F_{3,35} = 26.79$ ,  $P < 0.001$ ; Fig. 5.6), with many fewer mealworms taken from the Exclude All treatment compared to all other treatments (all  $P < 0.001$ ) and no difference between other treatments. There was no difference between sampling trips ( $F_{1,35} = 0.32$ ,  $P = 0.57$ ) and no interaction effect between treatment and sampling trip ( $F_{3,35} = 1.01$ ,  $P = 0.40$ ).

##### 5.4.4.2 Lycosid Burrow Surveys

The number of Lycosid burrows differed between treatments ( $F_{3,35} = 14.93$ ,  $P < 0.001$ ; Fig. 5.6) and sampling trips ( $F_{1,35} = 11.30$ ,  $P < 0.002$ ) but differences between treatments were consistent across sampling trips ( $F_{3,35} = 1.00$ ,  $P = 0.40$ ). There were significantly more Lycosid burrows in the Exclude All treatment compared to all other treatments ( $P < 0.05$ ) and more burrows were detected in November than October ( $P < 0.002$ ).

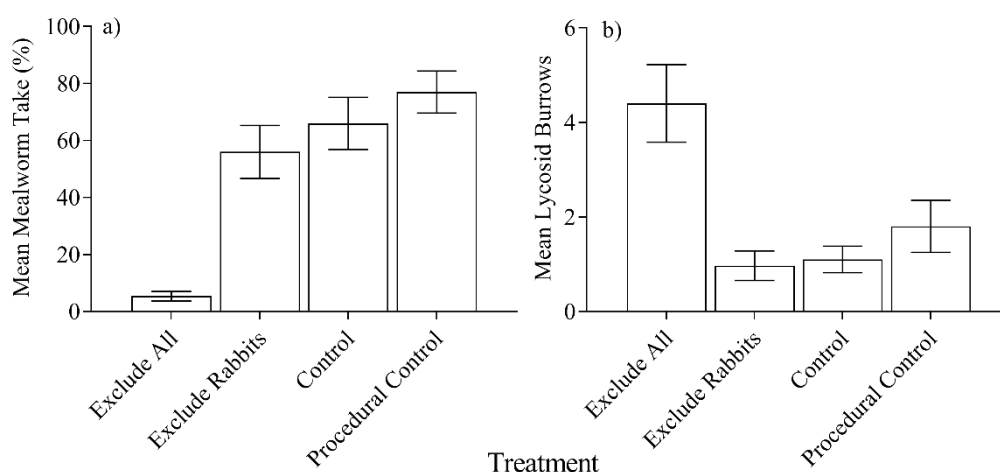


Figure 5.6 Effects of rodent exclusion on invertebrates: a) mean rates of mealworm take (%)  $\pm 1$  SE and b) mean counts of Lycosid burrows  $\pm 1$  SE.

#### 5.4.5 Nutritional Preferences

*Notomys fuscus* preferentially consumed different food types at each site. At Lindon, *N. fuscus* preferred the high protein food over both other treatments (high carbohydrate  $P < 0.01$ , equal carbohydrate-protein  $P = 0.057$ ; Fig. 5.7; Table 5.2). At Quinyambie *N. fuscus* consumed equal amounts of all foods. The presence of free water had no effect on food choice (Table 5.2).

At Lindon *N. fuscus* tracks were detected at 69% of high protein trays, 66% of high carbohydrate trays and 73% of equal carbohydrate-protein trays. At Quinyambie *N. fuscus* tracks were recorded at 75% of high protein trays, 72% of high carbohydrate trays and 63% of equal carbohydrate-protein trays. Birds, especially corvids, were the second most recorded visitor at both sites, and were recorded at 35% of trays at Quinyambie and 19% of trays at Lindon. Other visitors included *Dasyercus cristicauda*, *Canis dingo*, and unidentified rodents, and were recorded at less than 2% of trays at Quinyambie and 10% of trays at Lindon.

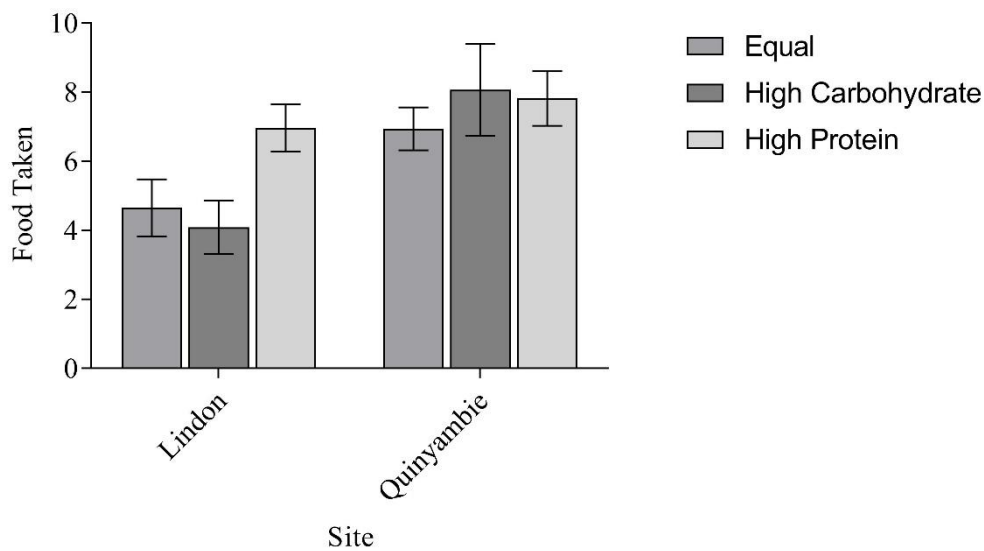


Figure 5.7 Amount of food taken between equal amounts protein and carbohydrate, high carbohydrate, and high protein at each study site.

Table 5.2 Results of generalised linear mixed-effects models

comparing take of different macronutrient diets and water availability across sites.

Factor	df(n)	df(d)	F	P
Food	2	133	3.69	<b>0.037</b>
Water	1	6	0.88	0.38
Site	1	146	21.11	<b>&lt;0.0001</b>
Food*Water	2	133	1.57	0.41
Water*Site	2	146	2.12	0.15
Food*Site	1	133	3.25	<b>0.04</b>

## 5.5 Discussion

Our study shows that *N. fuscus* is a true omnivore which preferred food resources with a high protein content but consumed a wide range of dietary items of varying macronutrient quality including seeds, herbage, flowers and invertebrates. However, contrary to our prediction that *N. fuscus* would only have measurable effects on protein-rich items, we found that *N. fuscus* had strong effects on both protein-rich

and protein-poor dietary items. Our results challenge the notion that omnivores should have weak effects on the species they consume (McCann & Hastings, 1997; Thompson et al., 2007) especially if they maintain the same feeding strategy throughout their life cycles (Kratina et al., 2012). Instead, we found that *N. fuscus* had strong effects on multiple food resources. Our results suggest that *N. fuscus* had a broad diet of low-quality resources and targeted high-quality resources as they became available.

The strong, focal effects we observed between *N. fuscus* and its food resources are enhanced because of the high densities at which *N. fuscus* populations persisted at our study sites. The ability to switch between resources is an advantage of having an omnivorous diet and may provide particular advantages to animals which live in high densities in strongly pulsed environments such as our desert study system (Murray & Dickman, 1994b). We suggest that omnivory facilitates the existence of *N. fuscus* at high population densities despite the unpredictability of their habitat.

At odds with our prediction that *N. fuscus* would prefer larger seeds, seed removal was not related to seed size. As an omnivore which can access multiple food resources, it is possible that factors other than seed size drive seed selection by *N. fuscus*. Such factors may include the presence of an eliasome or chemical defences, water content or the availability and nutritional content of other resources (Murray & Dickman, 1994a). Indeed, we found that *N. fuscus* took far fewer *Acacia ligulata* seeds when the eliasome had been removed. This finding indicates that the lipid rich eliasomes (Whitney & Lister, 2004) of this common shrub are attractive to *N. fuscus* and may provide an important food resource when they are available (Auld & Denham, 1999).

Our results show that *N. fuscus* reduced grass cover inside the fenced Exclude Rabbits (rodent access) treatment but not within the unfenced Control treatment. This finding was unexpected and may have been due to the fences altering the behaviour of *N. fuscus*, an effect that was not accounted for by our Procedural Control. We hypothesize that *N. fuscus* individuals may have perceived the surrounding fence as a refuge from predators and consequently allocated more time to foraging when inside the exclosures. This idea is supported by previous research showing that *N. fuscus* allocated more time to foraging when in sheltered microhabitats (Gordon, Feit, Gruber, & Letnic, 2015) and studies showing that rodents prefer to forage in places where larger mammals are excluded (Davidson & Lightfoot, 2006; Mills et al., 2019; Chapter 4). Because of the existence of this possible “fear” effect, we have unexpectedly detected a strong effect of *N. fuscus* on grass, a low-quality, low nitrogen resource (Murray & Dickman, 1994a).

Our finding that *N. fuscus* reduced the abundance of flowers on the ephemeral forb *B. pterosperma* when they were an abundant resource suggests that *N. fuscus* has focal effects in response to resource availability (Fagan, 1997). Ephemeral forbs are a highly pulsed resource in our study area that germinate and then grow and senesce rapidly after rainfall, usually in high abundances. That we were able to detect an effect of *N. fuscus* florivory on ephemeral forbs indicates that despite the relatively poor nutritional content of herbage (Murray & Dickman, 1994a), *N. fuscus* can have a strong, focal impact on poor-quality but abundant resources when available. Similarly, Gordon & Letnic (2016) found that consumption of seeds by *N. fuscus* had a strong effect on the abundance of *Dodonaea viscosa* seeds in the seed bank following seed fall. Our finding that rabbit grazing reduced the cover of ephemeral forbs but did not impact forb cover in our vegetation composition surveys, suggests

that rabbits, despite being obligate herbivores, also engage in resource-switching depending on resource availability. This dietary flexibility may be a factor that has contributed to the success of this introduced species in the Australian arid zone (Dawson & Ellis, 1994).

At our Lindon site we found that *N. fuscus* preferred the high protein macronutrient diet, confirming our prediction that protein, not water is a primary driver of food choice by *N. fuscus*. Taken together with our findings that *N. fuscus* had a marked effect on Lycosid burrow abundance and removed high numbers of mealworms, these findings demonstrate that *N. fuscus* has strong effects on food resources with nutrients that are encountered less frequently in the environment (Denno & Fagan, 2003). We do not know why results for macronutrient trays differed between study sites; however, there were differences in abundances of *N. fuscus* and rabbits between the two sites which may have altered nutritional demands via competition.

One caveat of our study is that with the exception of our foraging tray experiments, we did not directly link the impacts we describe here with a direct consumptive activity by *N. fuscus*. Therefore, we are only able to report the effects we have observed but are unable to identify the consumption niche related to those effects. For example, we do not know if spider burrows are more common in Exclude All treatments because of a landscape of fear effect whereby spiders were actively seeking habitats where rodents had been excluded (Rypstra, Schmidt, Reif, DeVito, & Persons, 2007) or if it is direct consumption by *N. fuscus* which influenced their abundance inside and outside of exclosures (Contos & Letnic, 2019). However, all of these activities have the potential to directly impact the abundance of specific food resources and although better understanding of the mechanisms by which *N. fuscus*

regulates its resources would provide valuable insight into the functional role of this species, it would not alter our findings that *N. fuscus* has strong effects on multiple components of their diet.

Although the implications of our findings on the functional extinction of mammals in arid Australia are beyond the scope of this study, other studies have demonstrated that shifts in vegetation communities, invertebrate communities and geomorphology can be attributed in part to the functional extinction of omnivorous native mammals which occur at high densities (Gordon & Letnic, 2016; Lyons, Mills, Gordon, & Letnic, 2018; Mills et al., 2018; Chapter 2). Our finding that omnivores in pulsed systems have strong effects on multiple prey items adds to a growing case that functional extinction of omnivores is an unappreciated driver of environmental change.

## 5.6 References

- Auld, T. D., & Denham, A. J. (1999). The role of ants and mammals in dispersal and post-dispersal seed predation of the shrubs *Grevillea* (Proteaceae). *Plant Ecology*, **144**, 201–213.
- Australian Bureau of Meteorology (2019). Retrieved from <http://www.bom.gov.au/> (Accessed 5 August 2019).
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48. doi: 10.18637/jss.v067.i01
- Brown, A. M., Warton, D. I., Andrew, N. R., Binns, M., Cassis, G., & Gibb, H. (2014). The fourth-corner solution - using predictive models to understand how species traits interact with the environment. *Methods in Ecology and Evolution*, **5**, 344–352. doi: 10.1111/2041-210X.12163



- Brown, J. H., & Heske, E. J. (1990). Control of a desert-grassland transition by a keystone rodent guild. *Science*, **250**, 1705–1707. doi: 10.1126/science.250.4988.1705
- Contos, P., & Letnic, M. (2019). Top-down effects of a large mammalian carnivore in arid Australia extend to epigeic arthropod assemblages. *Journal of Arid Environments*, **165**, 16–27.
- Davidson, A. D., & Lightfoot, D. C. (2006). Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography*, **29**, 755–765.
- Davis, M., Faurby, S., & Svenning, J.-C. (2018). Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proceedings of the National Academy of Sciences*, **115**, 11262–11267. doi: 10.1073/pnas.1804906115
- Dawson, T., & Ellis, B. A. (1994). Diets of mammalian herbivores in Australian arid shublands: seasonal effects on overlap between red kangaroos, sheep and rabbits and on dietary niche breadths and electivities. *Journal of Arid Environments*, **26**, 257–271.
- Denno, R. F., & Fagan, W. F. (2003). Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology*, **84**, 2522–2531. doi: 10.1890/09-2080.1
- Fagan, W. F. (1997). Omnivory as a stabilizing feature of natural communities. *The American Naturalist*, **150**, 554–567.
- Gordon, C. E., Eldridge, D. J., Ripple, W. J., Crowther, M. S., Moore, B. D., & Letnic, M. (2017). Shrub encroachment is linked to extirpation of an apex predator. *Journal of Animal Ecology*, **86**, 147–157. doi: 10.1111/1365-2656.12607
- Gordon, C. E., Feit, A., Gruber, J., & Letnic, M. (2015). Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20142870.

- Gordon, C. E., & Letnic, M. (2016). Functional extinction of a desert rodent: implications for seed fate and vegetation dynamics. *Ecography*, **39**, 815–824. doi: 10.1111/ecog.01648
- Griffiths, C. J., Jones, C. G., Hansen, D. M., Puttoo, M., Tatayah, R. V., Muller, C. B., & Harris, S. (2010). The use of extant non-indigenous tortoises as a restoration tool to replace extinct ecosystem engineers. *Restoration Ecology*, **18**, 1–7. doi: 10.1111/j.1526-100X.2009.00612.x
- Howard, K. S. C., Eldridge, D. J., & Soliveres, S. (2012). Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland. *Basic and Applied Ecology*, **13**, 159–168. doi: 10.1016/j.baae.2012.02.008
- Kratina, P., LeCraw, R. M., Ingram, T., & Anholt, B. R. (2012). Stability and persistence of food webs with omnivory: Is there a general pattern? *Ecosphere*, **3**, 1–18. doi: 10.1890/es12-00121.1
- Letnic, M. (2004). Cattle grazing in a hummock grassland regenerating after fire: the short-term effects of cattle exclusion on vegetation in South-Western Queensland. *The Rangeland Journal*, **26**, 34–48.
- Letnic, M., & Dickman, C. R. (2010). Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews*, **85**, 501–521. doi: 10.1111/j.1469-185X.2009.00113.x
- Lyons, M. B., Mills, C. H., Gordon, C. E., & Letnic, M. (2018). Linking trophic cascades to changes in desert dune geomorphology using high-resolution drone data. *Journal of the Royal Society Interface*, **15**, 20180327. doi: 10.1098/rsif.2018.0327
- McCann, K., & Hastings, A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society B: Biological Sciences*, **264**, 1249–1254.
- Mills, C. H., Gordon, C. E., & Letnic, M. (2018). Rewilded mammal assemblages

- reveal the missing ecological functions of granivores. *Functional Ecology*, **32**, 475–485. doi: 10.1111/1365-2435.12950
- Mills, C. H., Ooi, M., Tuft, K. D., & Letnic, M. (2019). The Rewilding-Jigsaw Dilemma: a rewilded mammal assemblage shapes a desert ecosystem in unexpected ways. *Manuscript Submitted for Publication*.
- Morton, S. R., & Baynes, A. (1985). Small mammal assemblages in arid Australia: a reappraisal. *Australian Mammalogy*, **8**, 159–169.
- Morton, S. R., Stafford Smith, D. M., Dickman, C. R., Dunkerley, D. L., Friedel, M. H., McAllister, R. R. J., ... Westoby, M. (2011). A fresh framework for the ecology of arid Australia. *Journal of Arid Environments*, **75**, 313–329. doi: 10.1016/j.jaridenv.2010.11.001
- Murray, B. R., & Dickman, C. R. (1994a). Food preferences and seed selection in two species of Australian desert rodent. *Wildlife Research*, **21**, 647–655. doi: 10.1071/WR9940647
- Murray, B. R., & Dickman, C. R. (1994b). Granivory and microhabitat use in Australian desert rodents: are seeds important? *Oecologia*, **99**, 216–225. doi: 10.1007/BF00627733
- Murray, B. R., Dickman, C. R., Watts, C. H. S., & Morton, S. R. (1999). The dietary ecology of Australian desert rodents. *Wildlife Research*, **26**, 857–858. doi: 10.1071/WR97046\_CO
- Pimm, S. L., & Lawton, J. H. (1978). On feeding on more than one trophic level. *Nature*, **275**, 542–544. doi: 10.1038/275542a0
- Polis, G. A., & Strong, D. R. (1996). Food web complexity and community dynamics. *The American Naturalist*, **147**, 813–846.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Raubenheimer, D., & Simpson, S. J. (1997). Integrative models of nutrient balancing: application to insects and vertebrates. *Nutrition Research Reviews*, **10**, 151–179. doi: 10.1079/nrr19970009

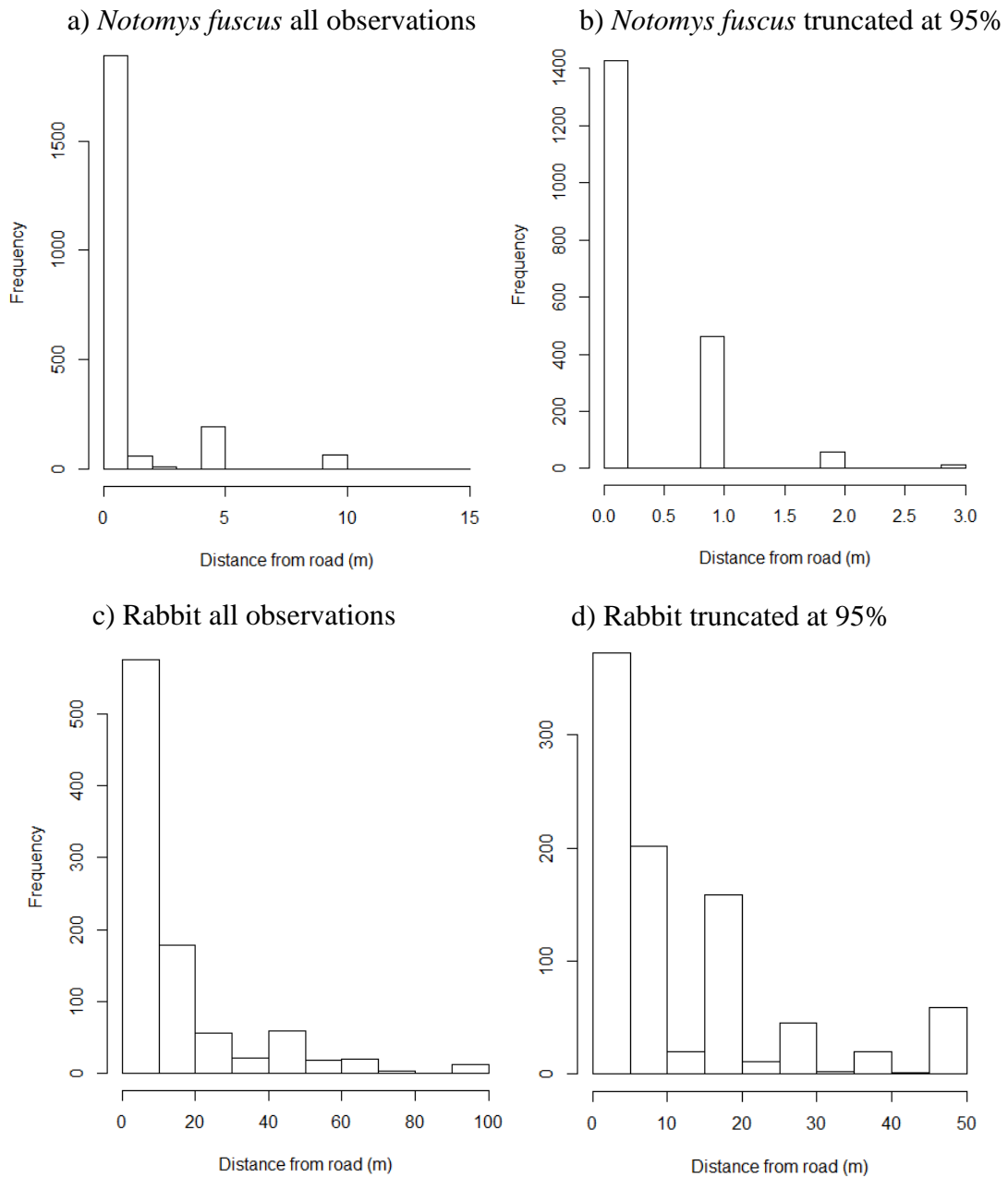
- Rees, J. D., Rees, G. L., Kingsford, R. T., & Letnic, M. (2019). Indirect commensalism between an introduced apex predator and a native avian predator. *Biodiversity and Conservation*, **28**, 2687–2700. doi: 10.1007/s10531-019-01787-8
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484. doi: 10.1126/science.1241484
- Rypstra, A. L., Schmidt, J. M., Reif, B. D., DeVito, J., & Persons, M. H. (2007). Tradeoffs involved in site selection and foraging in a wolf spider: Effects of substrate structure and predation risk. *Oikos*, **116**, 853–863. doi: 10.1111/j.0030-1299.2007.15622.x
- Simpson, S. J., & Raubenheimer, D. (2001). The geometric analysis of nutrient - allelochemical interactions: a case study using locusts. *Ecology*, **82**, 422–439. doi: 10.1890/0012-9658(2001)082[0422:TGAONA]2.0.CO;2
- Thompson, R. M., Hemberg, M., Starzomski, B. M., & Shurin, J. B. (2007). Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology*, **88**, 612–617.
- Vadas Jr, R. L. (1990). The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America. *Environmental Biology of Fishes*, **27**, 285–302.
- Van Dyck, S. M., & Strahan, R. (Eds.). (2008). *The Mammals of Australia* (3rd ed.). Sydney: Reed New Holland.
- Vandermeer, J. (2006). Omnivory and the stability of food webs. *Journal of Theoretical Biology*, **238**, 497–504. doi: 10.1016/j.jtbi.2005.06.006
- Wang, Y., Naumann, U., Wright, S. T., & Warton, D. I. (2012). Mvabund- an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, **3**, 471–474. doi: 10.1111/j.2041-210X.2012.00190.x
- Whitney, K. D., & Lister, C. E. (2004). Fruit colour polymorphism in *Acacia*

ligulata: seed and seedling performance, clinal patterns, and chemical variation. *Evolutionary Ecology*, **18**, 165–186. doi: 10.1023/B:EVEC.0000021153.64497.c1

Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences*, **112**, 4531–4540. doi: 10.1073/pnas.1417301112

Wootton, K. L. (2017). Omnivory and stability in freshwater habitats: does theory match reality? *Freshwater Biology*, **62**, 821–832. doi: 10.1111/fwb.12908

## 5.7 Supplementary Material



*Figure S5.1* Detection histograms for *Notomys fuscus* and rabbits. In b) and d) the top 5% of observations have been removed. Truncating around 5% of distances is standard procedure in density estimations using line transect sampling methods, because the top 5% of distances add little to the abundance while reducing the precision of the density. For more details see: Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Stringberg, S., Hedley, S.L, Bishop, J.R.B, Marques, T.A, & Burnham, K.P. (2010) *Journal of Applied Ecology*, **47**, 5-14.

Table S5.1 Seedbank and above ground vegetation species lists, traits and related references.

Species	Functional Group	Family	Seed Mass	Data Reference
<i>Acacia ligulata</i>	S	Fabaceae	27.6	SID*, SSA**
<i>Brassica tournefortii</i>	F	Brassicaceae	1.355	Jurado et al. 1991***
<i>Crotalaria eremaea</i>	F	Fabaceae	13.104	SID*, SSA**
<i>Enchylaena tomentosa</i>	S	Chenopodiaceae	4.35	SID*, SSA**
<i>Euphorbia porcata</i>	F	Euphorbiaceae	1.96	SID*, SSA**
<i>Nicotiana velutina</i>	F	Solanaceae	0.103	SID*, SSA**
<i>Phyllanthus fuernrohrrii</i>	F	Phyllanthaceae	1.67	SID*, SSA**
<i>Rhodanthe moschata</i>	F	Asteraceae	0.588	SID*, SSA**
<i>Salsola australis</i>	S	Chenopodiaceae	0.88	Jurado et al. 1991***
<i>Scaevola parvibarbata</i>	F	Goodeniaceae	8.41	SID*, SSA**
<i>Senecio gregorii</i>	F	Asteraceae	3.178	SID*, SSA**
<i>Sonchus oleraceus</i>	F	Asteraceae	0.3	SID*, SSA**
<i>Tetragonia eremaea</i>	F	Aizoaceae	9.39	SID*, SSA**
<i>Trachymene glaucifolia</i>	F	Araliaceae	5.08	SID*, SSA**
<i>Tribulus hystrix</i>	F	Zygophyllaceae	16.5	SID*, SSA**
<i>Zygophyllum simile</i>	F	Zygophyllaceae	7.69	SID*, SSA**

\*Royal Botanic Gardens Kew. (2018) Seed Information Database (SID). Version 7.1. <http://data.kew.org/sid/> (Accessed: 15 September 2018)

\*\* South Australian Seed Conservation Centre, Botanic Gardens of South Australia. (2018) The Seeds of South Australia. <https://spapps.environment.sa.gov.au/SeedsOfSA/home.html> (Accessed 15 September 2018)

\*\*\*Jurado, E., Westoby, M., & Nelson, D. (1991) Diaspore Weight, Dispersal, Growth Form and Perenniality of Central Australian Plants. *Journal of Ecology*, **79**, 811-828.

**Specialty Feeds**

3150 Great Eastern Hwy  
Glen Forrest  
Western Australia 6071  
P: +61 8 9298 8111  
F: +61 8 9298 8700  
Email: [info@specialtyfeeds.com](mailto:info@specialtyfeeds.com)

**Diet SF18-022**  
**Low Protein High Carbohydrate**  
**Mixed Herbivorous Diet**

A low protein high carbohydrate diet for mixed species herbivorous native animals designed on customer specification.

- Cellulose has been added as a filler

Calculated Nutritional Parameters	
Protein	7.0%
Total Fat	5.0%
Total Carbohydrate	35.0%
Crude Fibre	40.0%
AD Fibre	41.3%
Digestible Energy	8.1 MJ / Kg

Feeding Recommendations	
Feed ad-lib to animals of all ages.	

Diet Form and Features	
<ul style="list-style-type: none"> <li>Cereal grain base diet.</li> <li>4 mm diameter pellets.</li> <li>Pack size 5 Kg, vacuum packed in oxygen impermeable plastic bags, under nitrogen.</li> </ul>	
Bags are packed into cardboard cartons to protect them during transit.	
<ul style="list-style-type: none"> <li>Smaller pack quantity on request.</li> <li>Diet suitable for irradiation and for autoclave.</li> <li>Lead time 2 weeks for non-irradiation or 4 weeks for irradiation.</li> </ul>	

Ingredients	
A fixed formula ration using the following ingredients.	
Barley, Cellulose, Bran, Canola meal, Canola oil, Calcium carbonate, Dicalcium phosphate, Magnesium oxide, and a Vitamin and mineral premix.	

Added Trace Minerals	
Magnesium	100 mg/Kg
Iron	70 mg/Kg
Copper	16 mg/Kg
Iodine	0.5 mg/Kg
Manganese	70 mg/Kg
Zinc	50 mg/Kg
Molybdenum	0.5 mg/Kg
Selenium	0.1 mg/Kg

Table S5.2 Contents of food used in nutritional preference experiment

Added Vitamins		Calculated Total Minerals	
Vitamin A (Retinol)	10 000 IU/Kg	Calcium	0.80%
Vitamin D3 (Cholecalciferol)	2 000 IU/Kg	Phosphorous	0.70%
Vitamin K (Menadione)	20 mg/Kg	Magnesium	0.20%
Vitamin E (a Tocopherol acetate)	100 mg/Kg	Sodium	0.20%
Vitamin B1 (Thiamine)	80 mg/Kg	Potassium	0.40%
Vitamin B2 (Riboflavin)	30 mg/Kg	Sulphur	0.08%
Niacin (Nicotinic acid)	100 mg/Kg	Iron	130 mg/Kg
Vitamin B6 (Pyridoxine)	25 mg/Kg	Copper	25 mg/Kg
Calcium Pantothenate	50 mg/Kg	Iodine	0.5 mg/Kg
Biotin	300 ug/Kg	Manganese	103 mg/Kg
Folic Acid	5 mg/Kg	Zinc	80 mg/Kg
Vitamin B12 (Cyanocobalamin)	150 ug/Kg	Molybdenum	0.5 mg/Kg
		Selenium	0.2 mg/Kg

Calculated Amino Acids		Calculated Total Vitamins	
Valine	0.34%	Vitamin A (Retinol)	10 030 IU/Kg
Leucine	0.47%	Vitamin D (Cholecalciferol)	2 000 IU/Kg
Isoleucine	0.25%	Vitamin E (a Tocopherol acetate)	18 mg/Kg
Threonine	0.24%	Vitamin K (Menadione)	20 mg/Kg
Methionine	0.09%	Vitamin C (Ascorbic acid)	No data
Cystine	0.23%	Vitamin B1 (Thiamine)	82 mg/Kg
Lysine	0.30%	Vitamin B2 (Riboflavin)	31 mg/Kg
Phenylalanine	0.33%	Niacin (Nicotinic acid)	136 mg/Kg
Tyrosine	0.20%	Vitamin B6 (Pyridoxine)	27 mg/Kg
Tryptophan	0.08%	Pantothenic Acid	53 mg/Kg
Histidine	0.17%	Biotin	433 ug/Kg
		Folic Acid	5.2 mg/Kg
		Inositol	No data
		Vitamin B12 (Cyanocobalamin)	150 ug/Kg
		Choline	680 mg/Kg

Calculated Fatty Acid Composition	
Myristic Acid 14:0	No data
Palmitic Acid 16:0	0.44%
Stearic Acid 18:0	0.08%
Palmitoleic Acid 16:1	No data
Oleic Acid 18:1	2.61%
Gadoleic Acid 20:1	0.06%
Linoleic Acid 18:2 n6	1.32%
a Linolenic Acid 18:3 n3	0.49%
Total n3	0.51%
Total n6	1.32%
Total Mono Unsaturated Fats	2.67%
Total Polyunsaturated Fats	1.83%
Total Saturated Fats	0.52%





Specialty Feeds

3150 Great Eastern Hwy  
Glen Forrest  
Western Australia 6071  
p: +61 8 9298 8111  
F: +61 8 9298 8700  
Email: [info@specialtyfeeds.com](mailto:info@specialtyfeeds.com)

Diet  
SF18-023

Medium Protein Medium Carbohydrate  
Mixed Herbivorous Diet

A Medium protein medium carbohydrate diet for mixed species herbivorous native animals designed on customer specification.

- Cellulose has been added as a filler

Calculated Nutritional Parameters	
Protein	21.0%
Total Fat	5.0%
Total Carbohydrate	21.0%
Crude Fibre	38.5%
AD Fibre	40.3%
Digestible Energy	9.1 MJ / Kg

**Feeding Recommendations**  
Feed ad-lib to animals of all ages.

**Diet Form and Features**

- Cereal grain base diet.
- 4 mm diameter pellets.
- Pack size 5 Kg, vacuum packed in oxygen impermeable plastic bags, under nitrogen.

Bags are packed into cardboard cartons to protect them during transit.

- Smaller pack quantity on request.
- Diet suitable for irradiation and for autoclave.
- Lead time 2 weeks for non-irradiation or 4 weeks for irradiation.

**Ingredients**  
A fixed formula ration using the following ingredients.  
Wheat, Cellulose, Soya Bean Meal, Canola meal, Casein, Canola oil, Calcium carbonate, Dicalcium phosphate, Magnesium oxide, and a Vitamin and mineral premix.

Added Trace Minerals	
Magnesium	100 mg/Kg
Iron	70 mg/Kg
Copper	16 mg/Kg
Iodine	0.5 mg/Kg
Manganese	70 mg/Kg
Zinc	50 mg/Kg
Molybdenum	0.5 mg/Kg
Selenium	0.1 mg/Kg

Calculated Fatty Acid Composition	
Myristic Acid 14:0	Trace
Palmitic Acid 16:0	0.27%
Stearic Acid 18:0	0.10%
Palmitoleic Acid 16:1	Trace
Oleic Acid 18:1	2.76%
Gadoleic Acid 20:1	0.06%
Linoleic Acid 18:2 n6	0.96%
a Linolenic Acid 18:3 n3	0.49%
Total n3	0.51%
Total n6	0.96%
Total Mono Unsaturated Fats	2.82%
Total Polyunsaturated Fats	1.48%
Total Saturated Fats	0.37%

Added Vitamins		Calculated Total Minerals	
Vitamin A (Retinol)	10 000 IU/Kg	Calcium	0.70%
Vitamin D3 (Cholecalciferol)	2 000 IU/Kg	Phosphorous	0.70%
Vitamin K (Menadione)	20 mg/Kg	Magnesium	0.20%
Vitamin E (a Tocopherol acetate)	100 mg/Kg	Sodium	0.20%
Vitamin B1 (Thiamine)	80 mg/Kg	Potassium	0.80%
Vitamin B2 (Riboflavin)	30 mg/Kg	Sulphur	0.08%
Niacin (Nicotinic acid)	100 mg/Kg	Iron	150 mg/Kg
Vitamin B6 (Pyridoxine)	25 mg/Kg	Copper	26 mg/Kg
Calcium Pantothenate	50 mg/Kg	Iodine	0.6 mg/Kg
Biotin	300 ug/Kg	Manganese	111 mg/Kg
Folic Acid	5 mg/Kg	Zinc	90 mg/Kg
Vitamin B12 (Cyanocobalamin)	150 ug/Kg	Molybdenum	0.5 mg/Kg
		Selenium	0.3 mg/Kg
Calculated Amino Acids		Calculated Total Vitamins	
Valine	1.04%	Vitamin A (Retinol)	10 080 IU/Kg
Leucine	1.56%	Vitamin D (Cholecalciferol)	2 000 IU/Kg
Isoleucine	0.88%	Vitamin E (a Tocopherol acetate)	105 mg/Kg
Threonine	0.78%	Vitamin K (Menadione)	20 mg/Kg
Methionine	0.37%	Vitamin C (Ascorbic acid)	No data
Cysteine	0.27%	Vitamin B1 (Thiamine)	82 mg/Kg
Lysine	1.23%	Vitamin B2 (Riboflavin)	31 mg/Kg
Phenylalanine	0.97%	Niacin (Nicotinic acid)	135 mg/Kg
Tyrosine	0.78%	Vitamin B6 (Pyridoxine)	27 mg/Kg
Tryptophan	0.20%	Pantothenic Acid	56 mg/Kg
Histidine	0.55%	Biotin	500 ug/Kg
		Folic Acid	5.6 mg/Kg
		Inositol	No data
		Vitamin B12 (Cyanocobalamin)	150 ug/Kg
		Choline	1 580 mg/Kg



3150 Great Eastern Hwy  
Glen Forrest  
Western Australia 6071  
P: +61 8 9298 8111  
F: +61 8 9298 8700  
Email: [info@specialtyfeeds.com](mailto:info@specialtyfeeds.com)

Diet

SF18-024

High Protein Low Carbohydrate  
Mixed Herbivorous Diet

A high protein low carbohydrate diet for mixed species herbivorous native animals designed on customer specification.

- Cellulose has been added as a filler

Calculated Nutritional Parameters		Feeding Recommendations
Protein	35.0%	Feed ad-lib to animals of all ages.
Total Fat	5.0%	
Total Carbohydrate	7.0%	
Crude Fibre	38.6%	
AD Fibre	40.4%	
Digestible Energy	9.4 MJ / Kg	

Diet Form and Features	
<ul style="list-style-type: none"><li>Cereal grain base diet.</li><li>4 mm diameter pellets.</li><li>Pack size 5 Kg, vacuum packed in oxygen impermeable plastic bags, under nitrogen.</li></ul> <p>Bags are packed into cardboard cartons to protect them during transit.</p> <ul style="list-style-type: none"><li>Smaller pack quantity on request.</li><li>Diet suitable for irradiation and for autoclave.</li><li>Lead time 2 weeks for non-irradiation or 4 weeks for irradiation.</li></ul>	

Ingredients	
A fixed formula ration using the following ingredients. Cellulose, Soya Bean Meal, Canola meal, Casein, Canola oil, Calcium carbonate, Dicalcium phosphate, Magnesium oxide, and a Vitamin and mineral premix.	

Calculated Fatty Acid Composition	
Myristic Acid 14:0	Trace
Palmitic Acid 16:0	0.23%
Stearic Acid 18:0	0.10%
Palmitoleic Acid 16:1	Trace
Oleic Acid 18:1	2.79%
Gadoleic Acid 20:1	0.06%
Linoleic Acid 18:2 n6	0.81%
a Linolenic Acid 18:3 n3	0.48%
Total n3	0.51%
Total n6	0.81%
Total Mono Unsaturated Fats	2.85%
Total Polyunsaturated Fats	1.31%
Total Saturated Fats	0.33%

Added Trace Minerals	
Magnesium	100 mg/Kg
Iron	70 mg/Kg
Copper	16 mg/Kg
Iodine	0.5 mg/Kg
Manganese	70 mg/Kg
Zinc	50 mg/Kg
Molybdenum	0.5 mg/Kg
Selenium	0.1 mg/Kg

Added Vitamins		Calculated Total Minerals	
Vitamin A (Retinol)	10 000 IU/Kg	Calcium	0.70%
Vitamin D3 (Cholecalciferol)	2 000 IU/Kg	Phosphorous	0.70%
Vitamin K (Menadione)	20 mg/Kg	Magnesium	0.20%
Vitamin E (a Tocopherol acetate)	100 mg/Kg	Sodium	0.20%
Vitamin B1 (Thiamine)	80 mg/Kg	Potassium	0.79%
Vitamin B2 (Riboflavin)	30 mg/Kg	Sulphur	0.24%
Niacin (Nicotinic acid)	100 mg/Kg	Iron	140 mg/Kg
Vitamin B6 (Pyridoxine)	2.5 mg/Kg	Copper	25 mg/Kg
Calcium Pantothenate	50 mg/Kg	Iodine	0.6 mg/Kg
Biotin	300 ug/Kg	Manganese	104 mg/Kg
Folic Acid	5 mg/Kg	Zinc	92 mg/Kg
Vitamin B12 (Cyanocobalamin)	150 ug/Kg	Molybdenum	0.5 mg/Kg
		Selenium	0.3 mg/Kg
Calculated Amino Acids		Calculated Total Vitamins	
Valine	1.95%	Vitamin A (Retinol)	10 080 IU/Kg
Leucine	2.79%	Vitamin D (Cholecalciferol)	2 000 IU/Kg
Isoleucine	1.57%	Vitamin E (a Tocopherol acetate)	103 mg/Kg
Threonine	1.36%	Vitamin K (Menadione)	20 mg/Kg
Methionine	0.77%	Vitamin C (Ascorbic acid)	No data
Cysteine	0.29%	Vitamin B1 (Thiamine)	82 mg/Kg
Lysine	2.32%	Vitamin B2 (Riboflavin)	32 mg/Kg
Phenylalanine	1.63%	Niacin (Nicotinic acid)	130 mg/Kg
Tyrosine	1.50%	Vitamin B6 (Pyridoxine)	27 mg/Kg
Tryptophan	0.32%	Pantothenic Acid	55 mg/Kg
Histidine	0.93%	Biotin	518 ug/Kg
		Folic Acid	5.7 mg/Kg
		Inositol	No data
		Vitamin B12 (Cyanocobalamin)	153 ug/Kg
		Choline	1 710 mg/Kg

## Chapter 6: Discussion

### 6.1 Summary of findings

Australia's deserts became depauperate of mammal fauna before we understood the functional roles mammals played in the ecosystem. In this thesis, I have provided evidence that now rare native mammals once held important functional roles in arid Australia, and that their loss from large expanses of the continent may have had significant effects on vegetation community structure, composition and function which have until now been largely overlooked. I have shown that omnivorous marsupials and native rodents shape the vegetation communities in sand dune environments through seed predation (Chapters 2, 3 & 4), herbivory (Chapters 4 & 5) and selective consumption of plant parts (Chapters 4 & 5). In this thesis I have reassessed long-standing paradigms that were invoked based on data collected from mammal depauperate ecosystems (Chapters 2 & 3). Furthermore, I have found that much of our fundamental understanding of the organisation and function of arid Australia is a legacy of mammal decline.

In Chapter 2, I compared seed removal by mammals and ants on shrub seeds and the abundance of shrub seedlings in two rewilded desert ecosystems with adjacent areas possessing depauperate mammal faunas, testing the paradigm that ants hold primacy over mammals as seed predators in arid Australia (Morton, 1985). The results from this chapter demonstrate that in rewilded areas where mammals were abundant, mammals, especially the omnivorous *Bettongia lesueur* (bettong) and *Notomys alexis*, removed far more seeds than ants. Shrub seedlings were more abundant in areas with depauperate mammal faunas than in rewilded areas, and these results are consistent with prior research (Gordon et al., 2017; Gordon & Letnic, 2016; Noble,

Hik, & Sinclair, 2007) demonstrating that mammal decline and the associated relaxation of seed predation pressure may be an underappreciated driver of shrub encroachment.

In Chapter 3 I used a different rewilded mammal assemblage to further test the idea that ants are the dominant seed predators in arid Australia (Morton, 1985) and to investigate how the functional extinction of small and medium sized mammals has influenced our interpretation of other aspects of arid zone ecology, such as myrmecochory. Unlike the situation described on other continents (Giladi, 2006), the adaptive benefits of myrmecochory in an Australian context do not include avoiding seed predation by mammals (Davidson & Morton, 1984). My results in this chapter, namely that *Bettongia pennicillata* removed many more seeds than ants and removed seeds in winter when ants were inactive, refute the paradigm that ants are the dominant seed predator in arid Australia. My findings in Chapter 3 are concordant with my findings in Chapter 2 and similar studies (Gordon & Letnic, 2016), suggesting that mammals are the most important seed predators in arid Australia and that paradigms relating to seed predation, myrmecochory and the functional roles of mammals in arid Australia are prone to shifting baselines due to the devastation of our mammal fauna.

In Chapter 4, I used selective exclosures to test the effects that bettongs and the native rodents *Notomys fuscus* and *Pseudomys australis* have on above ground vegetation and the seed bank. I found that the interactions between rewilded mammals and vegetation were more complicated than predicted from prior knowledge of these species' functional roles (James, Eldridge, & Hill, 2009; Valentine et al., 2018; Chapters 2, 3). I found that mammal activity drove a shift in

the vegetation community from standing vegetation and longer-lived plants to increased litter and grass cover. I also found that native rodents and bettongs reduced the abundance of seeds of two forb species, were important pre-dispersal seed predators, and that rodents preferentially foraged in areas to which bettongs did not have access. The results from Chapter 4 add to Chapters 2 and 3 by enhancing our understanding of the ecological role of digging marsupials and native rodents and providing insight into previously unknown interspecific interactions. This chapter serves to highlight the uncertainty involved in rewilding programs, especially when we have insufficient information about species' ecosystem functions to set goals or predict the outcomes of ecosystem reassembly.

Finally, in Chapter 5, I used foraging trays and selective exclosures to determine the strength of interactions between the omnivorous rodent *Notomys fuscus* and its food resources. I found that *N. fuscus* has strong effects on food resources of varying protein content including seeds, herbage, flowers and invertebrates. My results demonstrate that omnivores in pulsed systems like the Australian arid zone exert strong effects on their food resources and through these strong interactions have the potential to shape the composition and structure of resources. When these results are viewed in concert with Chapters 2, 3 and 4, this Chapter supports my overall findings that the loss of mammals from the arid zone is an underappreciated driver of environmental change.

## 6.2 Mechanisms by which mammals can shape their ecosystem

The research contained within this thesis has demonstrated that the interactions between mammals, vegetation and the seed bank in arid landscapes is complex and responses are difficult to predict. Therefore, to frame my findings and other potential

interactions, I have adapted the Trigger-Reserve-Pulse model (TTRPM; Noy-Meir, 1973; Tongway & Ludwig, 1997) that was introduced in Chapter 1 to describe relationships between the seed bank, vegetation and mammal assemblages.

The TTRPM is a useful tool to inform our knowledge of how animals interact with resource pulses (Morris & Letnic, 2017). In the TTRPM (Fig. 1.1), the flow of nutrients and litter through the landscape is interrupted by vegetation patches which capture particles as they are carried past by wind or water. The vegetation patches then function as sinks for nutrients and litter to return to the reserve, and therefore the distribution of vegetation across the landscape can determine the distribution of resources and the ability of the landscape to respond during resource pulses (Noy-Meir, 1973; Tongway & Ludwig, 1997). Below I propose the Resource Pulse Consumer Compartment model (RPCC; Fig. 6.1) as an adaptation of the TTRPM which provides a framework for understanding how the removal of plant material and seeds by native rodents and digging marsupials, the creation of foraging pits, and the subsequent revisitation to foraging pits by native rodents and marsupials can all contribute to resource availability across the arid landscape.

According to the RPCC (Fig. 6.1), irregular rainfall events in the water-limited arid zone are triggers for plant growth and the germination of seeds in the reserve (Morton et al., 2011). If uninterrupted, vegetation growth after rainfall events culminates in the production of leaves, roots, stems, flowers and seeds, which provide litter and seeds for the reserve through the processes of senescence and dispersal. Foraging by animals such as digging marsupials and native rodents create pits for the reserve that capture litter and seeds (James et al., 2009; Valentine et al., 2018) and provide ideal germination sites for ephemeral species (Eldridge &

Simpson, 2002; Hobbs & Mooney, 1985). However, selective herbivory, granivory and pre-dispersal seed predation by the same animals reduces the seed production of palatable species and unpalatable plant parts remain to become litter (Chapters 2, 3, 4 & 5; Gordon et al., 2017; Valone & Balaban-Feld, 2018; Weltzin, Archer, & Heitschmidt, 1997).

Additionally, I hypothesise that digging marsupials and native rodents can directly impact a foraging pit's incorporation into the reserve compartment through the 'treasure effect', whereby they loot the litter that has accumulated in pits for morsels of food (Davies, Kirkpatrick, Cameron, Carver, & Johnson, 2019; James et al., 2009) or via trampling effects on the soil surface disrupting the pit structure.

Selective foraging by native mammals can therefore foreseeably shift the composition of the reserve compartment, driving changes in the vegetation community towards species of certain traits or life history strategies, for example, smaller seeds that are less attractive to granivores (Brown & Heske, 1990; Davidson & Lightfoot, 2006; Gordon et al., 2017). Because of the partitioning of roles between native rodents and digging marsupials in my experiments and the large ecosystems supported by similar mammals overseas (Chapters 4, 5; Davidson, Detling, & Brown, 2012), I anticipate that the strength of interactions described in the RPCC will also vary depending on the density of mammals and composition of the mammal assemblage (Davidson & Lightfoot, 2006; Decker, Eldridge, & Gibb, 2019; Sweeney et al., 2019).





### 6.3 Limitations

There is one main caveat that applies to the research contained within this thesis, and possibly any attempt at understanding the functional role of rare mammals in contemporary arid Australia. That is the problem of shifting baselines regarding our understanding of small and medium-sized mammal assemblages. Due to the severe losses in native mammal fauna experienced in the Australian arid zone (Woinarski, Burbidge, & Harrison, 2015), we simply do not know, and it is impossible to know, if the rewilded mammal communities in my study systems at Arid Recovery and Scotia Sanctuary are comparable to those that existed in pre-European times. I am therefore unable to make inferences about how the ecological functions discussed in this thesis would have influenced the vegetation community in a pre-European context.

The alternate states represented by my study sites demonstrate the variability of mammal densities in contemporary arid Australia. Inside fenced reserves such as Scotia Sanctuary and Arid Recovery, there is often a conspicuous absence of mammalian predators, and therefore reintroduced animals can attain high population densities (Moseby, Lollback, & Lynch, 2018). However, when compared to areas outside the reserves where mammalian predators persist, the density of bettongs within Arid Recovery during my study was comparable to that of the functionally similar introduced European rabbit (*Oryctolagus cuniculus*) outside the reserve (Mills, Gordon, & Letnic, 2018; Chapter 2), while native rodent populations were much higher inside the reserve than outside (Mills et al., 2018; Moseby, Hill, & Read, 2009; Chapter 2). At Scotia Sanctuary, European rabbit densities outside the reserve are much lower compared to the densities of bettong populations within the

reserve (Mills et al., 2018) and local native rodent assemblages are depauperate with just one species of native rodent present in low densities.

In my study site in the Strzelecki Desert (Chapter 5), small mammal assemblages were diverse and unfenced, and the ecosystem was mediated by the dingo (Letnic, Koch, Gordon, Crowther, & Dickman, 2009). The consistently high densities at which the rodent *Notomys fuscus* occurred during my study are unusual compared to similar sites in arid Australia (Dickman, Mahon, Masters, & Gibson, 1999; Greenville, Wardle, Nguyen, & Dickman, 2016; Letnic et al., 2011); however, small mammal densities resembling those reported in Chapter 5 have been observed at Arid Recovery, where the rodents *Notomys alexis* and *Pseudomys australis* have benefited from the removal of feral predators within the fenced reserve (Moseby et al., 2009), and in southern Northern Territory (Bennison, Godfree, & Dickman, 2018). By contrast, sites only 50 km from the study site at Lindon Station in Chapter 5 have extremely depauperate mammal assemblages (Contos & Letnic, 2019; Letnic, Crowther, & Koch, 2009).

#### 6.4 Future directions

As discussed in section 6.2, the effects that native mammals have on the vegetation and seed bank observed within this thesis and contained within the RPCC are likely to be context dependent (Davidson & Lightfoot, 2006; Decker et al., 2019). Because of the lack of certainty around historical mammal assemblages or densities, and the potential for density-dependent interactions, I suggest that future research should explore how the effects of mammals on vegetation and the seed bank shift in different contexts. Primarily, I suggest testing the pathways described in the RPCC (Fig. 6.1) using different mammal assemblages, between assemblages with different

densities, and in different habitats. The insights gained from further investigation into the functional roles of rare mammals would further inform the development of new paradigms describing the organisation and function of Australia's vast arid zone.

Australian conservation practitioners frequently provide novel solutions for the variety of threats which face wildlife (e.g. Hunter, Britz, Jones, & Letnic, 2015; Katherine E. Moseby, Blumstein, & Letnic, 2016; O'Donnell, Webb, & Shine, 2010; Read et al., 2019). For the foreseeable future; however, the key threats to wildlife will persist (Woinarski et al., 2015) and rewilding in fenced reserves will remain a cornerstone of Australian wildlife conservation (Legge et al., 2018; Sweeney et al., 2019). To further investigate pathways in the RPCC in different contexts, I propose that rewilding programs should install detailed monitoring programs and partition the ecosystem effects and interactions of different consumers. Having information about the ecological functions of native mammals in different contexts will enable informed decision making for ecosystem management and restoration (Hobbs et al., 2014; Nogués-Bravo, Simberloff, Rahbek, & Sanders, 2016; Schweiger, Boulangeat, Conradi, Davis, & Svenning, 2019).

## 6.5 Conclusions

I have, in this thesis, provided insight to the ecological functions of native mammals as consumers in arid Australia and demonstrated that many paradigms describing the function and organisation of Australia's deserts are in fact legacies of mammal decline and extinction. As demonstrated by the variety of mammal densities and assemblages described above in section 6.3 and the alternate states they represent (Chapter 1), it is impossible to discuss mammal assemblages without considering the

role that shifting baselines have had in our understanding of arid Australian ecosystems. Not only do we not know what pre-European mammal assemblages looked like in the Australian arid zone, but even if we did, it would be impossible to restore them due to the ongoing threat posed by introduced predators, and the complete extinction of a number of potentially functionally important species (Legge et al., 2018; Sweeney et al., 2019; Woinarski et al., 2015).

Contemporary ecosystem assemblages in arid Australia and around the world are the result of centuries of irreversible change wrought by humans (Bar-On, Phillips, & Milo, 2018; Dirzo et al., 2014; Sweeney et al., 2019). Rewilding and restoration have a role to play in a human-dominated landscape (Seddon, Griffiths, Soorae, & Armstrong, 2014; Svenning et al., 2015; Sweeney et al., 2019); however, due to contemporary conditions, that role inevitably includes the formation of novel ecosystems (Hobbs et al., 2014; Nogués-Bravo et al., 2016). With appropriate monitoring, rewilding affords us a window into both the unattainable past and the inevitable, novel, future. With this in mind, I suggest that rewilding and other ecosystem restoration programs embrace the novel ecosystems that they are creating, instead of seeking a past for which there is no baseline.

## 6.6 References

- Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences*, **115**, 6506–6511. doi: 10.1073/pnas.1711842115
- Bennison, K., Godfree, R., & Dickman, C. R. (2018). Synchronous boom-bust cycles in central Australian rodents and marsupials in response to rainfall and fire. *Journal of Mammalogy*, **99**, 1137–1148. doi: 10.1093/jmammal/gyy105
- Brown, J. H., & Heske, E. J. (1990). Control of a desert-grassland transition by a

- keystone rodent guild. *Science*, **250**, 1705–1707. doi: 10.1126/science.250.4988.1705
- Contos, P., & Letnic, M. (2019). Top-down effects of a large mammalian carnivore in arid Australia extend to epigeic arthropod assemblages. *Journal of Arid Environments*, **165**, 16–27.
- Davidson, A. D., Detling, J. K., & Brown, J. H. (2012). Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment*, **10**, 477–486. doi: 10.1890/110054
- Davidson, A. D., & Lightfoot, D. C. (2006). Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography*, **29**, 755–765.
- Davidson, D. W., & Morton, S. R. (1984). Dispersal adaptations of some *Acacia* species in the Australian arid zone. *Ecology*, **65**, 1038–1051.
- Davies, G. T. O., Kirkpatrick, J. B., Cameron, E. Z., Carver, S., & Johnson, C. N. (2019). Ecosystem engineering by digging mammals: effects on soil fertility and condition in Tasmanian temperate woodland. *Royal Society Open Science*, **6**, 180621. doi: 10.1098/rsos.180621
- Decker, O., Eldridge, D. J., & Gibb, H. (2019). Restoration potential of threatened ecosystem engineers increases with aridity: broad scale effects on soil nutrients and function. *Ecography*, **42**, 1–13. doi: 10.1111/ecog.04259
- Dickman, C. R., Mahon, P. S., Masters, P., & Gibson, D. F. (1999). Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildlife Research*, **26**, 389–403. doi: 10.1071/WR97057
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, **345**, 401–406. doi: 10.1126/science.1251817
- Eldridge, D. J., & Simpson, R. (2002). Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands.

*Basic and Applied Ecology*, **3**, 19–29. doi: 10.1078/1439-1791-00078

Giladi, I. (2006). Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos*, **112**, 481–492. doi: 10.1111/j.0030-1299.2006.14258.x

Gordon, C. E., Eldridge, D. J., Ripple, W. J., Crowther, M. S., Moore, B. D., & Letnic, M. (2017). Shrub encroachment is linked to extirpation of an apex predator. *Journal of Animal Ecology*, **86**, 147–157. doi: 10.1111/1365-2656.12607

Gordon, C. E., & Letnic, M. (2016). Functional extinction of a desert rodent: implications for seed fate and vegetation dynamics. *Ecography*, **39**, 815–824. doi: 10.1111/ecog.01648

Greenville, A. C., Wardle, G. M., Nguyen, V., & Dickman, C. R. (2016). Population dynamics of desert mammals: similarities and contrasts within a multispecies assemblage. *Ecosphere*, **7**, 1–19. doi: 10.1002/ecs2.1343

Hobbs, R. J., Higgs, E., Hall, C. M., Bridgewater, P., Chapin, F. S., Ellis, E. C., ... Yung, L. (2014). Managing the whole landscape: historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment*, **12**, 557–564. doi: 10.1890/130300

Hobbs, R. J., & Mooney, H. A. (1985). Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia*, **67**, 342–351.

Hunter, D. O., Britz, T., Jones, M., & Letnic, M. (2015). Reintroduction of Tasmanian devils to mainland Australia can restore top-down control in ecosystems where dingoes have been extirpated. *Biological Conservation*, **191**, 428–435. doi: 10.1016/j.biocon.2015.07.030

James, A. I., Eldridge, D. J., & Hill, B. M. (2009). Foraging animals create fertile patches in an Australian desert shrubland. *Ecography*, **32**, 723–732. doi: 10.1111/j.1600-0587.2009.05450.x

Legge, S., Woinarski, J. C. Z., Burbidge, A. A., Palmer, R., Ringma, J., Radford, J.

- Q., ... Tuft, K. D. (2018). Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. *Wildlife Research*, **45**, 627–644. doi: 10.1071/WR17172
- Letnic, M., Crowther, M. S., & Koch, F. (2009). Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? *Animal Conservation*, **12**, 302–312. doi: 10.1111/j.1469-1795.2009.00250.x
- Letnic, M., Koch, F., Gordon, C., Crowther, M. S., & Dickman, C. R. (2009). Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3249–3256. doi: 10.1098/rspb.2009.0574
- Letnic, M., Story, P., Story, G., Field, J., Brown, O., & Dickman, C. R. (2011). Resource pulses, switching trophic control, and the dynamics of small mammal assemblages in arid Australia. *Journal of Mammalogy*, **92**, 1210–1222. doi: 10.1644/10-mamm-s-229.1
- Mills, C. H., Gordon, C. E., & Letnic, M. (2018). Rewilded mammal assemblages reveal the missing ecological functions of granivores. *Functional Ecology*, **32**, 475–485. doi: 10.1111/1365-2435.12950
- Morris, T., & Letnic, M. (2017). Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20170111. doi: 10.1098/rspb.2017.0111
- Morton, S. R. (1985). Granivory in arid regions: comparison of Australia with North and South America. *Ecology*, **66**, 1859–1866. doi: 10.2307/2937381
- Morton, S. R., Stafford Smith, D. M., Dickman, C. R., Dunkerley, D. L., Friedel, M. H., McAllister, R. R. J., ... Westoby, M. (2011). A fresh framework for the ecology of arid Australia. *Journal of Arid Environments*, **75**, 313–329. doi: 10.1016/j.jaridenv.2010.11.001
- Moseby, K. E., Blumstein, D. T., & Letnic, M. (2016). Harnessing natural selection

to tackle the problem of prey naïveté. *Evolutionary Applications*, **9**, 334–343.  
doi: 10.1111/eva.12332

Moseby, K. E., Hill, B. M., & Read, J. L. (2009). Arid Recovery - a comparison of reptile and small mammal populations inside and outside a large rabbit, cat and fox-proof enclosure in arid South Australia. *Austral Ecology*, **34**, 156–169. doi: 10.1111/j.1442-9993.2008.01916.x

Moseby, K. E., Lollback, G. W., & Lynch, C. E. (2018). Too much of a good thing; successful reintroduction leads to overpopulation in a threatened mammal. *Biological Conservation*, **219**, 78–88. doi: 10.1016/j.biocon.2018.01.006

Noble, J. C., Hik, D. S., & Sinclair, A. R. E. (2007). Landscape ecology of the burrowing bettong: fire and marsupial biocontrol of shrubs in semi-arid Australia. *The Rangeland Journal*, **29**, 107–119.

Nogués-Bravo, D., Simberloff, D., Rahbek, C., & Sanders, N. J. (2016). Rewilding is the new Pandora's box in conservation. *Current Biology*, **26**, R87–R91. doi: 10.1016/j.cub.2015.12.044

Noy-Meir, I. (1973). Desert ecosystems: environment and producer. *Annual Review of Ecology and Systematics*, **4**, 25–51.

O'Donnell, S., Webb, J. K., & Shine, R. (2010). Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. *Journal of Applied Ecology*, **47**, 558–565. doi: 10.1111/j.1365-2664.2010.01802.x

Read, J. L., Bowden, T., Hodgens, P., Hess, M., McGregor, H., & Moseby, K. E. (2019). Target specificity of the felixer grooming “trap.” *Wildlife Society Bulletin*, **43**, 112–120. doi: 10.1002/wsb.942

Schweiger, A. H., Boulangeat, I., Conradi, T., Davis, M., & Svenning, J. C. (2019). The importance of ecological memory for trophic rewilding as an ecosystem restoration approach. *Biological Reviews*, **94**, 1–15. doi: 10.1111/brv.12432

Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: restoring species in a changing world. *Science*, **345**, 406–412. doi: 10.1126/science.1251818



- Svenning, J.-C., Pedersen, P. B. M., Donlan, J., Ejrnaes, R., Faurby, S., Galetti, M., ... Vera, F. W. M. (2015). Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences*, **113**, 898–906. doi: 10.1073/pnas.1502556112
- Sweeney, O. F., Turnbull, J., Jones, M., Letnic, M., Newsome, T. M., & Sharp, A. (2019). An Australian perspective on rewilding. *Conservation Biology*, **33**, 812–820. doi: 10.1111/cobi.13280
- Tongway, D., & Ludwig, J. (1997). The conservation of water and nutrients within landscapes. In J. Ludwig, D. Tongway, D. Freudenberger, J. Noble, & K. Hodgkinson (Eds.), *Landscape Ecology Function and Management* (pp. 13–23). Collingwood, Australia: CSIRO Publishing.
- Valentine, L. E., Ruthrof, K. X., Fisher, R., Hardy, G. E. S. J., Hobbs, R. J., & Fleming, P. A. (2018). Bioturbation by bandicoots facilitates seedling growth by altering soil properties. *Functional Ecology*, **32**, 2138–2148. doi: 10.1111/1365-2435.13179
- Valone, T. J., & Balaban-Feld, J. (2018). An experimental investigation of top–down effects of consumer diversity on producer temporal stability. *Journal of Ecology*, **107**, 806–813. doi: 10.1111/1365-2745.13064
- Weltzin, J. F., Archer, S., & Heitschmidt, R. K. (1997). Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology*, **78**, 751–763.
- Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences*, **112**, 4531–4540. doi: 10.1073/pnas.1417301112

## Appendix 1

### The Ecologists and the Australian Landscape

Charlotte Mills, after John Godfrey Saxe's "The Blind Men and the Elephant"

Six ecologists from New South Wales,  
Each specialised in a trait  
Went out to do their fieldwork  
(Though only in one State)  
That each by keen observing  
Might health of system rate.

The first inside a sanctuary  
Assesses bettong pits  
Finding always that they catch  
Rain, litter and seed bits.  
Exclaimed about their findings:  
"Rewilding – it's the s\*\*tz!"

The second out upon the plains  
Watches grass grow tall  
"Bring in sheep to moderate,"  
Is their frequent call.  
For we must help the Wanderer  
Or risk a breeding stall.

But further west the third can see  
How plentiful the roo.  
Aussie icons in great numbers  
A joy to witness too.  
"To cull would be a tragedy,  
This is a natural boon."

The fourth is sitting with the third,  
And can't help but disagree:  
"High abundances of herbivores  
Are not a source of glee,  
It took years of dingo cull  
To set the munchers free."

The fifth sets traps amongst the dunes  
Just past the dingo fence  
Sees all creatures large and small  
And each 'correctly' dense.  
Here predator-prey remains intact  
And nature just makes sense.

The sixth, jaded, has come to terms  
With a system ruled by goats:  
"This state is just one big goat farm  
Profitable for folks.  
Accepting ferals is the way  
Other stories are a hoax."

Upon return they all assessed  
Each other's theories broad:  
Of herbivores and pestilence,  
Of pits which may restore.  
What would the ideal system be?  
One boasting health galore?

One thing on which they did agree:  
Our goals are far from clear.  
We have seen our baselines shift  
To ecosystems near.  
To fight extinction is our test  
And the outcomes we can steer.



A particularly spectacular desert sunset.