Ryan, Natasha (2023) ***Effects of various grazing strategies on the shelter and forage site selection of rufous bettongs (Aepyprymnus rufescens)*****. Masters (Research) Thesis, James Cook University.**

Effects of various grazing strategies on the shelter and forage site selection of rufous bettongs (*Aepyprymnus rufescens*)

Natasha Ryan BAppSc

A thesis submitted for the degree of Master of Philosophy

College of Science and Engineering

James Cook University

April 2023

Acknowledgements

Like many before me can attest, the post-graduate research journey can rightly so, be likened to a rollercoaster. There are ups and downs, twists and turns, periods of calm and periods of immense stress. Through this journey it is your support network that keeps your wheels on the track, and to my support network, I am indebted to each and every one of you.

Firstly, I would like to thank my supervisors for their unwavering support, guidance and tolerance for my myriad of questions along the way. Professor Lin Schwarzkopf, thank you for being so inclusive and welcoming from the very first day I joined the Vertebrate Ecology Lab, and for sharing your wealth of knowledge and experience, which was fundamental to this project. You are an inspiration to myself, and all women in science and academia. To Dr. Eric Nordberg, I cannot even begin to express my immense gratitude for your assistance throughout this project. You have been a part of this journey since my first pilot field studies, providing invaluable advice, feedback, tuition and assistance. I cannot thank you enough for your contributions, but also your friendship and endless support. Dr. Heather Neilly, your very own thesis forged a path forward for the research I present here in my thesis. Your research intrigued and inspired me and I thank you for the valuable insights, and knowledge you offered me whenever I asked, no matter how long it was between emails or skype meetings. Dr. Ben Hirsch, thank you for your technical expertise, and helping with the commencement of the radio tracking which was pertinent to this research.

To Dr. Peter O'Reagain, John Bushell and all the staff at the Department of Agriculture and Fisheries, Charters Towers, thank you for your in-kind logistical support that made this research possible, but also for welcoming me into your office, offering me a workspace, and always extending an invite to "smokos" and industry events.

I would like to thank Michael and Michelle Lyons of Wambiana Station, on which this research was conducted. You were so welcoming and accommodating of myself and my volunteers while we were conducting fieldwork and you provided us with the perfect home away from home.

I am indebted to my volunteers who were a pivotal part of my fieldwork; without you, I would have no data to write this thesis. I must especially thank Eric and Hayley who dedicated numerous days and nights helping to build the foundations of this project. Amidst the trials and tribulations, you never failed to have a laugh and chat, and I could count on you no matter what. So thank you both for all your hard work, your patience, but more importantly, thank you for your friendship and for the all the laughter and the wonderful memories.

Finally, I would like to express my immense gratitude my beloved family, friends and partner. You have all been on this journey with me, vicariously living through the ups and downs, and you have stuck by my side through it all, cheering me on from the sidelines. Thank you for the unconditional love, support and encouragement that kept me going every step of the way. I would like to give a special shout out to my partner and say thank you for being my constant source of motivation and inspiration. You believed in me on the days I did not believe in myself and I am grateful for you, and the immense patience, understanding and unequivocal love you showed me, particularly in the final months - you are my rock.

Statement of contribution of others

Nature of Assistance	Contribution	Names, Titles *(if relevant)* and Affiliations of Co-Contributors
Intellectual support	Editorial assistance Data analysis Statistical support GIS Support	Professor Lin Schwarzkopf Dr. Eric Nordberg Dr. Heather Neilly Dr. Ben Hirsch Dr. Juan Mula Laguna
Financial Support	In kind support and equipment use	Dr. Peter O'Reagain, John Bushell and Department of Agriculture and Fisheries
	Equipment use and loans	Lexie Edwards
	Stipend	HDR Student Support Stipend (School of Science and Engineering)
Data Collection	Field work assistants	Dr. E. Nordberg, H. Goody, H. Wang, D. Donald, C. Kelly

Ethics statement

The research contained within this thesis was conducted under JCU Animal Ethics Committee permit number A2625 and Queensland Department of Environment and Science, Scientific Purposes Permit WA0016055.

Copyright Statement

Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

Abstract

The world is experiencing an extinction crisis, and Australia has one of the highest extinction rates in the world. Contributing to these species' declines are a range of factors, but one of the most significant pressures on wildlife in Australia, and across the globe, is agriculture because it profoundly disturbs natural ecosystems. Agriculture, in particular, livestock grazing, is Australia's primary land use, and one of our largest industries and global exports. Concerningly, amidst an extinction crisis, agriculture is set to expand in response to increasing global wealth and population size. With such a significant amount of land dedicated to livestock grazing, effective management of these production systems has the ability to significantly influence future production and conservation outcomes and should therefore be re-evaluated if we are to improve the future outcomes of both, simultaneously.

Sustainable grazing has been highlighted as a means of meeting production demands, whilst supporting biodiversity and enhancing ecosystem health and functioning. For Australia's beef production industry, determining and using appropriate grazing strategies and stocking rates could be the key to a sustainable and productive future, with reduced environmental impact. To achieve this, we need broad-scale adoption of sustainable grazing practices, and for that we need to continue providing industry with information about the benefits of sustainable land management to ecosystem health, functioning and ultimately, productivity. One aspect of this is better understanding how these sustainable grazing strategies directly influence the wildlife within these rangeland systems, and likewise, how wildlife benefit these systems.

For my thesis, I investigated the effect of various grazing strategies on the shelter and forage site selection of rufous bettongs (*Aepyprymnus rufescens*). Food and shelter are critical to the survival of all species, thus, understanding how grazing land management influences these factors is imperative if we want to safeguard the wildlife on these landscapes and improve biodiversity outcomes. In addition to forage and site selection, I also investigated and quantified the beneficial ecosystem services provided by the rufous bettong to rangelands. My research is pertinent to the ongoing global dilemma: how do we achieve production and biodiversity outcomes simultaneously?

Over two years, I tracked the diurnal and nocturnal locations of 15 rufous bettongs fitted with VHF radio collars, conducted 100 dig count transect surveys, deployed 80 Thermochron^{TM} iButton temperature loggers, measured the volume of 83 diggings and conducted vegetation composition assessments across five different grazing strategies and three vegetation types, in both wet and dry seasons.

I found that rufous bettongs were generally resilient to a range of grazing strategies; however, my data indicated a trend towards preferential selection of rotational spelling strategies, and avoidance of heavy stocking rate strategies. At a fine-scale vegetation level, I found that rufous bettongs preferred to shelter in the abundant, native shrub, *Carissa ovata*. Shelter sites themselves were an important buffer to highly variable, and sometimes extreme, ambient temperatures and thus, likely an important factor in the species' success in grazing landscapes. I also found that digging site selection was not affected by grazing strategy, and digging occurred at the same rate throughout the year. Finally, I determined that 72 m^3 of soil is moved by rufous bettongs at my study site annually; approximately 1.3m^3 soil/individual/year.

My findings suggest that rufous bettongs are a valuable ecosystem engineer within the grazing systems they inhabit due to their widespread digging behaviour, which occurs throughout the year and leads to a significant amount of soil displacement. The benefits of digging and soil turnover are well documented, therefore, having digging animals on resource-scarce rangelands could lead to significant, long-term landscape improvements. Therefore, I suggest that the rufous bettong is a species whose presence, and actions, could be a means of addressing the conundrum of meeting global beef production demands, while mitigating environmental risks and improving biodiversity outcomes.

To do this, there needs to be a mindset shift, and an adoption of a more holistic approach to the management of grazing on Australia's rangelands, such that there is consideration given to the interconnectedness of production systems and natural ecosystems. By making decisions that support biodiversity, such as reducing the clearing of *Carissa ovata*, or using moderate grazing strategies, species such as rufous bettongs, who provide invaluable ecosystem services, could coexist on the land while simultaneously improving landscape health and productivity. Broad-scale adoption of sustainable land management in the agricultural sector therefore has the potential to be a catalyst of change that sees the world better able to feed a growing population, while preserving and maintaining biodiversity and the benefits it provides.

Table of contents

List of Tables

List of Figures

Chapter 1 A review of the role and distribution of ecosystem engineers: Potoroidae, in northern Australian rangelands

Abstract

The global extinction crisis, and its associated losses, have become critical to many industries such as agriculture, that rely on the maintenance of landscape health, productivity and sustainability, and are suffering from the loss of species such as 'ecosystem engineers', which mediate ecosystem services and consequently maintain landscape health. In this chapter, I reviewed the role of ecosystem engineers, with particular focus on the family Potoroidae, within Australia's rangelands and determined, for each species, the percentage of habitat overlap with cattle grazing. I found that the rufous bettong (*Aepyprymnus rufescens*), the most abundant of all potoroids, was underrepresented in ecological research, and had the greatest overlap with cattle grazing (38%) of any Potoroidae species. Better understanding the ecological role of this species, particularly within agricultural systems, was identified as a key area for further research. I recommended that for biodiversity, and land health and functioning to be sustained in Australian rangelands, then developing a greater understanding of the ecology, and ecosystem role of this species, within grazing systems could be important. Utilising land management practices that support this species, and others, in grazing systems helps to achieve both biodiversity and agricultural production outcomes in the future.

Introduction

Australian wildlife face an uncertain future amidst a global extinction crisis of magnitude comparable to those that occurred in prehistoric times (Hooper et al. 2012; Tilman 1999). Since 1788, Australia has lost 11% of its endemic mammal fauna, equating to 50% of all mammal extinctions globally in that time (Hooper 2005; Woinarski, Burbidge, and Harrison 2015). The loss of just one species from an ecosystem can have a big impact. It can result in important ecological niches being vacated; niches upon which an unknown number of species, and ecosystem functions may rely. This accelerating biodiversity loss is negatively affecting landscape health, productivity and sustainability (Hooper et al. 2012; Tilman 1999; Hooper 2005), to such a degree that its effects equal, or exceed those of rising $C0_2$ levels and drought (Cardinale et al. 2012; Hooper et al. 2012). It is, therefore, an issue rivalling climate change, and needs further attention.

Australia is an isolated continent characterised by its arid climate, seasonal rainfall, ancient, weathered and low-fertility soils, and regular wildfires (Orians and Milewski 2007; Beeton et al. 2006). Although having evolved to withstand this distinct and challenging environment, Australia's unique ecological communities have a particularly low resilience to further environmental pressures, especially those that have ensued since European settlement (Beeton et al. 2006; Fleming et al. 2014; Orians and Milewski 2007; Martin 2003; Eldridge and James 2009; Claridge 2002). Land clearing, altered fire regimes, grazing and introduced species are just some of the novel pressures challenging native flora and fauna (Beeton et al. 2006; Martin 2003; Fleming et al. 2014; Cocklin and Dibden 2009). Among the groups most vulnerable to these effects are native marsupial and rodent species, which have experienced the highest extinction rate of all native Australian mammals; the family Potoroidae is one such example (Seebeck and Rose 1989; Woinarski, Burbidge, and Harrison 2015). As illustrated by Seebeck & Rose (1989) in Figure 1.1, the potoroids of genus *Bettongia*, formerly occupied most of southern Australia and the east coast. However, since the 1700's and the introduction of novel pressures such as livestock grazing and introduced predators, these species, and the rest of the Potoroidae family have suffered immense population attrition (Bradshaw 2012; Gretton and Salma 1996; Martin 2003; Cocklin and Dibden 2009). Many of these species would have had important ecosystem roles, and thus, could have contributed greatly to the health of their surrounding ecosystem (Woinarski, Burbidge, and Harrison 2015).

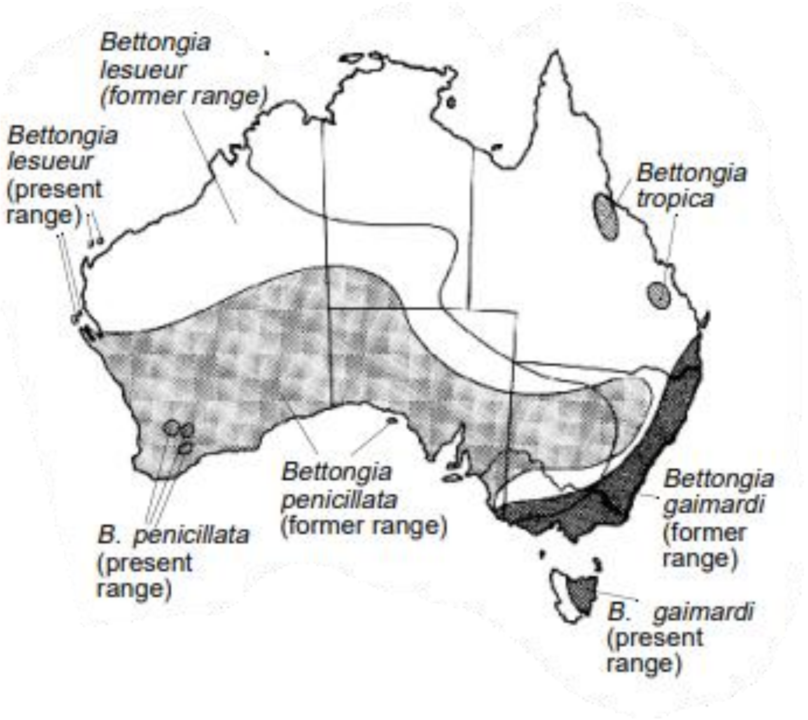

Figure 1.1 Historic distribution range compared to the modern day distribution range of Bettongia lesueur, Bettongia penicillata, Bettongia gaimardi and Bettongia tropica as at 1989 (adapted from Seebeck & Rose (1989)).

The species in the family Potoroidae can excavate large amounts of soil and thus have the ability to alter their environment significantly (Claridge et al. 1992; James and Eldridge 2007; James 2004; Eldridge and James 2009; Garkaklis, Bradley, and Wooller 2000, 2004). The effects of digging on the landscape are numerous, and can result in increased organic matter decomposition rates due to soil turnover, which exposes surface soil to sub-surface soil invertebrates and microbes (Eldridge and Mensinga 2007; Garkaklis, Bradley, and Wooller 2000; Killham 1994; Whitford and Kay 1999; Eldridge and James 2009). Studies show that digging also increases ecosystem heterogeneity by creating voids in often highly compacted surface crusts, in which seeds can accumulate, and more successfully germinate and grow, due to higher soil nutrients levels, lower temperatures, increased moisture levels and protection from weather and granivorous fauna (Valentine et al. 2017; Dundas et al. 2018; Eldridge and Mensinga 2007; James, Eldridge, and Moseby 2010; James, Eldridge, and Hill 2009; Fleming et al. 2014) (Noble 1993; Noble et al. 2007; James and Eldridge 2007) (Whitford and Kay 1999; James, Eldridge, and Hill 2009). Furthermore, the presence of digging mammals can lead to increased soil nutrients and soil enzyme activity (Decker et al 2019) and increased water infiltration (Whitford and Kay 1999; Eldridge and James 2009; Valentine et al. 2017). Overall, as a result of all these changes caused by digging, there is increased soil fertility and landscape heterogeneity where digging mammals are present (Eldridge and James 2009; Whitford and Kay 1999).

It has been suggested that the decline in digging mammals may be a factor contributing to the substantial declines in ecosystem function apparent today, particularly in arid and semi-arid Australia, where land stability and productivity are likely dependent on the maintenance of processes mediated by these ecosystem engineers (Martin 2003; Eldridge and James 2009; Fleming et al. 2014; Dundas et al. 2018). In Australia, our nutrient poor arid regions are utilised primarily for cattle grazing. Eighty-seven percent of all agricultural land in Australia are rangelands devoted to grazing, and this is set to increase or intensify as global wealth and demand for beef products rapidly increases (ABS 2018; McAlpine et al. 2009; MLA 2022; Lanz, Dietz, and Swanson 2018). Grazed environments are characterised by low rainfall and extreme heat, this, together with Australia’s weathered and nutrient poor soils, makes them vulnerable to erosion and degradation (Claridge 2002; Eldridge and James 2009; Orians and Milewski 2007). Grazing domestic livestock exacerbates pressure on this already fragile landscape and can lead to what Rapport & Whitford (1999) describe as landscape stress. Landscape stress is characterised by altered nutrient cycling, decreased productivity, vegetation loss, surface soil loss, increased wind and water erosion, soil compaction and reduced surface roughness, decreased landscape heterogeneity reduced species diversity, and a shift to more short-lived and invasive species of flora and fauna (Rapport, Regier, and Hutchinson 1985; Eldridge et al. 2017; Beeton et al. 2006; Nash, Jackson, and Whitford 2003; Tabeni and Ojeda 2003; Thrash 1998;

Whitford, Rapport, and deSoyza 1999; James, Landsberg, and Morton 1999). Overgrazing i.e. high cattle stocking rates over a prolonged period of time, further compounds these detrimental effects (Rapport and Whitford 1999; Fleischner 1994).

High stocking rates can alter plant species composition, often in favour of non-native, less palatable grasses and woody shrubs (Fleischner 1994; Rapport and Whitford 1999). The altered landscape disrupts habitat for vertebrates and invertebrates, resulting in reduced species richness and diversity (Fleischner 1994; Tabeni and Ojeda 2003; Eldridge, Poore, et al. 2016; James, Landsberg, and Morton 1999). For example, Eldridge et al (2012) found that grazing intensity affected the habitat preference of echidnas and goannas, with the lowest densities found on heavily grazed land. Similarly, grazing intensity (on a scale of low, moderate, and high) influenced habitat selection by the rufous bettongs, such that they avoided heavily grazed paddocks, instead opting for sites with low to moderate grazing intensity (Neilly and Schwarzkopf 2018).

Increasing consumer demand is putting pressure on the cattle industry, and as a result, so too the landscapes on which they occur (Bell et al. 2011; Cocklin and Dibden 2009; Beeton et al. 2006; Eldridge et al. 2017). This could result in more widespread and severe land degradation if it is not managed with consideration for the long-term health and sustainability of the landscape (O'Reagain et al. 2018; Jhariya, Meena, and Banerjee 2021; McAlpine et al. 2009). Failure to appropriately manage grazing land amidst global expansion and intensification of agriculture could result in reduced ecosystem health and functioning, loss of productivity and loss of biodiversity, including valuable ecosystem engineer species, such as bettongs (Lanz, Dietz, and Swanson 2018). To prevent this from occurring, and to ensure that Australia can meet increasing consumer demands, while maintaining biodiversity, it is imperative that we better understand the dynamic between cattle grazing, and biodiversity, particularly the valuable ecosystem engineers who contribute disproportionately more than other species to healthy ecosystem functioning.

In this chapter, I explore the valuable ecosystem role of each extant species within the family Potoroidae, and, based on occurrence data from confirmed sightings, determine the degree of habitat overlap each species has with cattle grazing. I also conduct a systematic review of literature to identify what we currently know and understand about the ecology and ecosystem services of the most abundant potoroid, the rufous bettong. I then discuss the relationship between ecosystem engineers, ecosystem health, and cattle grazing, and how this dynamic could be better managed and utilised to help achieve biodiversity and cattle production outcomes simultaneously.

Methods

Cattle grazing and habitat overlap

To determine the percentage of habitat overlap with cattle grazing for extant Potoroidae species, raw sighting data was downloaded from the Atlas of Living Australia (ALA). This data was then filtered using the following exclusion criteria: (i) Date of sighting: 1990-2019 (inclusive), (ii) Coordinate uncertainty: < 5000m, (iii) Location: exclusion of 'false' locations, and (iv) Taxonomy: exclusion of all 'false' taxonomic records. Records deemed to be 'false', were data points that did not meet the requirements of the data quality checks undertaken by ALA or its users (e.g. suspected outliers or incorrect identifications).

The filtered data was then imported to the mapping software program QGIS (3.4). A grazing land use 'layer', based on the Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES) land use data (Pintor et al. 2018), was then added to the map to determine where grazing land occurred. The overall percentage of habitat overlap with cattle grazing land, derived from confirmed ALA sighting data, was calculated for each Potoroidae species by dividing the number of sightings on grazing land, by the total number of sightings (occurring on a range of land types and localities).

Literature review

A range of databases were used to conduct this review including Scopus, Web of Science, SpringerLink, PubMed and CSIRO Publishing in addition to the JCU Library One search. For table one, each potoroid species' scientific and common name was searched in each database. The ecosystem services provided by potoroid species were categorised into one of five categories: mycophagism (fungi consumption), soil turnover, spore dissemination, soil physical properties, landscape. A summary of the main findings, under each category, and the associated authors were listed within the table.

For table two, Scopus, Web of Science, CSIRO Publishing and Scopus were searched using 'Aepyprymnus rufescens', 'rufous bettong' and 'rufous rat-kangaroo' to display results which were then searched individually for the same terms and the following exclusion criteria applied: the names 'Rufous bettong', 'Aepyprymnus rufescens', 'rufous rat-kangaroo' were in the subject of the paper; **or** mentioned over 10 times within a paper; **or** they were the topic of discussion; **or** they were listed in the keywords (N.B I did not include papers in which the species was mentioned briefly, e.g. in a species list, as a capture in a field study etc.). For the purpose of this chapter, those results were then categorised as: ecology, reproduction, parasitology, genetics, and only results relating to ‘ecology’ or ‘ecosystem engineer’ were tabulated and included here.

Key findings

Cattle grazing and habitat overlap

My examination of the degree of habitat overlap with cattle grazing for all extant Potoroidae species is summarised in Table 1.1. In brief summary, from the ALA occurrence data I assessed, I found that 38.12% of rufous bettong habitat overlaps with grazing land, the greatest degree of overlap of all species (Table 1.1). This was followed by Tasmanian bettong (*Bettongia gaimardi)* which had a 24.66% habitat overlap with grazing land. The other species had less than 10% of their habitat overlapping grazing land, with some species, Gilbert’s potoroo (*Potorous gilbertii)* and Burrowing bettong (*Bettongia lesueur)*, having no overlap with grazing land at all (Table 1.1).

Literature review

Potoroidae species

The ecosystem services provided by the species within family Potoroidae have been summarised in Table 1.1. In summary, the burrowing bettong appears to be the most widely researched and understood of the potoroid species, with a range of ecosystem services quantified and reported on by a range of authors. Likewise, the brush-tailed bettong had numerous studies quantifying the extent of its ecosystem services across all five categories. The Tasmanian bettong was also well represented in the literature, particularly, in regards to its mycophagism. Of the bettong species, the most under-represented in the literature, was the rufous bettong. That which was reported is summarised in Table 1.2 and was limited to the extent of their mycophagism and their role as spore disseminators. There were numerous papers outlining the ecosystem services provided by all three potoroo species; Long-footed potoroo (*Potorous longipes)*, Long-nosed potoroo (*Potorous tridactylus)* and Gilbert’s potoroo.

Rufous bettong (Aepyprymnus rufescens)

The literature available to describe the ecology and ecosystem services provided by the rufous bettong is summarised in Table 1.2 inclusive of the citation, sample size, study location and a summary of findings. At the time of this review, I found five studies that met my search criteria.

Table 1.1 Comparison of Potoroidae species conservation status, grazing overlap, and existing knowledge of ecological service

Species	*IUCN Conservation status*	*Percentage overlap with cattle grazing*	*Ecological services*	*References*
Long-footed potoroo *Potorous longipes*	Vulnerable (2016)	0.83	**Mycophagism** 82.6 ± 7.29% of diet is hypogeal fungi, with little seasonal variation [1,2,3] 90-100% of diet is fungi[8] 91.2 ± 4.4% of faecal remains contained fungi[6] Fungus is >80% of the diet all times of the year [7] **Spore dissemination** Spreads ectomycorrhizal spores in faeces[4,5]	[1]Nuske et al. (2017b) [2] Green et al. (1999) [3]Claridge, Tanton, and Cunningham (1993) [4]Claridge et al. (1992) [5](Reddell, Spain, and Hopkins 1997) [6](Green et al. 1999) [7] Johnson (1994b) [8] Scotts (1989)

Long-nosed potoroo *Potorous tridactylus*	Near Threatened (2016)	6.99	**Mycophagism** Hypogeal fungi are the primary food source, with less fungi consumed in Summer and Spring[1,2] Fungus forms a minimum of 50% of the diet all times of the year, with a peak in winter (92%), and low in summer (52%)[6] 33-82% of diet is fungi, with seasonal and site specific variation[7] **Soil turnover** Produce 2250 diggings/hectare/year[3] Excavates 0.34-1.1tonnes/ ha/individual of soil yearly [4] **Spore dissemination** Disperses viable ectomycorrhizal fungal spores in faeces[4,5]	[1]Bennett and Baxter (1989) [2] Claridge and Cork (1994) [3]Claridge, Cunningham, and Tanton (1993) [4]Claridge et al. (1992) [5]Reddell, Spain, and Hopkins (1997) [6]Tory et al. (1997) [7] Claridge, Tanton, and Cunningham (1993)

Burrowing bettong *Bettongia lesueur*	Near Threatened (2019)	0	**Mycophagism** 0.02% of diet comprised of fungi[9] Fungi forms 19-23% of the diet in Winter, and 2% of diet in Summer[10] **Soil turnover** Excavates 1.3-5.99 tonnes/ha/individual of soil yearly foraging [1,2] Excavates 2.8-9.8tonnes/ ha/individual of soil yearly burrowing[3] **Spore dissemination** Disperses viable ectomycorrhizal fungal spores in faeces[8] **Soil physical properties** Increased mineral nitrogen, carbon and sulphur content in digging pits[2] Increased soil moisture content in digging pits[2] Decreased subsurface soil temperature[4] **Landscape** Increased landscape heterogeneity[5,6,7] Increased biomass of native grasses[5,7]	[1]James and Eldridge (2007) [2]James (2004) [3]Eldridge and James (2009) [4]James, Eldridge, and Hill (2009) [5]Noble et al. (2007) [6]Noble (1993) [7]Burbidge, Short, and Fuller (2007) [8]Reddell, Spain, and Hopkins (1997) [9]Bice (2008) [10]Robley (2001)
Brush-tailed bettong	Critically Endangered (2016)	7.69	**Mycophagism** 54-76% of diet is fungi, with more consumed in autumn and winter[9]	[1]Garkaklis, Bradley, and Wooller (2004)

Bettongia penicillata			**Soil turnover** Excavates 2.7-9.7tonnes/ha/individual of soil yearly[1,2] Produce an average of 66 diggings/night; and 5000-16000 diggings/ha/year[1,2] **Spore dissemination** Dispersal and inoculation agent of ectomycorrhizal fungi via faeces[3,5,6,7] **Soil properties** May beneficially influence water infiltration[4] Decreased nitrate (NO_3^-) and ammonium (NH_4^-)[8] **Landscape** Possible role in post-fire spore dispersal and soil inoculation[7]	[2]Garkaklis, Bradley, and Wooller (2000) [3]Lamont, Ralph, and Christensen (1985) [4]Garkaklis, Bradley, and Wooller (1998) [5]Dundas et al. (2018) [6]Reddell, Spain, and Hopkins (1997) [7]Lamont, Ralph, and Christensen (1985) [8]Garkaklis, Bradley, and Wooller (2003) [9]Zosky et al. (2017)

Gilbert's potoroo *Potorous gilbertii*	Critically Endangered (2016)	0	**Mycophagism** Fungi forms a minimum of 70% of the diet with little seasonal variation [1,2,3] **Spore dissemination** Disperses viable ectomycorrhizal fungal spores in faeces[4]	[1]Nuske et al. (2017b) [2]Nguyen, Needham, and Friend (2005) [3]Bougher and Friend (2009) [4]Reddell, Spain, and Hopkins (1997)
Tasmanian bettong *Bettongia gaimardi*	Near Threatened (2016)	24.66	**Mycophagism** Feeds on at least 49 recorded fungi species[1] Mycophagist all year round[1] 40-90% of diet is fungi, with highest consumption in Winter[6] Females are more mycophagous than males: 1-28% more fungi present in faeces[6] Fungi form the greatest volume of faecal material - highest consumption in Spring, lowest in Winter[7] **Soil turnover** 0.38-4.57tonnes/ha/individual of soil yearly[2,3] Create up to 3000 diggings/ha[3] Create up to 200 diggings per night[5]	[1]Taylor (1991) [2]Eldridge and James (2009) [3]Johnson (1994a) [4]Reddell, Spain, and Hopkins (1997) [5]Munro et al. (2019) [6]Johnson (1994b) [7]Taylor (1992)

			Spore dissemination Disperses viable ectomycorrhizal fungal spores in faeces[4] **Landscape** Potent influence on maintaining hypogeous fungi species richness due to diversity of species consumed[1]	
Northern bettong *Bettongia tropica*	Endangered (2016)	9.97	**Mycophagism** Fungi form, on average, 50-60% of diet with individual consumption ranging from 34-85% [1,3] 23-67% of diet is fungi[7] Fungi forms the majority of faecal material content (~35-65%)[2] **Spore dissemination** Dispersal of ectomycorrhizal spores via faeces[4,5] Consumes and disperses a more diverse array of fungal species than other generalist species in the same habitat[4]	[1]Vernes, Castellano, and Johnson (2001) [2]McIlwee and Johnson (1998) [3]Nuske et al. (2017b) [4]Nuske et al. (2018) [5]Reddell, Spain, and Hopkins (1997) [7] Johnson and McIlwee (1997)

Rufous bettong *Aepyprymnus rufescens*	Least Concern (2016)	38.12	**Mycophagism** 9.3% of diet comprised of fungi[1] 84-95% of faecal material contains fungus in Autumn and Winter[3] Scats commonly contain ectomycorrhizal fungi spores[2,4] Fungus consumed more in the wet season[5] **Spore dissemination** Disperses ectomycorrhizal spores in faeces[2]	[1]Nuske et al. (2017b) [2]Reddell, Spain, and Hopkins (1997) [3]Vernes Vernes (2010) [4]Schlager (1982) [5]McIlwee and Johnson (1998)

Table 1.2 A summary of the research conducted on the ecological services provided by rufous bettongs (Aepyprymnus rufescens)

Citation	*Sample Size*	*Location*	*Summary*
Nuske, S. J., K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger and S. E. Abell (2017). "Redundancy among mammalian fungal dispersers and the importance of declining specialists." Fungal Ecology **27**: 1-13.	53 mammal species	James Cook University, Queensland	A meta-analysis to assess the importance of mammalian fungal dispersers to gain further understanding of how the substantial mammalian losses being encountered in Australia will affect plant-fungi interactions and fungal diversity. They concluded that fungal specialists (namely the Potoroidae family, except *Aepyprymnus rufescens* and *Bettongia lesueur)* contribute disproportionally more than other mammals to the dispersal of fungi in Australia.
McIlwee , A. P. and C. N. Johnson (1998). "The Contribution of Fungus to the Diets of Three Mycophagous Marsupials in Eucalyptus Forests, Revealed by Stable Isotope Analysis." Functional Ecology **12**(2): 223-231.	Not specified	North-eastern Queensland	Faecal samples were collected from three mycophagous marsupials to determine the dietary importance of fungus compared to other foods. Faecal composition indicated that *A. rufescens* consume more grass and less fungus than *Bettongia tropica*. Less fungus was present in scats during the dry season versus the wet. At this time, more roots, tubers and grass were evident.
Schlager, F. E. (1982). The Distribution, Status and Ecology of the Rufous Rat-Kangaroo, 'Aepyprymnus rufescens', in Northern New	Variable – wild and captive animals observed	Northern New South Wales	This unpublished thesis consists of a broad range of ecological observations on distribution and status, biology, habitat use, predation and effects of land use

South Wales. Masters Thesis University of New England			effects on *A. rufescens* in northern New South Wales.
Vernes, K. (2010). Mycophagy in a community of macropodoid species Macropods: the biology of kangaroos, wallabies, and rat-kangaroos. G. Coulson and M. Eldridge. Victoria CSIRO Publishing **1**.	54 scat samples	North-eastern New South Wales	Scat samples were collected from six species of wild and semi-wild macropods and potoroids to determine patterns of consumption among species and seasons. He found fungi in 84-95% of scat samples collected from *A. rufescens* in autumn and winter. There was a high diversity of fungal spores found in faeces.*
Reddell, P., A. V. Spain and M. Hopkins (1997). "Dispersal of Spores of Mycorrhizal Fungi in Scats of Native Mammals in Tropical Forests of North Eastern Australia." Biotropica **29**(2): 184-192.	6 scat samples	North-eastern Queensland	They collected samples from 17 mammal species to assess the presence of fungal spores. Of the samples collected from *A. rufescens*, three out of six samples contained arbuscular mycorrhizal fungi spores, and five out of six samples contained ectomycorrhizal fungi spores.*

(*) indicates when a summary of findings is only provided for A. rufescens specific results

Discussion

Australia's Potoroidae family has eight extant species, with many former species now extinct. Evidently, potoroids provide numerous ecosystem services, but the extent of their ecosystem engineering is understood to differing degrees, depending on the species (Table 1.1). Some of the difficulty in furthering this knowledge resides in the fact that all but one species, the rufous bettong (*Aepyprymnus rufescens),* are listed by the International Union for Conservation of Nature (IUCN) as a conservation concern (Table 1.1). This ranges from the Critically Endangered status of the Brush-tailed bettong *(Bettongia penicillata)* and Gilbert's potoroo *(Potorous gilbertii*), to the Near Threatened status of Long-nosed potoroo *(Potorous tridactylus),* Burrowing bettong *(Bettongia lesueur),* and Tasmanian bettong *(Bettongia gaimardi).* Hence, many of their distributions are very isolated in the wild, or non-existent without human intervention in the form of predator-proof sanctuaries, and this influences the extent of research that can be conducted (Anson 2018; Short & Turner 2000).

To date, research illustrates that in addition to roots, tubers, plant components and insects (Taylor 1992; Seebeck & Rose 1989; Schlager 1981; Claridge et al 1993; Bennett & Baxter 1989), all potoroids consume fungus, albeit differing quantities, with some showing a greater dependency on fungi as a primary food source (Table 1.1). For example, fungi makes up over 80% of the diet of long-footed potoroo (*Potorous longipes)* (Nuske et al. 2017b; Green et al. 1999; Claridge, Tanton, and Cunningham 1993), while it can make up as little as 9.3% of the diet of the rufous bettong depending on the time of year (Nuske et al. 2017b)(Table 1.1). This means that all species, to some extent, move soil in the landscape (biopedturbation) and hence can be classified as ecosystem engineers. However, at the time of this review, the extent of biopedturbation, in terms of the amount of soil moved, has only been quantified for four species, namely the long-nosed potoroo*,* burrowing bettong*,* brush-tailed bettong and Tasmanian bettong (Table 1.1). There is a disparity in the amount of literature, and thus the degree of biological and ecological understanding of the Potoroidae family. Some species, such as the burrowing bettong and Tasmanian bettong have been researched more extensively (Table 1.1), while other species, such as the rufous bettong are less understood.

Although it is the most abundant potoroid, surprisingly little is known about the rufous bettong. At the time of this review, there was a distinct lack of literature describing the ecology of, and ecosystem services provided by the species (Table 1.2). Given what we know about the fate of most species within the family Potoroidae, it is concerning how little we know about the most abundant extant species within this family.

Based on recorded ALA sighting data, my review of habitat selection by family Potoroidae revealed that rufous bettongs have the highest proportion of habitat overlapping grazing land of all potoroid species (Table 1.1). Given that agricultural land is typically a strong contributor to faunal declines (including bettongs) it is surprising that rufous bettongs seem resistant to this pressure (Beeton et al. 2006; Nash, Jackson, and Whitford 2003; Tabeni and Ojeda 2003; Thrash 1998; Whitford, Rapport, and deSoyza 1999). Rufous bettongs are the largest of the potoroids, which may reduce its vulnerability to predation, a significant cause of decline in other species (Dennis and Johnson 2008; Doherty et al. 2016). Studies also indicate that they have a variable dependence on fungi as a food source, with estimates ranging from 9-95% fungi consumption throughout the year (Nuske et al. 2017b; Vernes 2010)(Table 1.1). Perhaps a more generalist diet, one that incorporates more than just fungi, promotes resilience. Again, given what we know about the fate of most species within the family Potoroidae, it is concerning how little we understand about the rufous bettong, and what factors enable it to maintain a relatively stable population.

As a digging mammal, the rufous bettong, like other potoroids, is a source of biopedturbation within the landscape (Nuske et al. 2017b). Currently, the loss and destruction of biodiversity directly affects agricultural productivity (Cocklin and Dibden 2009). It is suggested that the decline in Australia’s ecosystem engineering species, especially digging mammals, could be a contributing factor which has led to the deterioration and reduced productivity of Australia’s semi-arid and arid rangelands on which most of the nation’s cattle production occurs (Eldridge and James 2009; Fleming et al. 2014; Dundas et al. 2018). Research suggests that ecosystem engineers not only play a pivotal role in maintaining landscape health and functioning, particularly in arid and semi-arid regions (Whitford and Kay 1999; Eldridge and James 2009), but they can also enhance productivity (Wright and Jones 2004).

With the increasing awareness of the importance of biodiverse ecosystems to agricultural productivity due to the abundance of species they support and the beneficial ecosystem services they provide (Gordon, Prins, and Squire 2017; Jhariya, Meena, and Banerjee 2021; Macdonald and Feber 2015; Gretton and Salma 1996; Filazzola et al. 2020; Woinarski, Burbidge, and Harrison 2015; Machovina, Feeley, and Ripple 2015; Tuomisto et al. 2015), and based on the findings of this review (Table 1.1), it is apparent that digging mammals provide a range of beneficial ecosystem services to the landscapes they inhabit. Therefore, to prevent further deterioration of Australia’s rangelands, and further productivity declines, management of these grazing systems should aim to support biodiversity, and species that provide valuable ecosystem services to these landscapes (Eldridge, Delgado-Baquerizo, et al. 2016). If populations of ecosystem engineers are supported on rangelands, then there is opportunity for industry to counteract the negative effects of grazing, and improve production (Halstead et al. 2019; Neilly and Schwarzkopf 2018). Furthermore, we could also see the cattle production industry mitigate its environmental impact, and in turn help achieve improved outcomes for biodiversity conservation.

Given what we understand about the fate of the Potoroidae family and their population and habitat range attrition since the commencement of agriculture in the 1700's (Figure 1.1), it is imperative that we take advantage of the last remaining, 'low conservation concern' potoroid. We need to better understand rufous bettongs and their role within rangeland systems so we can implement appropriate conservation and land management practices to preserve them and the beneficial services they provide, on these landscapes. My research demonstrates that although they are the most abundant and widespread potoroid (Seebeck and Rose 1989), surprisingly little is known about rufous bettongs, and the extent to which they 'engineer' the ecosystems they inhabit, and this needs be addressed (Table 1.1, Table 1.2). Rufous bettongs have experienced some decline (Schlager 1982; Short 1998), particularly in New South Wales, where they are now listed at the state level as threatened (Heritage 2018). Therefore, time is critical, and developing a better understanding of how they persist in agriculture, one of the biggest threats to biodiversity, while remaining the most abundant bettong species in Australia could help prevent future population declines or extinction of yet another ecosystem engineer, and loss of their valuable ecosystem services. As pointed out by Crain & Bertness (2006), making ecosystem engineers a conservation target is particularly beneficial, because through the conservation of a singular ecosystem engineer, such as the rufous bettong, we can positively influence entire ecological communities, due to the broad scale benefits engineers have on their surrounding environment.

We know that sustainable grazing, and utilising more moderate stocking rates is conducive to better environmental outcomes (Gordon, Prins, and Squire 2017; Jhariya, Meena, and Banerjee 2021; Macdonald and Feber 2015; Gretton and Salma 1996; Filazzola et al. 2020; Woinarski, Burbidge, and Harrison 2015; Machovina, Feeley, and Ripple 2015; Tuomisto et al. 2015). Furthermore, there is mounting evidence to suggest that these lower intensity grazing strategies better support ecosystem engineers including goannas, echidnas and the rufous bettong (Neilly and Schwarzkopf 2018; Eldridge et al. 2012). Therefore, in summary, I suggest that further research be dedicated to understanding rufous bettong ecology i.e. nesting behaviour, foraging behaviour and movement patterns across a range of grazing strategies. Furthermore, quantifying the amount of soil they move and when, would help to clarify the ecosystem services provided by the rufous bettong in grazing systems and highlight their value to these systems and broader ecosystem health, and thus productivity of landscape. If we can better understand the effect of different grazing land management strategies on rufous bettongs, then we can ascertain how we can best support and harness the services provided by these native ecosystem engineers. If we can better support nature, and the services it provides, we might be able to support and improve biodiversity and cattle production outcomes, simultaneously (Wright and Jones 2004).

Conclusion

This literature review highlights an opportunity we have to learn more about the ecosystem services provided by digging mammals using an abundant ecosystem engineer, the rufous bettong as a case study. Furthermore, we can investigate how the rufous bettong utilises grazing land of which a considerable amount of its habitat overlaps, and this could help target conservation efforts to prevent future population declines of this and other species in these landscapes. Further research on the ecology of rufous bettongs and the factors affecting their distribution and population size, especially on agricultural land, typically antagonistic to many species, would aid in the conservation of bettongs, potoroos and other ecosystem engineers.

Furthermore, with the impending expansion or intensification of agriculture in response to increasing global demands, it critical that we address how to manage agriculture, without further impacting biodiversity. I suggest that ecosystem engineers, such as the rufous bettong, who help to improve ecosystem health and functioning, could be a catalyst for change in the agricultural sector. By supporting such species, agricultural industries, such as grazing, could see improved productivity and profitability, which would help meet increasing consumer demands. They would also be simultaneously maintaining, if not improving biodiversity outcomes and thus help to mitigate the environmental impact of the industry. This would benefit the range of stakeholders involved and could see Australia recognised for its innovative, integrative approach to livestock production rather than its high rate of mammalian extinctions.

Chapter 2 Rufous bettong shelter site use, composition and importance in grazing systems

Introduction

Without adequate shelter, the threat of extreme weather, predators and competitors can be lethal to animals (MacGregor, Cunningham, and Lindenmayer 2015). Shelter sites, places that protect an organism from predators, weather, or both (Rutledge et al. 2022), can take many forms depending on the species, its habitat, and the climatic conditions specific to where it lives. Some animals use existing structures as shelter, such as logs, tree hollows and caves (Gibbons and Lindenmayer 2002; Cockle, Martin, and Weso łowski 2011; Wilkinson, Grigg, and Beard 1998), others create shelters like burrows and nests (Burbidge 1983; Haussmann 2017) and some animals do both.

Protection from the elements is particularly important for small- to medium-sized mammals, who compared to larger mammals have higher surface-to-volume ratios, higher metabolic rates, produce more heat per gram of tissue, and require more water to effectively cool down *via* evapotranspiration (Schmidt-Nielsen and Schmidt-Nielsen 1952; Fuller et al. 2021; MacGregor, Cunningham, and Lindenmayer 2015). If physiological adaptations such as evaporative cooling cannot reduce core body temperature, and shelter is unavailable, the risk of mortality greatly increases in smaller species (Mitchell et al. 2018; Fuller et al. 2021). Because maintaining core body temperature in unfavourable conditions is energetically expensive for mammals, finding and using appropriate shelter sites can be a far more efficient use of energy, and thus a more advantageous strategy to manage exposure to heat, cold, wind, or rain, compared to increasing metabolic rate (Poole et al. 2015). Thus, understanding shelter site use is critical to understanding the small mammals success in various environments.

The difficulty with relying on shelter as a mechanism to manage body temperature, is its availability. Finding suitable shelter can be difficult for a range of reasons, such as scarcity or unavailability of shelter materials, often resulting from anthropogenic causes such as land clearing or climate change. For example, tree hollows required for nesting and shelter are becoming increasingly rare due to logging and land clearing, which poses a significant ecosystem threat (Gibbons and Lindenmayer 2002; Lindenmayer, Laurance, and Franklin 2012). Similarly, changes to land use, for agriculture, urban development, and forestry, alter natural ecosystems and can inhibit, destroy or hinder access to adequate shelter sites for wildlife (Theobald, Miller, and Hobbs 1997; Davies et al. 2010; Goldie and Betts 2014; Tilman and Clark 2015). Arguably, agriculture is the most important of such disturbances, as it covers the largest land area worldwide (Ritchie and Roser 2013). Often, land is cleared or managed to maximise productivity, rather than for sustainable environmental outcomes, thus, decreasing biodiversity and reducing ecosystem function (Tilman and Clark 2015; O'Reagain et al. 2009; Eldridge, Delgado-Baquerizo, et al. 2016; Neilly and Schwarzkopf 2017). However, some shelter-building small mammal species manage to exist within agricultural systems (Neilly and Schwarzkopf 2018). Understanding the factors allowing native species to persist in agricultural landscapes is important for promotion of sustainable land management in this industry.

Rufous bettongs (*Aepyprymnus rufescens*) belong to the family Potoroidae, and are the only species in this group not listed by the International Union for Conservation of Nature (IUCN) as a conservation concern. Rufous bettongs are nocturnal, and build shelters made from grass, or use existing structures such as hollow logs as shelter during the day (Johnson 1980a; Schlager 1982). These shelters are likely critical to their survival, but little is known about their shelter materials or characteristics, particularly in northern Australian rangelands. Importantly, rufous bettongs occupy more agricultural land than any other potoroid and other studies have found that rufous bettongs were least abundant in areas of high cattle utilisation, suggesting that high cattle density may compromise access to resources, or ability to make shelters (Neilly and Schwarzkopf 2017). Therefore, the impact of agriculture on shelter use and availability could play a pivotal role in their success or demise in this landscape in the future, particular amidst the possible expansion or intensification of agriculture in response to increasing consumer demands (McAlpine et al. 2009; MLA 2022; Lanz, Dietz, and Swanson 2018; Godfray and Garnett 2014).

To determine the factors allowing native mammals and agriculture to co-occur, and to inform future land management strategies, I examined the characteristics of rufous bettong shelter sites and their capacity to act as thermal buffers in an experimental agricultural system. I predicted that shelter sites would act to buffer ambient temperatures. I also quantified shelter site selection and composition in relation to randomly selected sites across five different grazing strategies. I predicted that rufous bettong shelter sites would more commonly occur in areas utilising moderate grazing strategies, where cattle densities were lowest.

Methods

Study Site

This study was conducted on a Queensland Department of Agriculture and Fisheries grazing research trial at Wambiana Cattle Station, located approximately 70km southwest of Charters Towers. This savanna woodland is characterised by a prominent wet and dry season. There are five different grazing strategies trialed on site (Table 2.1), two replicates of each strategy across 10 paddocks ranging in size from 97-117ha (Figure 2.1).

Table 2.1 Wambiana grazing trial stocking rates

Grazing strategy	Number of hectares (ha) per animal equivalent (AE*)
Heavy stocking rate (HSR)	4 ha/AE
Moderate stocking rate (MSR)	8 ha/AE
Rotational Spelling (R.Spell)	8 ha/AE rotated among 6 sub paddocks
Flexible + Wet Season Spelling (Flex.S)	4-12 ha/AE rotated among 6 sub paddocks
Flexible (no spelling) (Flex)	4-12 ha/AE

**Animal equivalents (AEs) = 450kg steer (O'Reagain et al. 2018)*

There are two dominant vegetation types at the site: Reid River Box (*Eucalyptus brownii)* and Silver-leaf Ironbark (*Eucalyptus melanophloia),* with an additional narrow band of Brigalow (*Acacia harpophylla)* extending across the trial, separating the two dominant vegetation types. The trial paddocks are designed so that there are equal areas of each vegetation type in each paddock (O'Reagain et al. 2018))(Figure 2.1).

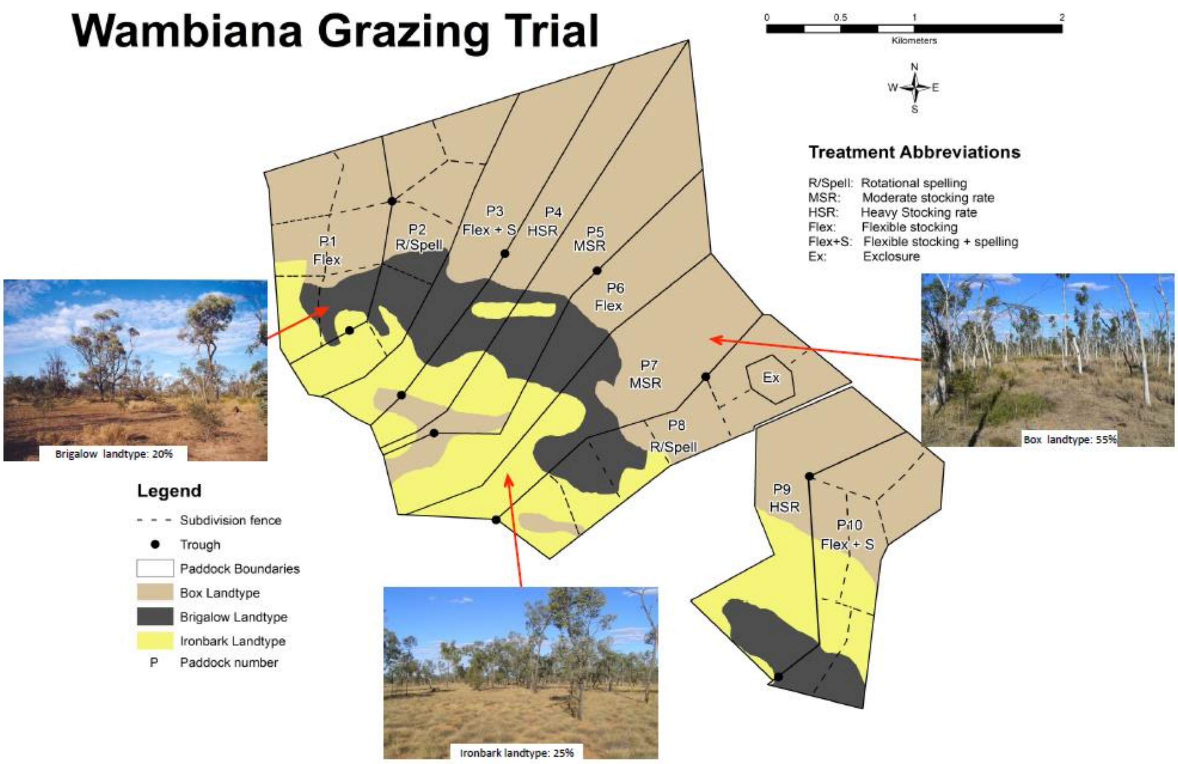

Figure 2.1 Vegetation types and paddocks within the Wambiana grazing trial (O'Reagain and Bushell 2015).

Landscape-scale shelter site selection

The locations of diurnal shelter sites were collected by attaching LiteTrack 40 VHF radio-tracking collars (Lotek NZ Ltd) to 15 rufous bettongs (6 males, 9 females). To attach the transmitters, individuals were captured using cage traps baited with standard bait (balls of peanut butter, oats and vanilla essence). Collared individuals were tracked using a three-element Yagi antenna and a Telonics^{TM} R-1000 telemetry receiver between January 2020 and May 2021. Animals were relocated during the day 1-2 times per fortnight to identify diurnal shelter sites. Once an animal was located, a waypoint was recorded on a handheld Garmin GPS.

Statistical analysis

To assess whether bettong shelter sites occurred in each grazing strategy in proportion to their availability, or if there were preferences for, or avoidance of, any of the grazing strategies I used a WIDESI Manly selectivity measure using the R package '*AdehabitatHS*' (Version 0.3.15; Calenge 2011). I chose the WIDES Type I selectivity analysis model to assess shelter site selection because I wanted to investigate the effect of grazing strategy at a population level, rather than an individual level (which are WIDES type II or III analyses). In the model, I used the GPS waypoints from each individual shelter site as the 'used' habitat data, and I used a QGIS random point generator tool to generate an equal number of random points, within a defined habitat range, as the 'available' data in the model.

Fine-scale shelter site selection

A habitat assessment was conducted at each shelter site. The proportions of fine woody debris (FWD), bare-ground (BG), grass (G), leaf-litter (LL), shrubs or saplings (Sap.shrub), *Carissa Ovata* shrub (*C. ovata*), log, tree, and termite mound within a 0.5 x 0.5m quadrat were recorded. To assess canopy cover, I took a photo approximately 1 m above the shelter site with the camera facing upwards at the sky, and used this image to determine the proportion of canopy cover. A paired random location, 50 m from the shelter in a randomly generated direction, was also assessed using the same methods. All random sample sites were within the grazing trial study site.

Statistical Analysis

To assess the pairwise dissimilarity between diurnal shelter sites and random sites, I created a non-metric multi-dimensional (NMDS) ordination plot. The ordination plot, created using the 'Vegan' package in R (v2.5-7; Oksanen et al, 2020), is based on the Bray-Curtis dissimilarity matrix and shows the vegetation composition among sample sites. I used a multivariate analyses of variance (MANOVA;

R Core Team, 2019) to test whether there was a significant difference between the composition of shelter sites and random sites, and also whether shelter site composition varied significantly between seasons. I used the proportions of fine-scale habitat features recorded (e.g., leaf litter, bare-ground, grass etc.) as the response variables in the model, and location (shelter sites and random sites), or season as grouping variables.

Shelter Site Temperature

Shelter site temperatures were recorded using Thermochron^{TM} iButtons, programmed to record temperatures hourly, before being sealed in a waterproof wax coating. Each iButton was deployed in a small calico bag placed within a shelter, or at a random point outside the shelter, but within a 2m radius. All iButtons were secured to the ground using an aluminum garden peg placed through the calico bag and into the ground. A total of 40 iButtons (20 in shelters and 20 at a random point outside the shelter) were deployed in both the dry season (July-October) of 2020, and the wet season (December – March) of 2020-2021.

Statistical analysis

To account for the large dataset and high degree of variation among recorded temperatures across my study site, I firstly determined the coefficient of variation (CV) for the mean daily temperatures at shelter and random sites. I used this as my response variable in a linear mixed effect model to determine if there was a significant difference in the mean temperature CV between locations (shelter site or random site), between periods (day or night) in shelter and random sites, between seasons (wet and dry) in shelter and random sites, and among sampled months in shelter and random sites. The linear mixed effects models were created in R using the 'lme4' package (v1.1-26; Bates et al., 2015) and significance assessed using the anova function and type II sum of squares, in the 'car' package (v3.1-0; Fox and Weisberg, 2019)(Fox and Weisberg 2019). In the model, location, season and period were fixed effects, and month was a crossed random effect. I also accounted for the paired design of this study by giving each pair of iButtons (consisting of one in a shelter site and one in a random site) a unique identification code and making this identification code a crossed, random factor in the model.

Results

Shelter site selection

Rufous bettong shelter sites were comprised of a shallow pit, excavated by the animal, approximately 10-20 cm deep and approximately 30 cm in diameter (pers. obs.). These pits were covered by a thick layer of grass, collected by the animal in its prehensile tail (Schlager 1982; Southgate 1980; pers. obs.) which acted like a 'lid' on top of the pit and enclosed the shelter site (Figure 2.2). I found rufous bettongs had a network of shelters between which an animal would move, and sometimes reuse weeks later. Nests only contained one animal, except in the case of one female and joey who shared a shelter for the duration of my study (pers. obs.)(Johnson 1980b).

Figure 2.2 Example of a rufous bettong nest found at Wambiana Station study site (Photograph: Natasha Ryan).

Landscape-scale shelter site selection

Animals were tracked for an average of 168 days (22 – 429 days, min-max). There was no statistically significant effect of grazing strategy on the selection of shelter sites by rufous bettongs at my study site. However, there was a trend for bettongs to utilise the rotational spelling (R.SPELL) grazing strategy more than would be expected by chance (Figure 2.3). The flexible (FLEX), moderate (MSR), and flexible with spelling (FLEX.S) grazing strategies were used approximately as much as would be expected by chance, and the heavily grazed (HSR) paddocks were used less than would be expected by chance (Figure 2.3). The heavily grazed paddock had the greatest disparity between use and availability, indicating a trend towards avoidance of this paddock (Figure 2.3).

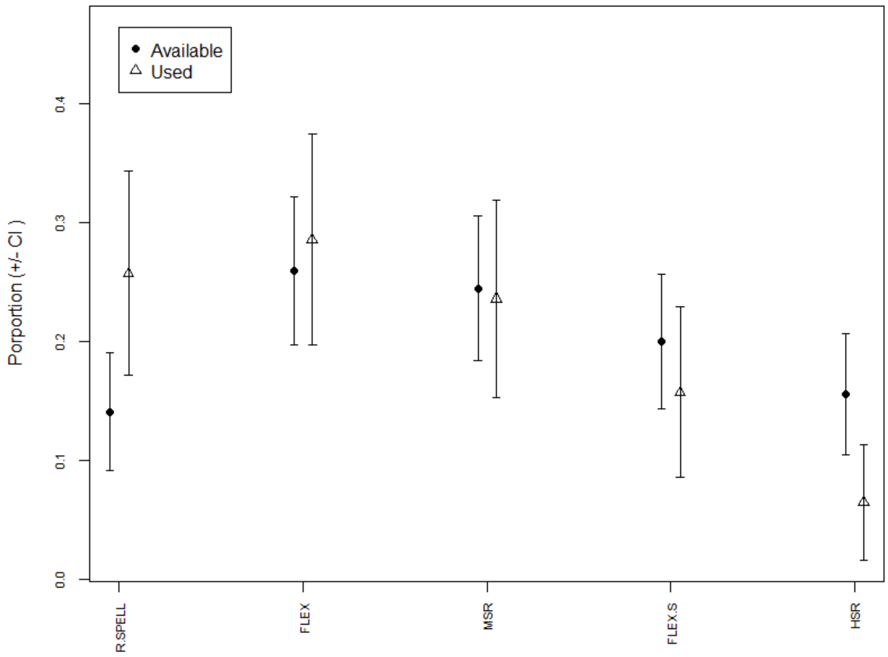

Figure 2.3 Proportion of area 'used' by rufous bettongs for shelter sites, versus the proportion of area 'available' to them at a grazing strategy level: rotational spelling (R.SPELL), flexible stocking rate without spelling (FLEX), flexible stocking rate with wet season spelling (FLEX.S), moderate (MSR), heavy (HSR).

Fine-scale shelter site selection

In 2021-2022, 170 shelter sites and 316 random sites were surveyed over the wet and dry seasons. The structural composition of shelter sites was significantly different from random sites (MANOVA; $F_{10,\,360} = 38$, $p < 0.0001$). Shelter sites were most commonly characterised by a high proportion of *C. ovata,* while random sites had a lower proportion of *C.ovata*, but higher proportions of bare-ground, grass and leaf litter (Figure 2.4). There was no significant difference in tree canopy cover between shelter and random sites (Figure 2.4).

Rufous bettong shelters did not occur exclusively in *Carissa ovata*, they also occurred in, or directly beside logs, termite mounds, and thick grass. Shelter site composition varied significantly between the wet and dry season (MANOVA; $F_{10,157} = 3.55$, $p < 0.0003$), where bettongs used termite mounds and logs more commonly in the wet season, and *C. ovata* more in the dry season (Figure 2.5).

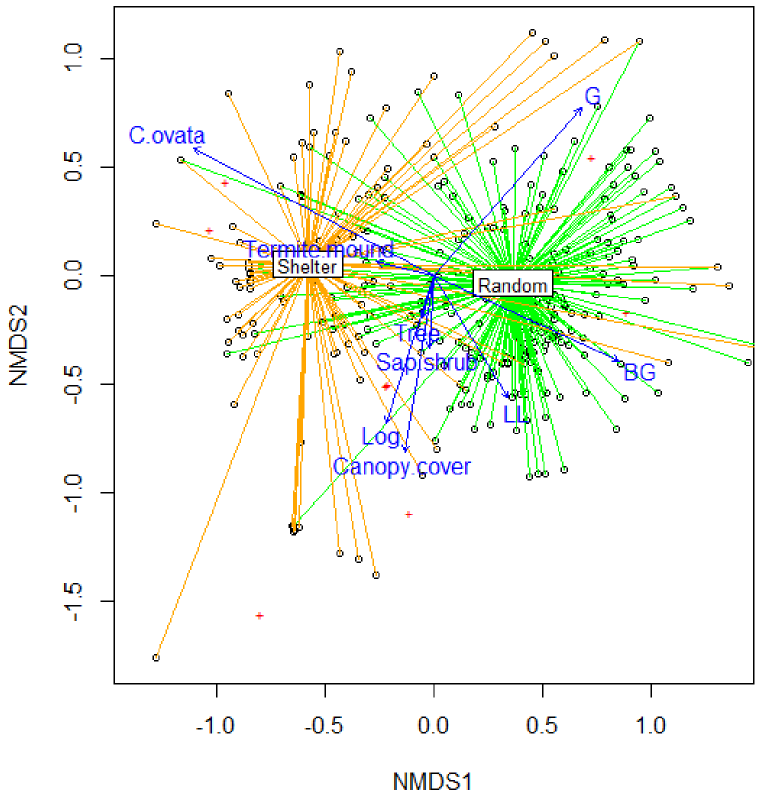

Figure 2.4 Vegetation composition among shelter sites and random sample sites. 'Shelter' sites (orange) represent sites that were used by bettongs and 'random' sites (green) represent random points used to identify the distribution of available fine-scale habitat components. The Bray Curtis stress estimate was 0.13 representing a good fit (Dugard, Todman, and Staines 2010).

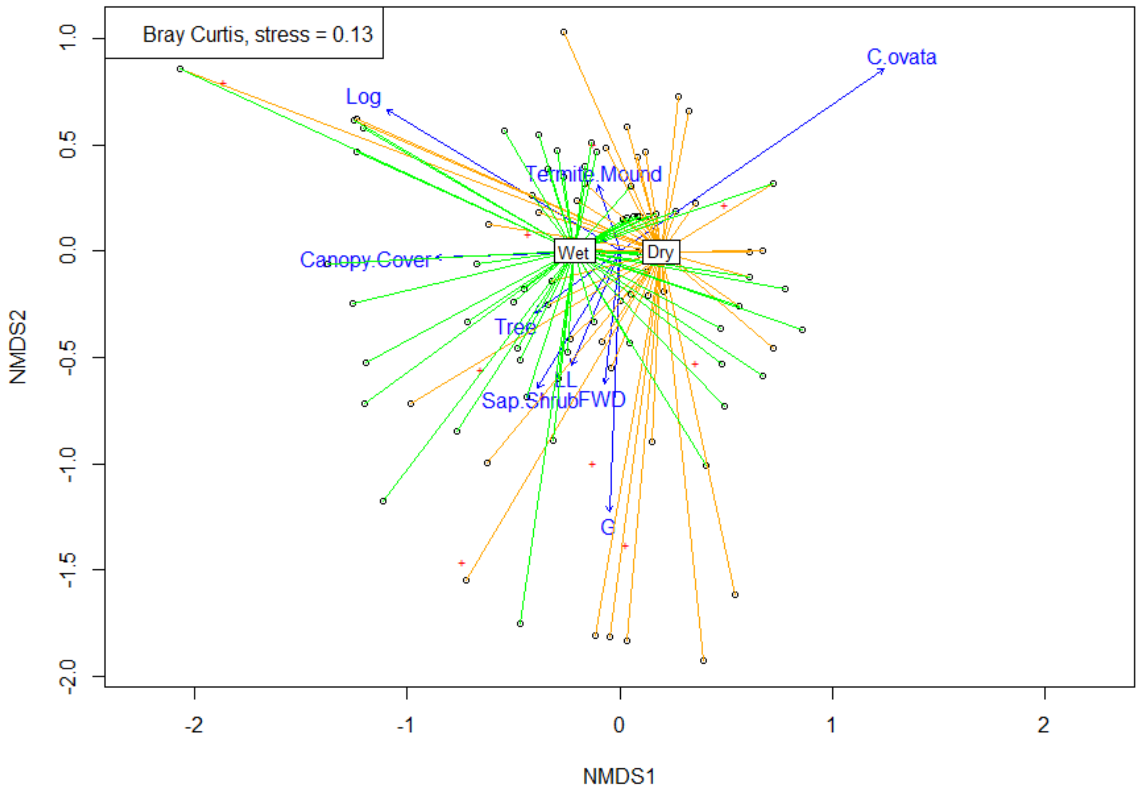

Figure 2.5 Vegetation composition of rufous bettong shelter sites in the wet season (green), and dry season (orange). The Bray Curtis stress estimate was 0.13 representing a good fit (Dugard, Todman, and Staines 2010).

Shelter site temperatures

During the 2020 dry season (July – October) 20,480 environmental temperatures were collected from shelter sites and 16,384 temperatures from random sites. During the wet season (December 2020 – February 2021) 16,002 environmental temperatures were recorded in shelter sites and 16,000 temperatures from random sites. The mean temperature within nests ranged from 22.2°C – 29.6°C, while for random sites a greater variability was observed, with temperatures ranging from 21.6°C - 31.6°C, over a 24hr period within both wet and dry seasons (Figure 2.6). The average hourly temperature recorded over a 24hr period also showed that temperatures within nests were less variable than the temperatures recorded at random sites, this was particularly evident for the hours leading up to and proceeding midday (Figure 2.7).

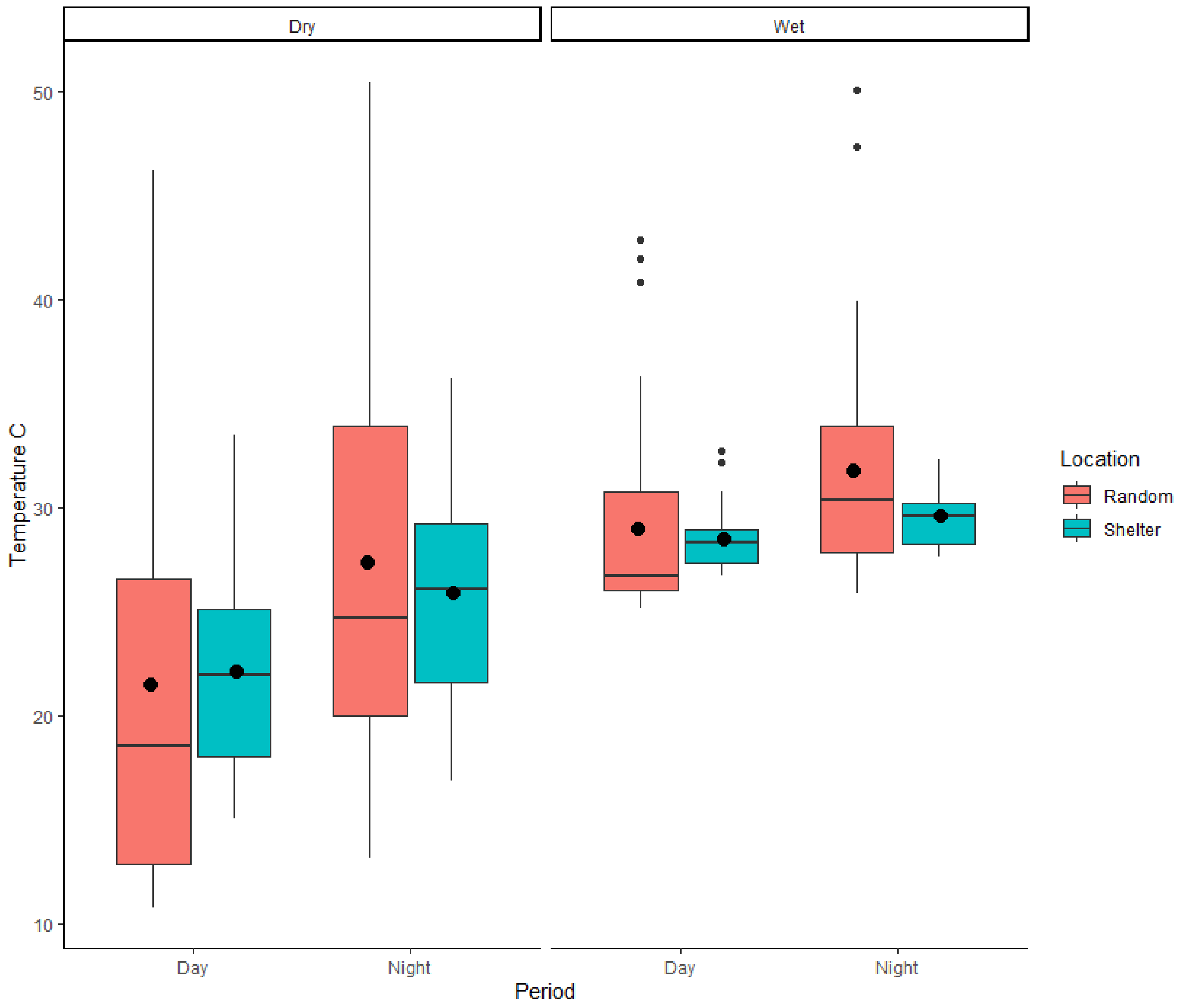

Figure 2.6 Temperature (C°) recorded in random (orange) shelter sites (blue) during day and night periods, across the wet and dry season, with means outlined (•).

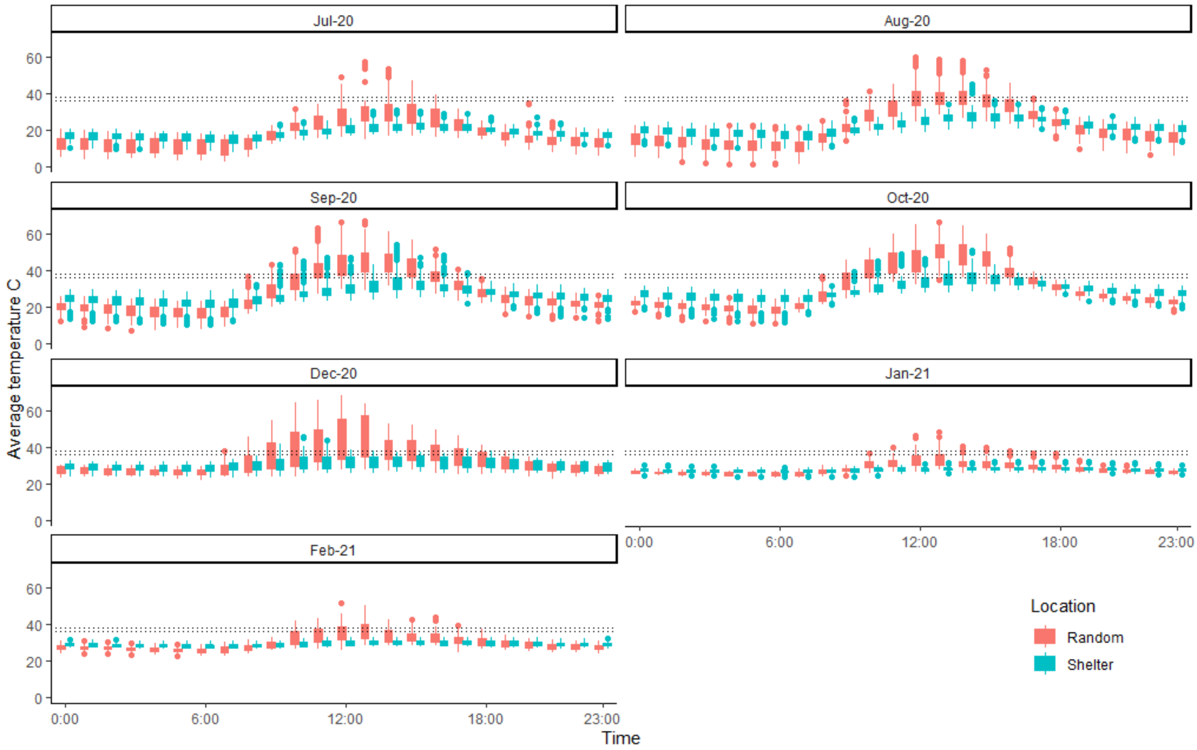

Figure 2.7 Average temperature range over a 24hr period at shelter sites and random sites each sampled month, with the approximate mean core temperature of rufous bettongs (36-38°C) outlined (Rübsamen, Hume, and Rübsamen 1983

Overall, the temperature coefficient of variation (here forth referred to as 'temperature variation') differed significantly between random and shelter sites (ANOVA; $F_{1,3739}$ = 4576; P< 0.0001)(Figure 2.8). There were also significant differences found between the day and night time recorded variation in temperatures (ANOVA; $F_{1,\ 3730}$ = 211; P < 0.0001) (Figure 2.8). Season (wet or dry) also had a significant effect on temperature variation ($F_{1,\ 15.7}$ = 20.6; P = 0.0003). Notably, the dry season had significantly higher and more variable day time temperatures at random sites both day and night (Figure 2.8). Overall, the wet season had less temperature variability, particularly so at shelter sites (Figure 2.8).

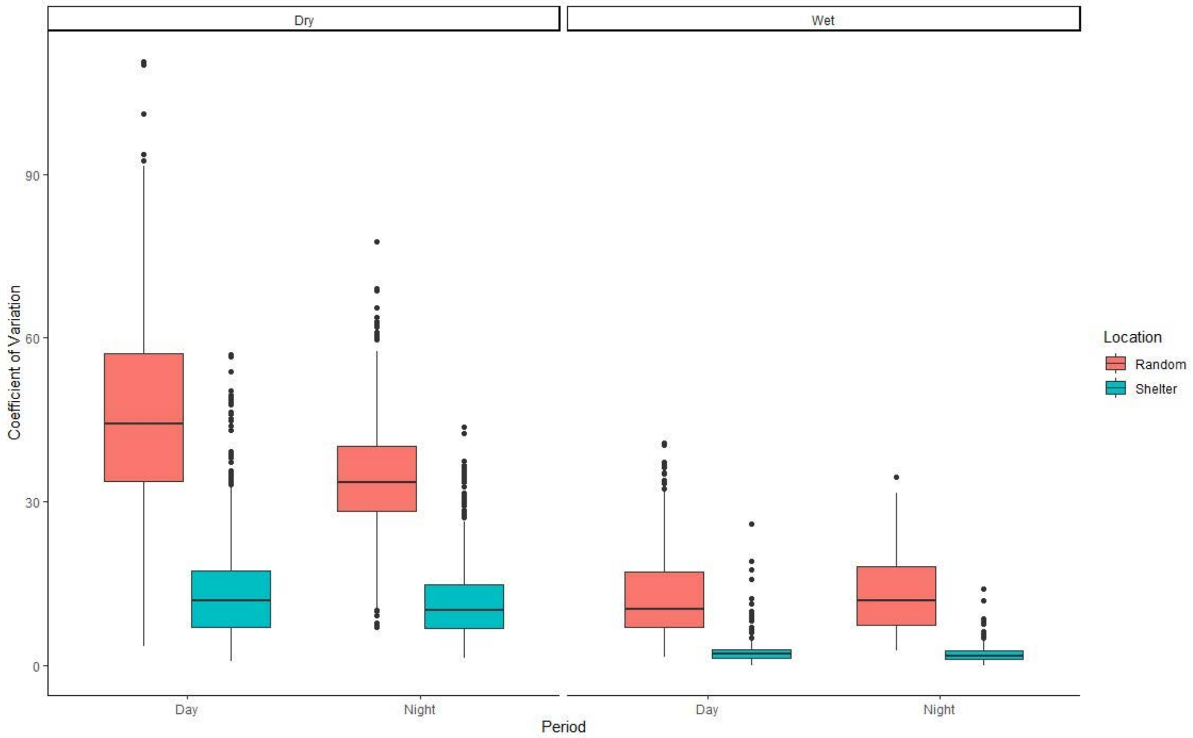

Figure 2.8 Coefficient of variation for daily mean temperatures at random (orange) and shelter (blue) sites, day and night over the wet and dry season of 2020 and 2021.

Lastly, I also found a significant effect of month on recorded temperature variation ($F_{6,167} = 30$; $P<0.001$). The sampled months of July, August, September, October and December had significantly greater temperature variation than those recorded in January and February (Figure 2.9).

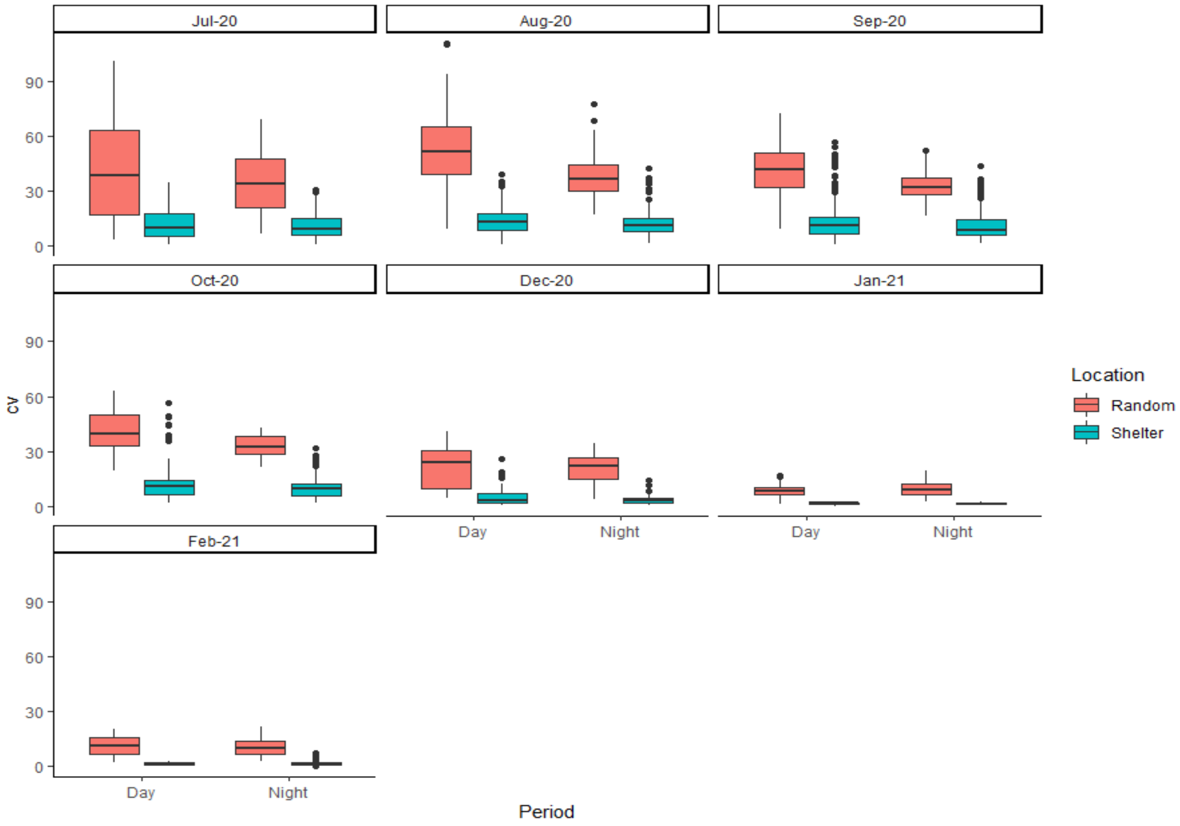

Figure 2.9 Coefficient of variation for daily mean temperatures at random (orange) and shelter (blue) sites over seven sampled months (July-October 2020; December 2020-February 2021).

Discussion

I predicted that rufous bettong shelter sites would more commonly occur in areas utilising moderate grazing strategies, where cattle densities were lowest. However, I found that grazing strategy did not affect shelter site selection significantly at my study site, although there was a trend for bettongs to select sites most often in the rotational spelling grazing strategy, and to avoid sheltering in the heavy grazing strategy. Conversely, I did find strongly significant differences in the composition of shelter sites compared to randomly selected sites, suggesting that rufous bettongs require specific shelter site characteristics and prefer shrubs as shelters. I also found differences in shelter site characteristics between the wet and dry seasons, indicating that bettongs use available shelters, such as hollow logs more frequently in the wet season. Finally, I found that, compared to randomly chosen sites, bettong shelters provided significant buffering from daily and monthly temperature extremes, suggesting that the shelters are critical to a medium-sized mammal living in a hot terrestrial environment.

Landscape-scale shelter site selection

The Wambiana grazing trial consists of a series of adjacent 97-117 ha paddocks subjected to different grazing strategies. In this study, individual rufous bettong movements encompassed at least two or three strategies, suggesting that they could easily move from one paddock type to another. Thus, from the point of view of a bettong, the trial is a mosaic of various grazing intensities. The use of various paddocks and strategies might be due to the 'good' conditions during which my study was conducted. Previous studies at the Wambiana grazing trial have found that rufous bettongs avoided the heavy grazing strategies (Neilly and Schwarzkopf 2017), however, those studies were undertaken during drought years (O'Reagain et al. 2018) during which there is a more distinct, and stark contrast between the land condition of the various grazing strategies. I did find a trend for bettongs to prefer sheltering in the rotational spelling paddock, while avoiding the heavily grazed paddocks, however, these trends were not statistically significant. Again, perhaps strong avoidance of certain grazing strategies was masked by the favourable climatic conditions, and replication of this study during periods of drought might yield different results. Alternatively, the lack of statistical significance could have been caused by a small sample size, i.e., I did not have the statistical power to detect weak influences. Further research, in which more detailed, daily movements and habitat use data could be recorded over a longer period, would help to better determine whether rufous bettongs avoid heavily grazed areas or areas with characteristics typical of heavy grazing. A more in-depth study could also help to identify whether there are seasonal differences in habitat selection, and more specifically, how rufous bettongs respond to climate variability and the effect of drought, as this is factor potentially influencing their shelter site selection, and overall habitat selection. In addition, further detailed research could provide insight into the reuse of shelter sites in different grazing treatments, and the fitness of animals using shelter sites exposed to different grazing intensities. This would shed further light on the shelter site requirements of rufous bettongs in relation to grazing strategy.

Fine-scale shelter site selection

My research found that rufous bettongs selected habitat with a high proportion of the shrub *Carissa ovata (C. ovata).* This native shrub has leathery leaves and thorny stems and often forms dense thickets that can be several metres tall and wide (Department of Agriculture and Fisheries 2020). These thickets are nearly impenetrable, making them excellent refuge for small mammals, such rufous bettongs (Poole et al. 2015; Fisher 2000; Christensen and Leftwich 1980). It is likely that *C. ovata* is preferred because it provides concealment and protection from predators that occur at my site, including dingoes, wild dogs and cats (Fisher 2000; Day and Elwood 1999). Similarly, sheltering within *C. ovata* protects bettongs from trampling by cattle. Previous studies have also identified cattle trampling as a likely factor influencing habitat selection (Neilly and Schwarzkopf 2018).

I found that bettongs were more likely to use *C. ovata* as shelter in the dry season. At the end of the dry season in 2020 and 2021, pasture yields across the different paddocks were on average 201 kg/ha and 397 kg/ha, respectively, compared to the 2020 and 2021 post-wet season averages of 639 kg/ha and 774 kg/ha. These reduced pasture yields following the dry season, in conjunction with continued consumption by cattle, reduces grass availability. Because rufous bettongs rely on grass to form their shelters (Johnson 1980b; Schlager 1982), reduced grass availability following the dry season possibly leads to an increased reliance on *C. ovata* to form adequate shelter. Other studies have also found that shelter site selection is dependent on the availability of natural cover and suitable shelter-making materials (Schlager 1982).

Using *C. ovata* as shelter in the dry season may also help reduce daily energy expenditure by reducing time spent searching for sufficient nesting materials, particularly so when there is reduced grass availability. At my study site, *C. ovata* was the dominant shrub species, so I could not determine whether rufous bettongs were obligate or opportunistic users of the shrub. Other studies have found shrubs to be a preferred shelter site for some small mammals, such as quokkas and wallabies (Poole et al. 2015; Fisher 2000). Determining whether *C. ovata* specifically is an obligate or opportunistic choice, would provide valuable insight into rufous bettong shelter site selection.

In addition to *C. ovata*, termite mounds and logs were also used as shelter, especially during the wet season. I postulate that the increased use of solid structures in the wet season might mitigate the threat of shelter site flooding and displacement during torrential wet season rains and possibly mitigate the severity of the summer temperatures.

Shelter site temperatures

I predicted that internal shelter site temperatures would be milder than ambient temperatures. I found that the temperatures recorded within shelters were less variable and less extreme than, and differed significantly from, ambient temperatures. Therefore, it is clear that shelters provide a buffer against daily temperature extremes, and do so throughout year, as I found a significant difference between shelter site and ambient temperature variation among months and between seasons.

I found that the highest temperature variation recorded in this study occurred in the hours leading up to and immediately following midday. Importantly, the temperature variation at this time, was far lower in shelter sites than at random sites. As the rufous bettong is a nocturnal species, spending most of its time within its shelter during the day, this finding illustrates how important these shelters are for refugia and survival of rufous bettongs. These findings align with other studies which also suggest that variation in shelter site temperatures differs significantly from external landscape temperatures and thus provide wildlife valuable refuge from potentially lethal temperature extremes (Hovick et al. 2014; Christensen and Leftwich 1980; Isaac, De Gabriel, and Goodman 2008; Kerth, Weissmann, and Konig 2001; Kay and Whitford 1978).

I postulate that the extremes in temperature variation I recorded during the dry season could be associated with the fine-scale habitat composition of shelters during this time. I found that the greatest temperature variability occurred during the dry season which also coincides with the period of lowest grass availability (P. O'Reagain, personal communications, 12 December 2022). At this time, shelters could have been formed with less grass, due to its reduced availability, resulting in a thinner grass 'lid' and thus less insulation and protection from ambient temperatures compared to wet season shelters made from more grass. Additionally, during the dry season, I found greater use of *C. ovata,* with reduced usage of logs, termite mounds and other solid structures. I had insufficient data to properly understand the thermal protection provided by *C. ovata*, but it is thought to be minimal compared to these other solid structures, which are more commonly used in the wet season. Therefore, use of *C. ovata* during the dry season may result in shelter site temperatures more closely resembling the highly variable temperatures outside the shelter. Conversely, the slightly increased usage of logs in the wet season could be the reason for the lower temperature variability recorded during this time. Logs are thicker, and sheltering within them minimises the influence of direct sunlight and soil surface temperatures on shelter site temperature. Further investigation into the thermal protection provided by selected fine-scale habitat components in my study would be of value for ongoing conservation and management of rufous bettong habitat.

Conclusion

This study provides new insight into shelter use by rufous bettongs in agricultural systems. Learning more about rufous bettong habitat use has enhanced our understanding of the elements essential for their survival, and potentially that of other species too. This study highlights the importance of understanding and considering what shelter sites provide to an animal (i.e. thermal protection etc.). It is also important to acknowledge that what a shelter site provides to an animal may be very specific and unique to the particular habitat it occupies and the climate and weather conditions at that location. As such, at a time in which land needs to support a growing human population and biodiversity concurrently, whilst also facing the challenges of an increasingly unpredictable climate; conservation efforts need to be adaptable and account for existing, site-specific challenges. Whether it be the influence of grazing animals, fire, drought, domestic animals or human land use; we need to improve our knowledge of how humans and wildlife can coexist across a range of landscapes and land uses. This starts with developing a much greater ecological understanding of the wildlife occupying land used extensively for anthropogenic uses. It is this knowledge that will help shape and improve conservation efforts in the future.

Chapter 3 - Rufous bettong digging and its benefit to grazing systems

Introduction

The area of earth occupied by agricultural land, including rangelands, is set to expand by over 1 million km^2 by 2050 in response to increasing global wealth and population size (Tuomisto et al. 2015; Jantz et al. 2015; Lanz, Dietz, and Swanson 2018). This expansion comes at a time when there is more emphasis on and effort dedicated to counteracting the negative effects of agriculture, and preserving biodiversity. Agriculture, and more specifically, rangelands are one of the biggest contributors to global biodiversity declines (Tilman and Clark 2015; Macdonald and Feber 2015). Rangelands are places where anthropogenic land use, primarily livestock grazing, occurs on long-existing, natural ecosystems typically supporting a plethora of wildlife (Neilly 2017). Depending on a species' biology and ecological requirements, their responses to land use change vary, but for most animals, rangelands have resulted in population declines (Buesching et al. 2015; Beeton et al. 2006; Cocklin and Dibden 2009) therefore, how these landscapes are managed is more critical than ever before (Gordon, Prins, and Squire 2017; Jhariya, Meena, and Banerjee 2021). This is in part due to the growing awareness of the impacts of agriculture on biodiversity, but also expanding knowledge suggesting that healthy and biodiverse ecosystems can enhance agricultural outputs, especially for agriculture in natural systems such as rangelands (Gordon, Prins, and Squire 2017; Jhariya, Meena, and Banerjee 2021; Macdonald and Feber 2015; Gretton and Salma 1996; Filazzola et al. 2020; Woinarski, Burbidge, and Harrison 2015; Machovina, Feeley, and Ripple 2015; Tuomisto et al. 2015).

Biodiverse ecosystems support a myriad of species that perform a range of ecosystem services (Hooper 2005; Tilman and Clark 2015; Romero et al. 2015). For example, digging mammals, through their natural behaviour, contribute to increased soil turnover, seed capture and successful germination of grasses, reduced water runoff and erosion, increased water infiltration, and increased soil turnover which increases microbial activity and organic matter breakdown (Valentine et al. 2017; Dundas et al. 2018; Whitford and Kay 1999; Eldridge and James 2009; Fleming et al. 2014). Furthermore, digging mammals also play a crucial role in the dispersal of belowground fungal bodies, which are almost solely reliant on spore dispersal by vertebrates who excavate, eat and then disseminate the spores in their faeces (Claridge and May 1994; Fogel and Trappe 1978; Claridge 2002; Vernes 2007; Vernes 2010; Malajczuk, Trappe, and Molina 1987; Nuske et al. 2017b). These fungal bodies commonly form symbiotic relationships with eucalyptus trees, which help to support the health of the ecosystem amidst the challenges of low moisture and nutrient-poor soils (Danks et al. 2020; Malajczuk, Dell, and Bougher 1987; Dundas et al. 2018; Claridge 2002; Horton et al. 2013).

The extensive range of ecosystem services provided by digging mammals are particularly important in arid or semi-arid regions where water and soil nutrients are scarce resources (Eldridge and James 2009; James, Eldridge, and Hill 2009; Eldridge and Whitford 2009; Romero et al. 2015). In Australia, these regions are predominately used for livestock grazing (McKeon et al. 2009; ABS 2018); a land use that further compounds the detrimental effects of low rainfall, extreme temperatures and nutrient-poor soils, by causing increased soil compaction and erosion (Claridge 2002; Eldridge and James 2009; Orians and Milewski 2007). Livestock grazing systems are also a major contributing factor to species decline in Australia and abroad (Filazzola et al. 2020; Woinarski, Burbidge, and Harrison 2015; Machovina, Feeley, and Ripple 2015).

One particular digging mammal, the rufous bettong (*Aepyprymnus rufescens)*, inhabits rangelands more than any other species within its family: Potoroidae, while also remaining a species of least conversation concern (Chapter 1) (IUCN 2023). How rufous bettongs successfully use, and survive within extensive grazing systems is still poorly understood (Chapter 1). My research suggests that rufous bettongs prefer to shelter in paddocks using more sustainable grazing strategies i.e., rotational grazing (R.Spell), rather than those that were heavily grazed (Chapter 2). Similarly, Neilly and Schwarzkopf (2017) found that rufous bettongs were negatively affected by heavy grazing in particular vegetation types. However, it remains unclear exactly how rufous bettongs survive within agricultural systems. We know that they respond to, and therefore might be affected by, different management strategies, but we are yet to fully understand this dynamic. As a likely ecosystem engineer, due to the incidental benefits of digging for food; including fungi, roots and tubers (Vernes 2010; McIlwee and Johnson 1998; Schlager 1982; Johnson 1978), it is important that we better understand how rufous bettongs successfully inhabit these resource scarce rangelands. As a likely ecosystem engineer, correct land management and conservation of this species alone, could positively influence an entire ecosystem and the industry relying upon it (Johnson 1978).

In this chapter, I aim to better understand the ecosystem services provided by rufous bettongs to rangeland landscapes, by investigating and quantifying the amount of soil moved by the species within a grazing system. I also assess the effect of grazing strategy, vegetation type and season on the amount and location of digging, and thus, the provision of ecosystem services. Based on previous research, I expect to find an effect of all, or a combination of these factors, on digging site selection and digging abundance.

Methods

Study site

This study was conducted approximately 70 km southwest of Charters Towers, Queensland, at the Department of Agriculture and Fisheries grazing research trial located on Wambiana Station. The 1000 ha research trial is comprised of 10 separate paddocks, each 97-110 ha in size. There are five grazing strategies being trialed on site, with two replicates of each (Table 2.1).

Wambiana Station is situated within northern Queensland's savanna woodlands, where there is a distinct wet season (December – April) and dry season (May - November). For my study I have broken these seasons down further into pre-wet (September – November) and post wet (March – May). There are three vegetation types at the site, Reid River Box (*Eucalyptus brownii)* and Silver-leaf Ironbark (*Eucalyptus melanophloia)*, with a small Brigalow (*Acacia harpophylla)* belt in the middle. The trial was designed with equal proportions of each vegetation type within each paddock (Figure 2.1).

Digging site selection – replicate transect surveys

Survey design

I conducted two transect surveys, one in September 2020 (pre-wet) and the other in April 2021 (post-wet). The same 50 transects were surveyed in both seasons, with 10 transects assessed in each grazing strategy (five transects per paddock), across the three vegetation types (Figure 3.1). Each transect (100 m long and 2 m wide) was walked in the same cardinal direction (north, south, east or west) each survey period to ensure replication. Cardinal directions were chosen at random during the initial (September 2020) transect surveys.

Transect data collection

In September 2020, the total number of fresh diggings found within the 100 x 2 m transect survey area were counted and their dimensions (length, width and depth) recorded. Digging by rufous bettongs was observed in the field prior to transect surveys being undertaken to ensure rufous bettong diggings could be correctly identified. Additionally, there are few other digging mammals that coexist at my study site and those that do, mainly bandicoots and echidnas, are less abundant and have distinctly different digging characteristics. Bettong diggings are typically shallower and less acute than bandicoots (Schlager 1982; pers. obs.) and echidnas have distinctly wide and circular diggings (Dundas et al 2022).

When sighted, a digging was categorised as fresh if there was a clear adjacent heap of loose and friable excavated soil, and the digging contained little to no leaf litter (Claridge, Cunningham, and

Tanton 1993; Valentine et al. 2013). For the first five instances of digging (defined as a singular digging or multiple diggings within 1m^2) a quadrat was placed over the digging site and the vegetation and ground cover was assessed. The proportion of fine woody debris (FWD), bare-ground (BG), grass (G), leaf-litter (LL), shrubs or saplings (Sap.Shrub), *Carissa ovata* shrub (*C. ovata*), logs, trees, and termite mounds (T.Mound) within a 0.5 x 0.5 m quadrat were recorded. Quadrats measuring the same habitat features where there were no diggings were also assessed at 0, 25, 50, 75 and 100m along every transect. In the April 2021 survey, diggings found in the transect surveys area were counted but no dimensions were measured due to time and weather limitations.

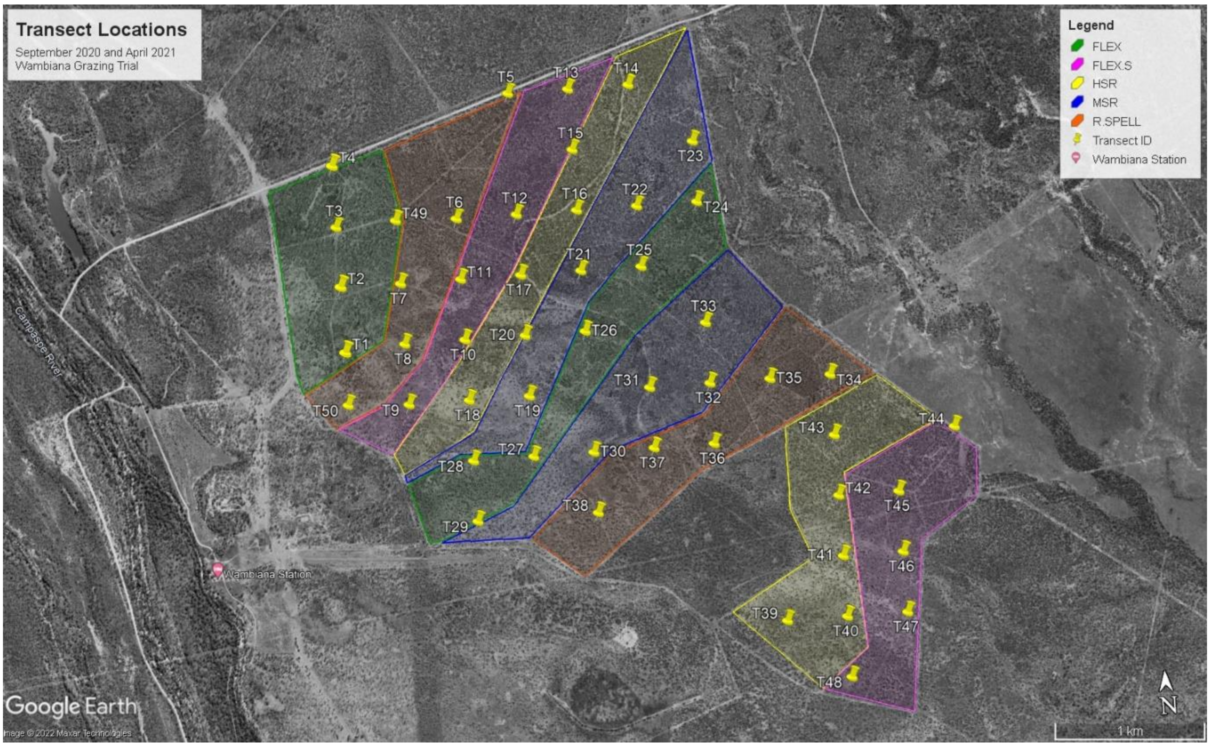

Figure 3.1 Map outlining the starting location for each of the 50 transects (T1-T50).

Data analysis - digging site selection

Landscape-scale digging site selection

I used generalised linear mixed effects modelling using the *glmer* function in package *lme4* (Bates et al 2020; version 1.1-26) to examine whether digging occurred across the entire survey area or whether grazing strategy, season or vegetation type influenced the location of diggings. Dig counts, derived from transect surveys in September and April, were used as the response variable, transect ID was a random effect, and grazing strategy, season and vegetation type were fixed effects. Significance was assessed using the *anova* function and type II sum of squares, in the 'car' package (v3.1-0; Fox and Weisberg, 2019) and I used pseudo R^2 values to determine the goodness of fit for my model with the *rsquared* function in the 'piecewiseSEM' package (v2.0.2; Lefcheck, Byrnes & Grace, 2018). A

Pearson’s Chi-squared goodness-of-fit test, performed using the *chisq.test* from the ‘stats’ package (v3.6.2; R Core Team), was used to test if diggings occurred in equal proportion in the various vegetation types and grazing strategies.

Fine-scale composition of digging sites

I created a non-metric multi-dimensional (NMDS) ordination plot to assess the pairwise dissimilarity between quadrats where diggings were present, and quadrats where diggings were absent. My ordination plot was created using the ‘Vegan’ package in R (v2.5-7; Oksanen et al, 2020). The plot is based on the Bray-Curtis dissimilarity matrix and shows the vegetation composition at sites where diggings were absent or present. I used a multivariate analysis of variance (MANOVA; R Core Team, 2019) to test whether there was a significant difference between the fine-scale composition at sites with, versus sites without, diggings. The features assessed in my model, at both sites, included fine woody debris (FWD), bare-ground (BG), grass (G), leaf-litter (LL), shrubs or saplings (Sap.shrub), *Carissa ovata* shrub (*C. ovata*), logs, and termite mounds (T.Mound). The habitat feature ‘tree’ was not included in my MANOVA as there were no recorded instances.

Soil displacement

I collected length, depth, and width measurements for all fresh diggings found along 50 individual transects during September 2020 surveys.

Calculating soil displacement

I created moulds, using Plaster of Paris, for a subset of these diggings (n = 34) to later calculate their volumes using the water displacement method; whereby each mould was submerged in water and the amount of water displaced (mL) was recorded.

I plotted the water displacement volumes against the volumes calculated using the equation for the volume of an elliptical cone:

$$(\frac{1}{3}\pi \left((\frac{dig.length}{2}) * (\frac{dig.width}{2}) * dig.depth \right)$$

I determined, through the coefficient of determination ($R^2 = 0.70$) that the elliptical cone volume estimate was strongly correlated to the volume of my diggings, and therefore I used this equation to calculate the volume of all diggings (n=83) using their length, width and depth measurements when I did not have a plaster mould and water displacement measurement.

Using these calculated volumes, I determined the amount of soil displaced from each digging by multiplying the dig volume by the density of the soil type where it was located. The average soil density values I used for Reid River Box, Ironbark and Brigalow soils were 1.515g/cm^3, 1.645g/cm^3 and 1.263g/cm^3 respectively (Fraser and Stone 2016; Thornton and Shrestha 2021).

Total soil displacement, attributed to bettong diggings, across my study site was calculated as follows:

$$\begin{aligned} &Soil\ displacement\ (cm^3)\ per\ 1m^2 \\ &\qquad = \frac{Sum\ of\ soil\ displaced\ by\ measured\ diggings\ (cm^3)}{Survey\ area\ (m^2)} \end{aligned}$$

$$\begin{aligned} &Soil\ displacement\ across\ study\ site\ (cm^3) \\ &\qquad = \left(soil\ displaced\ (cm^3)\ per\ 1m^2\ \times grazing\ trial\ area\ (m^2)\right) \\ &\qquad \times number\ of\ surveys\ (2) \end{aligned}$$

Annual soil displacement was converted to m^3 for analysis of results.

Results

Landscape-scale digging site selection

I found that there was no significant effect of season, grazing strategy or vegetation type, nor were there any significant interaction effects on the number of diggings (Marginal $R^2 = 0.18$; Conditional $R^2 = 0.88$). There was a slight trend towards more digging in the flexible stocking rate (Figure 3.2), and in the Reid-river box habitat (Figure 3.3), however my chi-square contingency tests indicated that there was no significant difference in the number of diggings in different grazing strategies ($x^2 = 0.35$, $df = 4$, $p = 0.99$) or vegetation types ($x^2 = 0.48$, $df = 2$, $p = 0.79$). Therefore, digging by rufous bettongs appears to occur evenly across the paddock types, with no apparent influence of season, grazing strategy, or vegetation type (Figure 3.4).

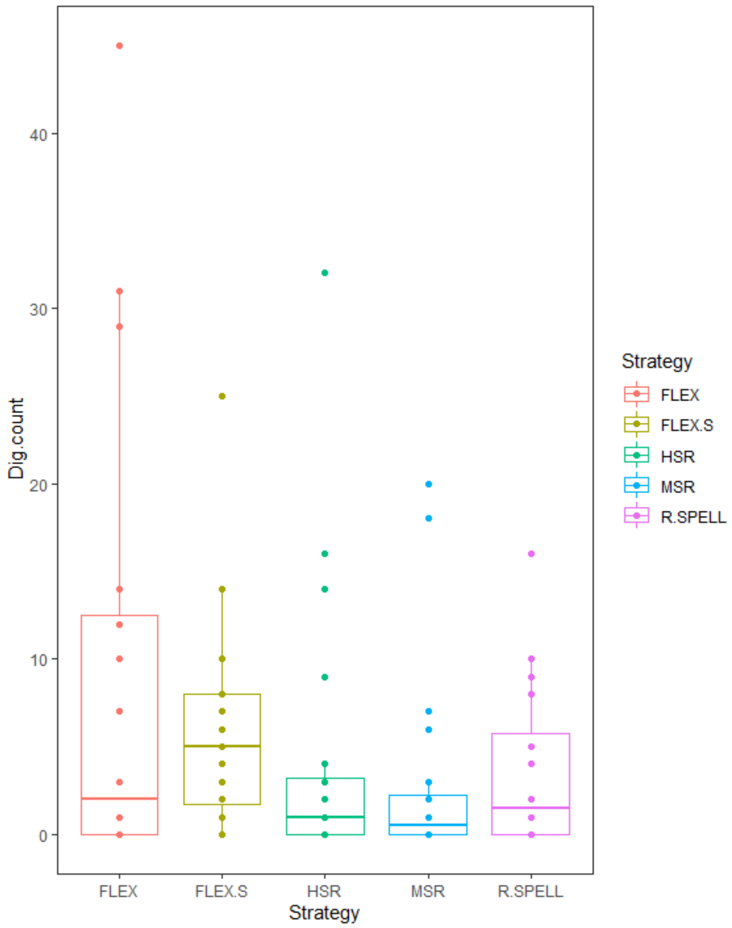

Figure 3.2 Dig counts across the grazing strategies: FLEX (flexible), FLEX.S (flexible + wet season spelling), HSR (heavy stocking rate), MSR (moderate stocking rate), R.SPELL (rotational spelling).

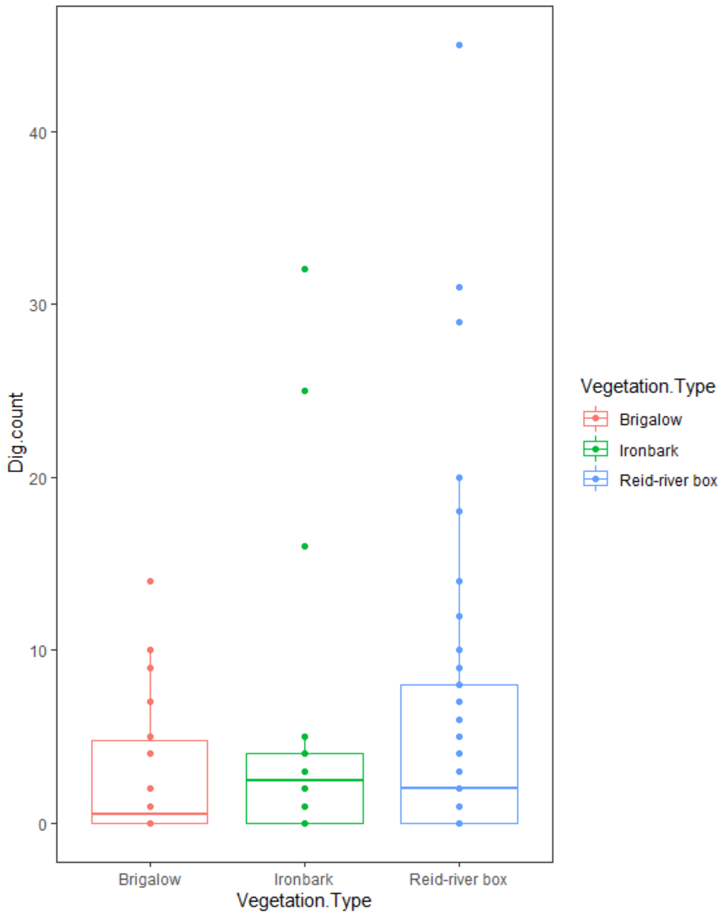

Figure 3.3 Dig counts across the vegetation types.

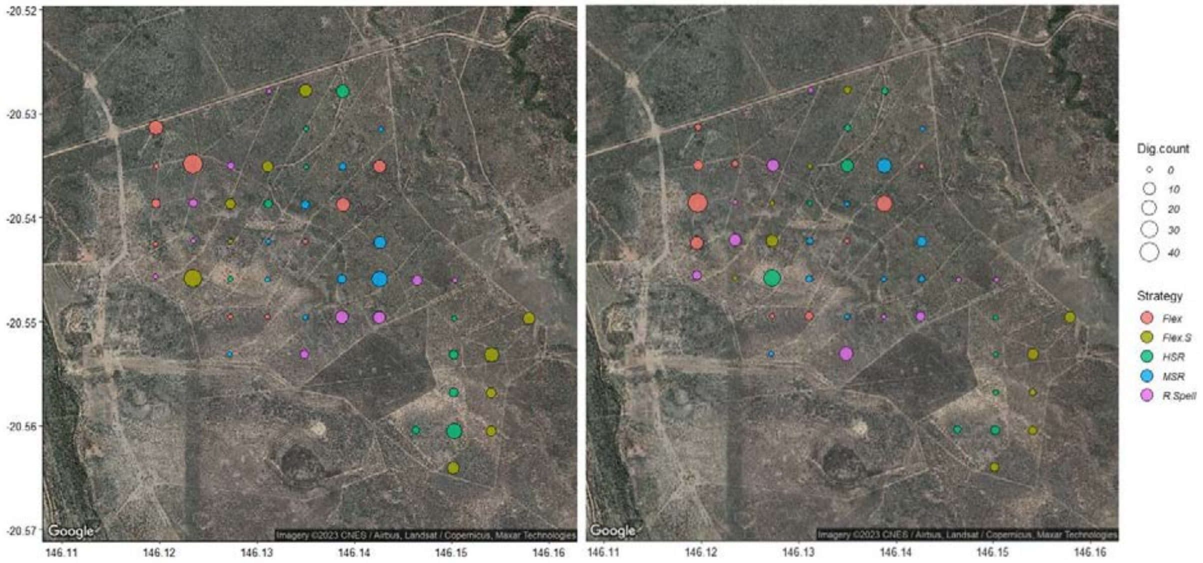

Figure 3.4 Digging occurrences in September (pre-wet) 2020 and April (post-wet) 2021, respectively, across the five grazing strategies at the study site (Flex, Flex.S, HSR, MSR and R.Spell).

Fine-scale composition of digging sites

I found that there was a significant difference in the fine-scale composition of sites where diggings were present compared to sites where diggings were absent (MANOVA; $F_{9, 178} = 7$, $P < 0.0001$). Sites where diggings were present commonly had a higher portion or leaf litter (LL) and bare-ground (BG), while sites where diggings were absent had higher portions of *C. ovata*, fine woody debris (FWD), saplings and shrubs (Sap.Shrub), termite mounds (T.Mound) and logs (Figure 3.5). This difference also occurred between seasons as I found a significant difference in fine-scale digging site composition between my April and September surveys (MANOVA; $F_{9, 178} = 5$, $P < 0.0001$). In April, digging more commonly occurred in areas with a higher proportion of bare-ground, while in September, digging also occurred where there were higher proportions of grass and leaf litter (Figure 3.6).

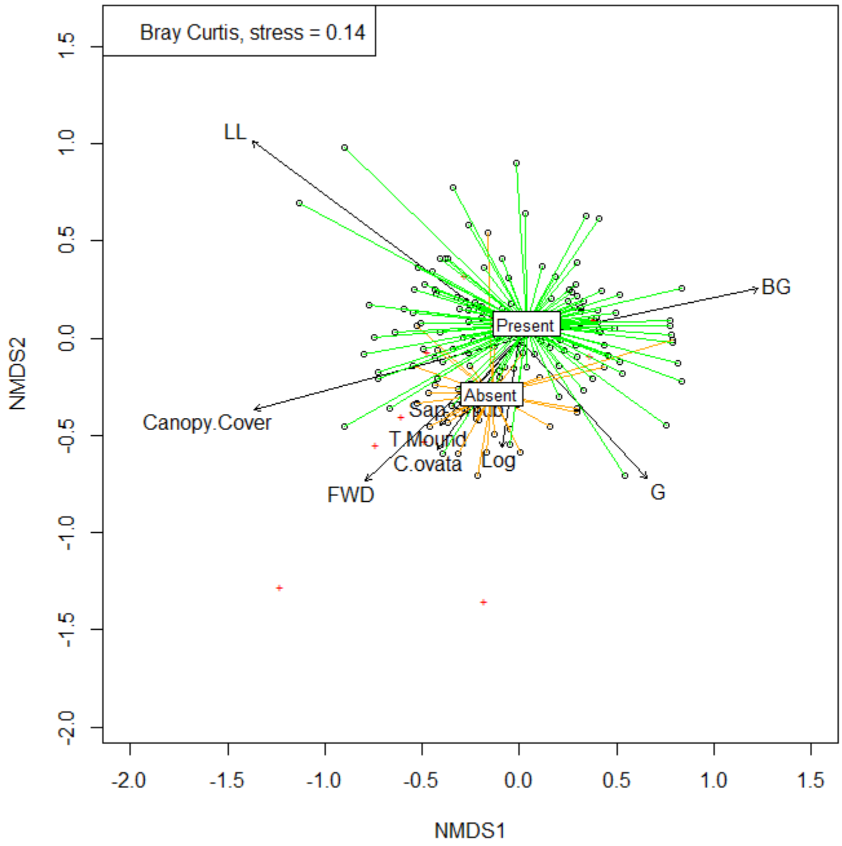

Figure 3.5 Fine-scale site composition where diggings is present and where digging is absent. 'Present' sites are where quadrats were placed over found diggings and 'Absent' sites are where quadrats contained no diggings and occurred at 0, 25, 50, 75 and 100m along my transects. The Bray Curtis stress estimate is 0.14 representing a good fit (Dugard, Todman, and Staines 2010).

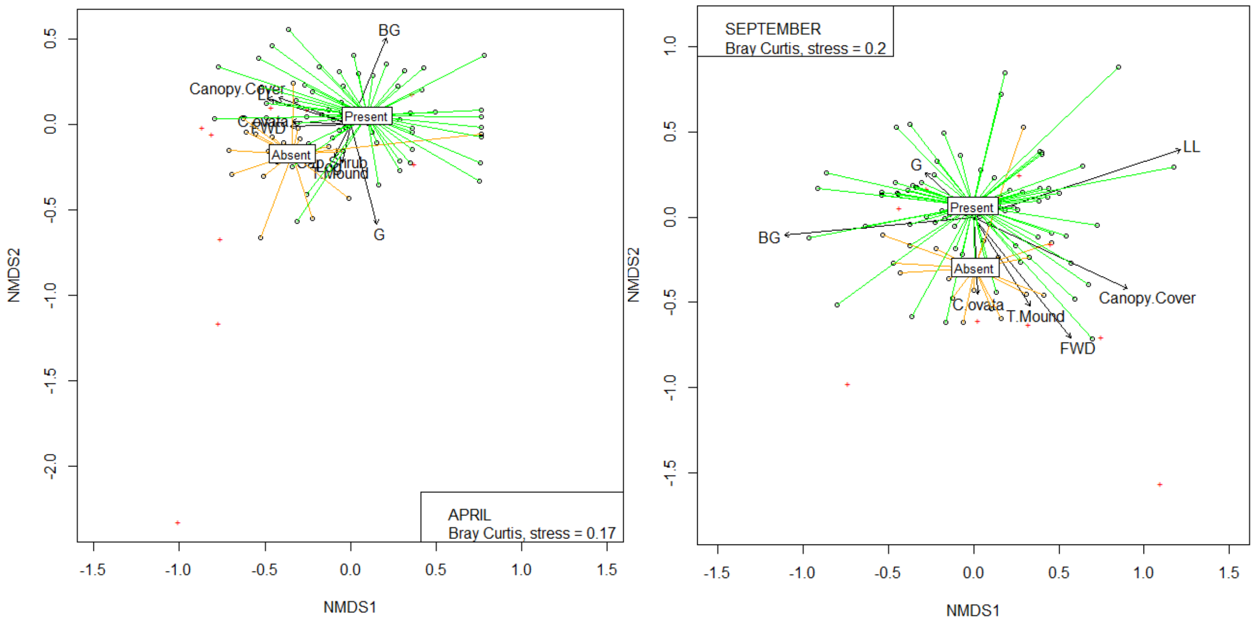

Figure 3.6 Seasonal variation (April and September) in the fine-scale site composition at sites where diggings were present and sites where diggings were absent. Bray Curtis stress estimates of 0.17 and 0.2 represent a good fit (Dugard, Todman, and Staines 2010).

Soil displacement

I collected length, width, and depth measurements from 83 diggings during the September sampling period. The mean ± standard error dimensions were: length 7.4 ± 0.33 cm, width 4.8 ± 0.26 cm and depth 2.4 ± 1.7 cm. The average volume per digging was 24.3 cm^3, and the average amount of soil moved from a digging (accounting for transect specific soil density) was 36.41 g/cm^3. Overall, in the 83 diggings measured, across my total transect survey area of 10,000 m^2, there was 3021.78 cm^3 of soil displaced. This equates to $6m^3$ over my two sampling periods. Based on the assumption that a digging would appear 'fresh' for no more than two weeks, that is, it has no signs of degradation, or accumulation of leaf litter, I extrapolated this figure to determine that the average yearly soil displacement rate of rufous bettongs at my study site is $72m^3$. Based on historical population estimates at my study site (Neilly and Schwarzkopf 2018), this equates to $1.3m^3$ soil/animal/year.

Discussion

Landscape-scale digging site selection

I found that there was no significant effect of season, grazing strategy, or vegetation type on the location or abundance of diggings. I found that bettongs prefer to dig in areas with more bare-ground and grass than in areas with shrubs or other features, such as termite mounds and logs. In general, rufous bettongs moved a significant amount of soil in my study area (an estimated 72 m^3 of soil per year, or 1.3 m^3 per bettong per year), and it is likely this represents an important ecosystem service to agricultural land.

I expected to find an effect of season on digging site selection, as has been observed in other studies on a range of digging species, due to seasonal diet shifts, or vegetation composition changes, however this was not the case (Danks et al. 2020; Claridge, Cunningham, and Tanton 1993; Vernes, Cooper, and Green 2015; McIlwee and Johnson 1998). My study commenced after a drought period (2013-2018) (O'Reagain et al. 2018), and therefore had comparatively more rain than the previous years. Precipitation and soil moisture are major drivers of truffle production, a food source for a range of digging mammals including rufous bettongs (Vernes 2010; McIlwee and Johnson 1998; Schlager 1982; Johnson 1978; Bateman, Abell-Davis, and Johnson 2011) and therefore, in the comparatively wetter years of my study, this belowground fungi might have been more widespread, and therefore, so too rufous bettong diggings. As a result, any variation in the number of diggings found among grazing strategies, vegetation types or between seasons may have been masked by truffle abundance during this time.

Interestingly, some studies have found a correlation between dig counts, the density of mature *Eucalypt* tree species (Johnson 1994a) and food availability (Claridge, Cunningham, and Tanton 1993). Belowground fungal bodies form symbiotic relationships with trees, particularly, *Eucalypt* species (Danks et al. 2020; Malajczuk, Trappe, and Molina 1987; Dundas et al. 2018; Horton et al. 2013; Claridge 2002; Nuske et al. 2017a). Due to the abundance of *Eucalyptus* trees at my study site, there may be a greater abundance of fungal bodies then places with less of these trees. As such, differences in digging abundance or occurrence caused by grazing strategy, seasons, or vegetation type may have been masked by the widespread availability of the fungal bodies that are symbiotically linked to the most common and widespread tree species at my study site. This is an avenue worth investigating further and could be done by conducting another similar study, but at a location with a lower density, or absence of *Eucalyptus* trees, or trees altogether. Faecal analysis would provide additional, valuable insight into whether the food chosen by rufous bettongs at my study site is the same, or is available, throughout all seasons and among all grazing strategies, producing the aseasonal pattern in my results. Of course, it is also possible that season has no effect on the digging behaviour and diet of rufous bettongs. Further research would help to determine whether this is the case.

As with seasonal differences, I did not find any effect of grazing strategy on digging in bettongs. No other studies have examined the impact of grazing strategies on digging in this group, but the apparent negative impact of farming on potoroids more generally suggests that many species may be sensitive to grazing impacts on food availability. Rufous bettongs in this study foraged in all the available grazing strategies, in both seasons, which might be a factor contributing to their successfully coexistence with grazing systems, but further studies on the diet of rufous bettongs, across different grazing strategies, would help clarify this. It is important to note that my study was conducted between 2020 and 2021, which were neither particularly dry nor wet years (Bureau of Meteorology 2022). Previous studies found that rufous bettong avoided using heavy grazing strategies (Neilly and Schwarzkopf 2017), however these studies were conducted in a drought period from 2013-2018 (O'Reagain et al 2018). In years of drought, there are stark differences among the various grazing strategies, reflecting the different responses to grazing pressure by vegetation and the landscape as a whole (O'Reagain et al 2018). For my study, these differences were perhaps less stark, allowing widespread utilisation of all grazing strategies for feeding by rufous bettongs.

Fine-scale composition of digging sites

I found a significant effect of fine-scale habitat features on digging, such that diggings occurred more commonly in areas comprised of bare-ground and leaf litter. Other studies have also found digging to occur more commonly in areas with minimal groundcover, in addition to areas with a high proportion of mature trees, low soil fertility and soil moisture (Johnson 1994a). My study was conducted in northwestern Queensland, so it is possible that these factors also influenced my findings. My whole study site has a high density of *Eucalypt* species, is located in a region of low soil fertility (Eldridge et al. 2018; Orians and Milewski 2007; Claridge 2002), and experiences a wet and dry seasonal rainfall pattern, thus facing extended dry periods.

It is also possible that the areas of bare-ground and high leaf litter used to forage by rufous bettongs in my study, contain a higher proportion of belowground biomass, rather than aboveground biomass i.e. grass. In addition to fungal bodies that occupy the subsurface, my study site includes a high proportion of perennial grass species. Perennial grasses store carbohydrate reserves in their tillers (bases) and roots between leaf growth phases and, therefore, when the aboveground biomass is low, the belowground biomass is high (Miller et al. 2022). As roots are another food source for rufous bettongs (Claridge 2002; Schlager 1982; Johnson 1978), this could explain why diggings occurred in areas of bare soil. Dietary, faecal and subsurface soil analysis was beyond the scope of my study, but this would be a valuable addition to future similar research in order to better understand what it is that determines digging sites selection.

Soil displacement

I estimated that 72 m^3 of soil was moved by rufous bettongs at my study site. Based on historical population estimates from this study site (Neilly and Schwarzkopf 2018), this equates to 1.3m^3 soil/animal/year displaced as a result of foraging for food. This volume of soil is much less than that recorded for other digging mammals who purportedly move several tonnes of soil per year (Valentine et al. 2013; James and Eldridge 2007; Claridge et al. 1992; James 2004; Eldridge and James 2009; Garkaklis, Bradley, and Wooller 2000, 2004, 1998). However, my soil displacement estimates are only for the digging associated with food acquisition. They do not account for soil moved by rufous bettongs while building their shelters, which involves digging shallow, body-sized pits that are far larger then foraging diggings. Further to this, some of the other species, such as the burrowing bettong, who have much larger soil displacement figures, are species that dig burrows for shelter and therefore displace significantly more than the rufous bettong.

Conclusion

My study found that rufous bettongs in grazing systems can move approximately 72m^3 of soil in a year. Although this is less than burrowing species, rufous bettong diggings were not seasonal, and there was no evidence of landscape-scale habitat or site selection preferences, suggesting that the beneficial effects of their digging are widespread if bettongs are present. At a smaller scale, bettong diggings commonly occurred in areas comprised of bare-ground, grass and leaf litter. This vegetation composition is not uncommon in the grazing landscape and suggests that the effects of bettongs that result from their digging could be widespread for graziers who have bettongs on their land. These beneficial ecosystem services could lead to improved ecosystem functioning and improved production outcomes. I believe further research examining the effect of grazing land management, and agricultural management as a whole, on abundant digging wildlife species should be undertaken to understand this dynamic further. Other digging species, such as goannas and echidnas also inhabit these landscapes and could be the focus of other similar research. If we can further understand, and educate agricultural producers on the importance of sustaining populations of digging wildlife on their properties, we could begin taking steps towards meeting increased production demands while at least maintaining, if not improving, biodiversity and environmental outcomes.

Chapter 4 - Synthesis and conclusion

Thesis summary

The conservation of biodiversity is a growing concern around the world, with extinction rates across all taxonomic groups increasing at an unprecedented rate (Ceballos et al. 2015; Ceballos, Ehrlich, and Raven 2020), particularly in Australia, where extinction rates are disproportionately greater than elsewhere in the world (Wintle et al. 2019; Woinarski et al. 2014; Johnson 2006).

There are a range of factors that have contributed to these species' declines, for example: invasive species, human disturbance and over-exploitation, but one of the greatest contributors, globally and in Australia, is agriculture (Woinarski et al. 2014; Kearney et al. 2019; Maxwell 2016). Agriculture is a globally significant land use. It encompasses approximately 40% of the earth's land mass, and of this, two-thirds is dedicated to livestock grazing (Food and Agriculture Organization of the United Nations 2020). With such a large amount of land dedicated to this purpose, how this land is managed has the potential to make a big difference to global food production and biodiversity outcomes (Cocklin and Dibden 2009). This is particularly so given that agriculture, and its associated land use changes, are critical factors to which global biodiversity loss and species declines have been attributed (Filazzola et al. 2020; Bell et al. 2011; Garnett et al. 2010).

Agriculture, and more specifically, cattle grazing, are commonly associated with decreased diversity of flora and fauna, degraded soil health and structure, and high levels of greenhouse gas emissions (Godfray and Garnett 2014; Garnett et al. 2010; Filazzola et al. 2020; Jones and Barmuta 2000; Eldridge et al. 2017; Eldridge et al. 2015; Sciences 2021; Tilman and Clark 2015). The threats and pressures placed on ecosystems by agriculture are only going to increase as the need for land and greater productivity to meet the demands of exponential human population growth also grow (Bell et al. 2011; Sciences 2021; Lanz, Dietz, and Swanson 2018). Greater pressure will be placed on my existing agricultural systems, and thus, so too the land and the ecosystems they rely upon. As such, it is critical that we determine ways in which we can meet both production and conservation needs concurrently.

For cattle grazing in Australia's semi-arid and arid rangelands, there is increasing awareness that in order to maximise production within these challenging, and often resource-limited environments, determining and using appropriate grazing strategies, and stocking rates is key (Garnett et al. 2010; Wang et al. 2020). Stocking cattle at suitable, sustainable rates can ensure that land condition is maintained and thus the landscape responds effectively to rain, and produces good pasture yields (O'Reagain et al. 2018; O'Reagain and Bushell 2015; Hall, Silcock, and Mayer 2020). This, in turn helps minimise runoff and erosion, which can, if not managed, lead to rapid and severe land degradation or loss (Hunt et al. 2014). Maintaining good land condition enables the system to support the livestock, as well as at least some of the flora and fauna native to the area, and this is where we start to see the beneficial effects of appropriate and sustainable land management on biodiversity conservation. Supporting biodiversity ensures that there are species filling ecosystem roles, and contributing to healthy ecosystem functioning (Crain and Bertness 2006; Lanz, Dietz, and Swanson 2018; Beeton et al. 2006; Fleming et al. 2014; Eldridge and James 2009; Martin 2003; Valentine et al. 2017). In turn, through the occupancy of valuable ecosystem roles by a biodiverse plethora of native flora and fauna, the landscape is healthier, produces better pasture yields and has increased resilience to stressors such as drought (Whitford and Kay 1999; Eldridge and James 2009; Eldridge, Delgado-Baquerizo, et al. 2016; Minns et al. 2001; Gordon, Prins, and Squire 2016).

To better understand the relationship that exists between cattle grazing strategies and biodiversity, I investigated the rufous bettong, a species that inhabits rangelands, and which likely provides valuable ecosystem services to these systems. Across three chapters, my research aimed to:

1) Determine the extent of habitat overlap between ecosystem engineers: the Potoroidae family, and grazing land using known occurrence data

2) Determine how grazing strategies influence rufous bettong shelter site selection

3) Determine what factors influence foraging areas for rufous bettongs and to quantify soil turnover through digging

Chapter 1 - A review of the role and distribution of ecosystem engineers: Potoroidae, in rangelands

In my first chapter, I discuss the relationship between ecosystem engineers, ecosystem health and cattle grazing; an increasingly vital dynamic to understand to meet the needs of a growing human population, while mitigating the environmental impact of agriculture (Lanz, Dietz, and Swanson 2018; Willem Erisman et al. 2016; Cocklin and Dibden 2009). Ecosystem engineers are organisms, which, directly or indirectly increase the availability of resources to other living organisms through the creation, modification and maintenance of habitats (Jones, Lawton, and Shachak 1994). Digging wildlife are commonly referred to as ecosystem engineers because their digging can lead to improved water infiltration, plant germination, organic matter breakdown, seed and spore dispersal, and can create habitat or refugia for other species (Martin 2003; Whitford and Kay 1999; Eldridge and James 2009; Huston 1994; Schooley, Bestelmeyer, and Kelly 2000; Wright, Jones, and Flecker 2002; Fleming et al. 2014). These ecosystem services are highly beneficial to all landscapes, but particularly

Australia's rangelands where the effects of a nutrient poor, arid landscape are exacerbated by the negative effects of cattle grazing.

I reviewed the current understanding of ecosystem services provided by species within the family Potoroidae and found a lack of literature describing the ecology, and ecosystem services of the rufous bettong *Aepyprymnus rufescens,* despite it being the most abundant of all the potoroids. I also analysed the habitat range of all extant potoroids for the past 30 years, alongside current Australian land-uses and I found that 38% of assessed rufous bettong habitat occurs on grazing land; the greatest degree of overlap of all potoroids (Table 1.1).

It is likely, yet still insufficiently quantified, that the rufous bettong provides beneficial ecosystem services like the other Potoroidae species. Given it is the most abundant potoroid and has the greatest degree of habitat overlap with cattle grazing land, this species could, if supported on rangelands, be a catalyst for change. Through its digging, and the ecosystem services it provides, the rufous bettongs could help to enhance ecosystem functioning, which better supports production outcomes, while simultaneously improving biodiversity outcomes also. I identified this as an avenue of future research pertinent to the current global challenges of feeding a growing population while mitigating environmental impact.

Chapter 2 - Rufous bettong shelter site use, composition and importance in grazing systems

In chapter two, I examined shelter site selection and the effect of landscape-scale factors: grazing strategy, vegetation type, and season, on shelter site selection. I also looked at fine-scale shelter site composition to determine whether there was any selection for leaf litter, bare-ground, grass, fine-woody debris, *Carissa ovata (C. ovata),* saplings or shrubs, trees, termite mounds or canopy cover. I also investigated the importance of shelter sites at my rangeland study site by assessing shelter temperatures compared to ambient temperatures.

My analysis revealed that at a landscape-scale, there was a trend suggesting a preference for paddocks using rotational spelling as a grazing strategy, and an avoidance of paddocks using the heavy stocking rate strategy, although these effects were not statistically significant. These trends were consistent with previous research suggesting rufous bettongs on this property avoided the heavy grazing paddocks (Neilly and Schwarzkopf 2018). Bettongs may prefer more conservatively grazed paddocks as they often support more grass than the other strategies (P. O'Reagain, personal communications, 12 December 2022), and rufous bettongs often build their nests from grass. At a fine-scale, shelter sites were characterised by high proportions of *C. ovata* compared to randomly selected areas. This may occur because these shrubs are thorny and nearly impenetrable and thus may provide protection from predators and trampling by cattle. There was a significant effect of season on shelter site selection composition. I found that greater proportions of logs and termite mounds were used in the wet season, possibly to mitigate the threat of shelter flooding during this time. I also found that *C. ovata* was used more in the dry season. Possibly, because rufous bettongs rely on grass to form their shelters (Johnson 1980b; Schlager 1982), the reduced grass availability following the dry season leads to increased reliance on *C. ovata* to form adequate shelter.

When analysing shelter site temperature coefficient of variation, I found that the variation in temperatures within shelter sites were significantly less than the variation in ambient temperatures recorded at random sites outside the shelter. I found that the variation in temperature between these two sites varied significantly over a 24-hour period, among months, and between seasons. Overall, variation in temperatures within shelters was less, and temperature means were less extreme in shelters. Thus, shelter sites are important to rufous bettongs as they provide important protection from ambient temperatures.

Overall, my findings in chapter two highlighted the importance of understanding and considering the function of shelter sites (i.e., thermal protection etc.), particularly in an agricultural landscape as we grapple with improving biodiversity outcomes, while simultaneously increasing agricultural production.

Chapter 3 - Rufous bettong digging and its benefit to grazing systems

In Chapter three, I investigated the digging behaviour of rufous bettongs, by determining the factors that influence digging site selection, at a landscape and fine-scale. I also provided new insight into the ecosystem services provided by the rufous bettong, by quantifying the amount of soil they can move in grazing systems as a result of digging for food.

When examining the effect of landscape-scale factors on digging site selection, I found that there was no significant effect of season, grazing strategy or vegetation type on the numbers of diggings in various locations. However, at a fine-scale, I found a significant difference between sites where diggings were present, versus sites where diggings were absent, which has also been noted by other authors (Johnson 1996). Digging site composition was characterised by a higher proportion of leaf litter and bare-ground compared to sites where digging was absent. When examining the extent of rufous bettong digging, I found that rufous bettongs displaced approximately 72m^3 annually; equating to 1.3m^3 of soil, per animal, per year by digging for food (estimated population size based on earlier work in this area (Neilly and Schwarzkopf 2018)). Therefore, I concluded that the rufous bettong provides valuable ecosystem services to this landscape in terms of soil turnover and, therefore, targeted conservation and land management that supports the species could not only improve biodiversity conservation outcomes, but also improve ecosystem health and functioning that could enhance agricultural productivity simultaneously.

Management implications

The management of grazing systems in northern Australian rangelands is undoubtedly a challenging task. Adding to this is growing pressure for Australian agricultural practices to mitigate their environmental impact, while also enhancing production in response to growing consumer demands (Sciences 2021; Godfray and Garnett 2014). The management of this land is therefore, more critical than ever, as it has the capacity to significantly contribute to either positive, or negative, long-term biodiversity and production outcomes.

We know that sustainable grazing management is associated with benefits to land condition, soil health, vegetation structure and composition, and long-term profitability (O'Reagain et al. 2014). Increasingly, we are also aware of the benefits of these sustainable practices to biodiversity (Neilly et al. 2018; Godfray and Garnett 2014). As such, I suggest that more consideration is given to the long-term sustainability of grazing land, and importantly, the ecosystem as a whole; inclusive of the often ill-considered native flora and fauna that predated the existence of cattle in these areas. Importantly, there needs to be increased awareness that managing land for production and biodiversity can be achieved simultaneously (Godfray and Garnett 2014; Tilman et al. 2011; Jhariya, Meena, and Banerjee 2021; Gordon, Prins, and Squire 2017).

My research provides valuable insight into how different grazing strategies, and their associated landscape structure and vegetation composition, affect the rufous bettong, a beneficial ecosystem engineer. Notably, I identified that the native shrub, *C. ovata,* was a very important feature within the landscape as it was used significantly more than all other vegetation. This is a significant finding because this shrub is commonly despised by graziers in northern Australian rangelands because it can reduce pasture production (Department of Agriculture and Fisheries 2020). Therefore, to discover that it provides important refuge to a valuable ecosystem engineer gives cause to reconsider its removal, or at least minimise the extent of its removal. Instead of seeing *C. ovata* as an intrusive, undesirable plant with no benefits, it could in fact be an indirect facilitator of improved land condition, pasture growth, and thus productivity due to the species it supports. Given the time and effort required to remove this shrub, my insights may prove highly valuable to the management of grazing systems, as it could enable graziers to allocate their time and efforts elsewhere, knowing the presence of this shrub is not as directly linked to productivity declines as was once thought.

Through my research, I also found that rufous bettongs showed a preference for grazing strategies that used low-to-moderate stocking densities, further supporting what is currently understood about the benefits of sustainable grazing. This provides further justification for why these grazing strategies should be used. Not only do they benefit land condition, long-term profitability and biodiversity, but more specifically by supporting biodiversity, we see ecosystem engineers, who contribute disproportionately to the improved health and functioning of these systems, successfully inhabit these landscapes (Crain and Bertness 2006; Eldridge and Mensinga 2007; James, Eldridge, and Moseby 2010; James, Eldridge, and Hill 2009; Fleming et al. 2014; Noble et al. 2007; Noble 1993; James and Eldridge 2007; Eldridge and James 2009; Whitford and Kay 1999). My research alters the narrative and highlights the benefits of wildlife, and biodiverse ecosystems to agricultural systems through healthy ecosystem functioning.

In order to see Australian grazing systems keep up with growing consumer demands, while also managing the complexities of growing consumer demand for, and industry pressure to, mitigate the environmental impact of farming; change is required. My research provides further justification for why there should be widespread adoption of sustainable long-term grazing strategies, as the results are mutually beneficial to industry and the environment.

Future research

Future research into effective, concurrent improvements to both biodiversity and production outcomes in Australia is imperative. With the need to protect Australia's unique, world-renowned, flora and fauna, and one of its largest industries, the stakes could not be higher. My research provided new insight into the interrelationship between grazing systems and an ecosystem engineer, which could help to inform the management of rangelands, such that they can achieve both production and conservation outcomes. However, there is still more to be learnt and understood and therefore, it would be beneficial to do a longer-term study, across multiple seasons to measure the effect of drought, climate variability, and other potential longer-term influences on long-term landscape and fine-scale site selection patterns of rufous bettongs. Similarly, more extensive investigation of the long-term, direct effect of digging on the landscape, inclusive of pasture yields, water runoff rates and vegetation composition, could help to better understand, and thus better educate stakeholders on the benefit of digging animals to these landscapes, and why supporting them is mutually beneficial.

Furthermore, my research examined rufous bettong digging, but only that which results from digging for food. I did not investigate the digging that results from shelter creation and the associated pits dug by rufous bettongs. These pits are significantly larger than digging pits, so examining and quantifying these would be valuable to furthering our knowledge of the ecosystem services provided by rufous bettongs. This may strengthen the argument for their conservation on grazing land. In addition to rufous bettongs, we could also explore the interrelationship of a range of other digging species and grazing systems. Other digging animals, such as goannas and echidnas, inhabit these landscapes, and further investigation of their role within these systems could provide more scope to the benefits of biodiversity within rangelands.

Conclusion

My research shows that the interaction between wildlife and grazing systems is complex and multifaceted, with many factors to be considered when understanding the extrinsic pressure of an anthropogenic land use on the natural ecosystems and wildlife within them. I found that rufous bettongs were relatively resilient to the direct, broad-scale effects of grazing strategy, however, these strategies can alter the landscape structure and vegetation composition, and I found these factors to be of significance to shelter and digging site selection. Therefore, moving forward, we need to take a more holistic approach when making management decisions in these grazing systems and consider the interconnectedness of natural and anthropogenic systems.

In understanding the history of wildlife extinctions in Australia, we know that small digging mammals are at high risk of extinction and thus, we are at high risk of losing the beneficial ecosystem services they provide. Through the findings of my research, it is evident that management decisions such as opting for more sustainable grazing strategies (i.e., rotational spelling), could better support ecosystem engineers like the rufous bettong. Similarly, considering the value of seemingly undesirable species such as *C. ovata*, before removing it, is imperative as we now know that this shrub provides valuable refuge for species who offer highly beneficial services to the surrounding ecosystem.

These mindset shifts, and associated changes to management decisions, would contribute to supporting ecosystem engineers like rufous bettongs, and other valuable species on these landscapes. These species provide ecosystem services that improve ecosystem functioning and land condition and thus benefit productivity and profitability. Improved land condition and production for farmers, and more inhabitable land to support a plethora of flora and fauna; this is the goal. Not only is there no loss to farmers, but they would in fact benefit, just as the natural ecosystems that coexist on these rangelands would too. These changes in management decisions are how we can address the conundrum of meeting increasing consumer demands, while trying to minimise risk to and loss of biodiversity.

Chapter 5 References

ABS. 2018. 'Land Management and Farming in Australia, 2016-2017', Australian Bureau of Statistics https://www.abs.gov.au/ausstats/abs@.nsf/mf/4627.0

Bateman, Brooke L., Sandra E. Abell-Davis, and Christopher N. Johnson. 2011. 'Climate-driven variation in food availability between the core and range edge of the endangered northern bettong (Bettongia tropica)', *Australian Journal of Zoology*, 59: 177-85.

Bates, Douglas , Martin Machler, Benjamin Bolker, and Steven Walker. 2015. "lme4: Linear Mixed-Effects Models Using Eigen and S4." In.

Beeton, RJS , Kristal I Buckley, Gary J Jones, Denise Morgan, Russell E Reichelt, and Denis Trewin. 2006. "Australia State of the Environment 2006." In. Canberra: Australian State of the Environment Committee

Bell, Alan W., Edward Charmley, Robert A. Hunter, and Jason A. Archer. 2011. 'The Australasian beef industries—Challenges and opportunities in the 21st century', *Animal Frontiers*, 1: 10-19.

Bennett, A. F., and B. J. Baxter. 1989. 'Diet of the long-nosed potoroo, Potorous tridactylus (Marsupialia: Potoroidae), in south-western Victoria', *Australian Wildlife Research*, 16: 263-71.

Bice, J. 2008. 'Diets of the re-introduced greater bilby (Macrotis lagotis) and burrowing bettong (Bettongia lesueur) in the Arid Recovery Reserve, Northern South Australia', *Australian Mammalogy*, 30: 1-12.

Bougher, N. L., and J. A. Friend. 2009. 'Fungi consumed by translocated Gilbert's potoroos (Potorous gilbertii) at two sites with contrasting vegetation, south coastal Western Australia', *Australian Mammalogy*, 31: 97.

Bradshaw, Corey J. A. 2012. 'Little left to lose: deforestation and forest degradation in Australia since European colonization', *Journal of Plant Ecology*, 5: 109-20.

Buesching, Christina D., Eleanor M. Slade, Thomas Merckx, and David W. Macdonald. 2015. 'Local and landscape-scale impacts of woodland management on wildlife.' in David W. Macdonald and Ruth E. Feber (eds.), *Wildlife Conservation on Farmland Volume 1: Managing for nature on lowland farms* (Oxford University Press).

Burbidge, A. A. 1983. 'Burrowing bettong, *Bettongia lesuer*.' in Ronald Strahan (ed.), *Complete Book of Australian Mammals* (Angus and Robertson Sydney).

Burbidge, Andrew, Jeff Short, and Phillip Fuller. 2007. 'Relict Bettongia lesueur warrens in Western Australian deserts', *Australian Zoologist*, 34: 97-103.

Bureau of Meteorology. 2022. 'Climate statistics for Australian locations - Charters Towers Airport ', Accessed 5 October 2022. http://www.bom.gov.au/jsp/ncc/cdio/cvg/av?p_stn_num=034084&p_prim_element_index=1

8&p_display_type=statGraph&period_of_avg=ALL&normals_years=allYearOfData&staticPage=.

Calenge, Clement. 2011. "Exploratory Analysis of the Habitat Selection by the Wildlife in R." In. France.

Cardinale, Bradley J., J. Emmett Duffy, Andrew Gonzalez, David U. Hooper, Charles Perrings, Patrick Venail, Anita Narwani, Georgina M. Mace, David Tilman, David A. Wardle, Ann P. Kinzig, Gretchen C. Daily, Michel Loreau, James B. Grace, Anne Larigauderie, Diane S. Srivastava, and Shahid Naeem. 2012. 'Biodiversity loss and its impact on humanity', *Nature (London)*, 486: 59-67.

Ceballos, Gerardo, Paul R. Ehrlich, Anthony D. Barnosky, Andrés García, Robert M. Pringle, and Todd M. Palmer. 2015. 'Accelerated modern human-induced species losses: Entering the sixth mass extinction', *Science advances*, 1: e1400253.

Ceballos, Gerardo, Paul R. Ehrlich, and Peter H. Raven. 2020. 'Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction', *Proceedings of the National Academy of Sciences*, 117: 13596-602.

Christensen, P., and T. Leftwich. 1980. 'Observations on the nest-building habits of the brush-tailed rat-kangaroo or woylie (Bettongia penicillata)', *Journal of the Royal Society of Western Australia*, 63: 33-38.

Claridge, A. W., and S. J. Cork. 1994. 'Nutritional-Value of Hypogeal Fungal Sporocarps for the Long-Nosed Potoroo (Potorous-Tridactylus), a Forest-Dwelling Mycophagous Marsupial', *Australian Journal of Zoology*, 42: 701-10.

Claridge, A. W., R. B. Cunningham, and M. T. Tanton. 1993. 'Foraging patterns of the long-nosed potoroo (Potorous tridactylus) for hypogeal fungi in mixed-species and regrowth eucalypt forest stands in southeastern Australia', *Forest Ecology and Management*, 61: 75-90.

Claridge, A. W., and T. W. May. 1994. 'Mycophagy among Australian mammals', *Australian Journal of Ecology*, 19: 251-75.

Claridge, A. W., M. T. Tanton, and R. B. Cunningham. 1993. 'Hypogeal fungi in the diet of the long-nosed potoroo (Potorous tridactylus) in mixed-species and regrowth eucalypt forest stands in south-eastern Australia', *Wildlife Research*, 20: 321-38.

Claridge, A. W., M. T. Tanton, J. H. Seebeck, S. J. Cork, and R. B. Cunningham. 1992. 'Establishment of ectomycorrhizae on the roots of two species of Eucalyptus from fungal spores contained in the faeces of the long-nosed potoroo (Potorous tridactylus)', *Australian Journal of Ecology*, 17: 207-17.

Claridge, Andrew W. 2002. 'Ecological role of hypogeous ectomycorrhizal fungi in Australian forests and woodlands', *Plant and Soil*, 244: 291-305.

Cockle, Kristina L., Kathy Martin, and Tomasz Weso łowski. 2011. 'Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide', *Frontiers in Ecology and the Environment*, 9: 377-82.

Cocklin, Chris, and Jacqui Dibden. 2009. 'Systems in peril: Climate change, agriculture and biodiversity in Australia', *IOP Conference Series: Earth and Environmental Science*, 8.

Crain, Caitlin Mullan, and Mark D. Bertness. 2006. 'Ecosystem Engineering across Environmental Gradients: Implications for Conservation and Management', *BioScience*, 56: 211-18.

Danks, Melissa A., Natalie Simpson, Todd F. Elliott, C. E. Timothy Paine, and Karl Vernes. 2020. 'Modeling mycorrhizal fungi dispersal by the mycophagous swamp wallaby (Wallabia bicolor)', *Ecology and Evolution*, 10: 12920-28.

Davies, Kendi F., Brett A. Melbourne, Craig D. James, and Ross B. Cunningham. 2010. 'Using traits of species to understand responses to land use change: Birds and livestock grazing in the Australian arid zone', *Biological Conservation*, 143: 78-85.

Day, Richard T., and Robert W. Elwood. 1999. 'Sleeping Site Selection by the Golden-handed Tamarin Saguinus midas midas: The Role of Predation Risk, Proximity to Feeding Sites, and Territorial Defence', *Ethology*, 105: 1035-51.

Dennis, A.J , and P.M Johnson. 2008. 'Rufous Bettong, *Aepyprymnus Rufescens,* (Gray, 1837).' in Steve Van Dyck and Ronald Strahan (eds.), *The Mammals of Australia* (Reed New Holland Australia).

Department of Agriculture and Fisheries. 2020. "Currant Bush (Blackberry, burrum bush or conkberry), -*Carissa ovata* and *Cairssa lanceolata*." In, edited by Queensland Government, 2.

Doherty, Tim S., Alistair S. Glen, Dale G. Nimmo, Euan G. Ritchie, and Chris R. Dickman. 2016. 'Invasive predators and global biodiversity loss', *Proceedings of the National Academy of Sciences*, 113: 11261-65.

Dugard, Pat, John B. Todman, and Harry Staines. 2010. *Approaching multivariate analysis : a practical introduction / Pat Dugard, John Todman, Harry Staines* (Routledge: London).

Dundas, Shannon J., Anna J. M. Hopkins, Katinka X. Ruthrof, Natasha E. Tay, Treena I. Burgess, Giles E. St J. Hardy, and Patricia A. Fleming. 2018. 'Digging mammals contribute to rhizosphere fungal community composition and seedling growth', *Biodiversity and Conservation*, 27: 3071-86.

Eldridge, D. J., and W. G. Whitford. 2009. 'Soil disturbance by native animals along grazing gradients in an arid grassland', *Journal of Arid Environments*, 73: 1144-48.

Eldridge, David J., Manuel Delgado-Baquerizo, Samantha K. Travers, James Val, Ian Oliver, and Paul Kardol. 2017. 'Do grazing intensity and herbivore type affect soil health? Insights from a semi-arid productivity gradient', *Journal of Applied Ecology*, 54: 976-85.

Eldridge, David J., Manuel Delgado-Baquerizo, Jason N. Woodhouse, Brett A. Neilan, and Kim Cuddington. 2016. 'Mammalian engineers drive soil microbial communities and ecosystem functions across a disturbance gradient', *Journal of Animal Ecology*, 85: 1636-46.

Eldridge, David J., and Alex I. James. 2009. 'Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes', *Ecological Management & Restoration*, 10: S27-S34.

Eldridge, David J., Terry B. Koen, Aaron Killgore, Niki Huang, and Walter G. Whitford. 2012. 'Animal foraging as a mechanism for sediment movement and soil nutrient development: Evidence from the semi-arid Australian woodlands and the Chihuahuan Desert', *Geomorphology*, 157-158: 131-41.

Eldridge, David J., Fernando T. Maestre, Terry B. Koen, and Manuel Delgado-Baquerizo. 2018. 'Australian dryland soils are acidic and nutrient-depleted, and have unique microbial communities compared with other drylands', *Journal of Biogeography*, 45: 2803-14.

Eldridge, David J., and Anna Mensinga. 2007. 'Foraging pits of the short-beaked echidna (Tachyglossus aculeatus) as small-scale patches in a semi-arid Australian box woodland', *Soil Biology and Biochemistry*, 39: 1055-65.

Eldridge, David J., Alistair G. B. Poore, Marta Ruiz-Colmenero, Mike Letnic, and Santiago Soliveres. 2015. 'Ecosystem structure, function and composition in rangelands are negatively affected by livestock grazing', *Ecological Applications*.

Eldridge, David J., Alistair G. B. Poore, Marta Ruiz-Colmenero, Mike Letnic, and Santiago Soliveres. 2016. 'Ecosystem structure, function, and composition in rangelands are negatively affected by livestock grazing', *Ecological Applications*, 26: 1273-83.

Filazzola, Alessandro, Charlotte Brown, Margarete A. Dettlaff, Amgaa Batbaatar, Jessica Grenke, Tan Bao, Isaac Peetoom Heida, James F. Cahill, and Eric Seabloom. 2020. 'The effects of livestock grazing on biodiversity are multi-trophic: a meta-analysis', *Ecology Letters*, 23: 1298-309.

Fisher, D. O. 2000. 'Effects of Vegetation Structure, Food and Shelter on the Home Range and Habitat Use of an Endangered Wallaby', *The Journal of applied ecology*, 37: 660-71.

Fleischner, Thomas L. 1994. 'Ecological Costs of Livestock Grazing in Western North America', *Conservation Biology*, 8: 629-44.

Fleming, Patricia A., Hannah Anderson, Amy S. Prendergast, Michael R. Bretz, Leonie E. Valentine, and Giles E. StJ Hardy. 2014. 'Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function?', *Mammal Review*, 44: 94-108.

Fogel, Robert , and James M Trappe. 1978. 'Fungus Consumption (Mycophagy) by Small Animals ', *Northwest Science*, 52: 1-31.

Food and Agriculture Organization of the United Nations. 2020. 'Land use in agriculture by the numbers'. https://www.fao.org/sustainability/news/detail/en/c/1274219/.

Fox, John, and Sanford Weisberg. 2019. "An R Companion to Applied Regression." In. Oaks CA.

Fraser, G. W., and G. S. Stone. 2016. 'The effect of soil and pasture attributes on rangeland infiltration rates in northern Australia', *The Rangeland Journal*, 38: 245-59.

Fuller, Andrea, Duncan Mitchell, Shane K. Maloney, Robyn S. Hetem, Vinicius F. C. Fonsêca, Leith C. R. Meyer, Tanja M. F. N. van de Ven, and Edward P. Snelling. 2021. 'How dryland mammals will respond to climate change: The effects of body size, heat load and a lack of food and water', *Journal of experimental biology*, 224.

Garkaklis, Mark J., J. S. Bradley, and R. D. Wooller. 1998. 'The effects of Woylie (Bettongia penicillata) foraging on soil water repellency and water infiltration in heavy textured soils in southwestern Australia', *Australian Journal of Ecology*, 23: 492-96.

———. 2000. 'Digging by vertebrates as an activity promoting the development of water-repellent patches in sub-surface soil', *Journal of Arid Environments*, 45: 35-42.

———. 2003. 'The relationship between animal foraging and nutrient patchiness in south-west Australian woodland soils', *Australian Journal of Soil Research*, 41: 665+.

———. 2004. 'Digging and soil turnover by a mycophagous marsupial', *Journal of Arid Environments*, 56: 569-78.

Garnett, Stephen T., John C. Z. Woinarski, Gabriel M. Crowley, and Alex S. Kutt. 2010. 'Biodiversity Conservation in Australian Tropical Rangelands.' in, *Wild Rangelands*.

Gibbons, P., and David Lindenmayer. 2002. *Tree hollows and wildlife conservation in Australia* (CSIRO Publishing: Melbourne).

Godfray, H. Charles J., and Tara Garnett. 2014. 'Food security and sustainable intensification', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369: 20120273.

Goldie, Jenny, and Katharine Betts. 2014. *Sustainable futures : linking population, resource and the environment* (Csiro Publishing: Collingwood, Victoria).

Gordon, I. J., Herman de Prins, and G. R. Squire. 2017. *Food production and nature conservation : conflicts and solutions* (Routledge: London, United Kingdom ;).

Gordon, Iain J., Herbert H. T. Prins, and Geoff R. Squire. 2016. 'Nature’s role in feeding the 10 billion: how biodiversity can benefit agriculture.' in (Taylor & Francis Group: United Kingdom).

Green, K., M. K. Tory, A. T. Mitchell, P. Tennant, and T. W. May. 1999. 'The diet of the long-footed potoroo (Potorous longipes)', *Australian Journal of Ecology*, 24: 151-56.

Gretton, Paul, and Umme Salma. 1996. "LAND DEGRADATION AND THE AUSTRALIAN AGRICULTURAL INDUSTRY." In. Canberra

Hall, Trevor J., Richard G. Silcock, and David G. Mayer. 2020. 'Grazing pressure and tree competition affect cattle performance and native pastures in Eucalypt woodlands of Queensland, north-eastern Australia', *Animal production science*, 60: 953-66.

Halstead, Lauren M., Duncan R. Sutherland, Leonie E. Valentine, Anthony R. Rendall, Amy L. Coetsee, and Euan G. Ritchie. 2019. 'Digging up the dirt: Quantifying the effects on soil of a translocated ecosystem engineer', *Austral Ecology*, n/a.

Haussmann, Natalie S. 2017. 'Soil movement by burrowing mammals: A review comparing excavation size and rate to body mass of excavators', *Progress in Physical Geography*, 41: 29-45.

Heritage, Office of Environment and. 2018. 'Rufous Bettong - Profile ', NSW Government https://www.environment.nsw.gov.au/threatenedSpeciesApp/profile.aspx?id=10033.

Hooper, D. U. 2005. 'EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING: A CONSENSUS OF CURRENT KNOWLEDGE', *Ecological monographs*, 75: 3-35.

Hooper, David U., E. Carol Adair, Bradley J. Cardinale, Jarrett E. K. Byrnes, Bruce A. Hungate, Kristin L. Matulich, Andrew Gonzalez, J. Emmett Duffy, Lars Gamfeldt, Mary I. O'Connor, fakulteten Naturvetenskapliga, Sciences Faculty of, Biological Department of, Sciences Environmental, universitet Göteborgs, miljövetenskap Institutionen för biologi och, and University Gothenburg. 2012. 'A global synthesis reveals biodiversity loss as a major driver of ecosystem change', *Nature*, 486: 105-08.

Horton, Bryony M., Morag Glen, Neil J. Davidson, David Ratkowsky, Dugald C. Close, Tim J. Wardlaw, and Caroline Mohammed. 2013. 'Temperate eucalypt forest decline is linked to altered ectomycorrhizal communities mediated by soil chemistry', *Forest Ecology and Management*, 302: 329-37.

Hovick, Torre J., R. Dwayne Elmore, Brady W. Allred, Samuel D. Fuhlendorf, and David K. Dahlgren. 2014. 'Landscapes as a moderator of thermal extremes: a case study from an imperiled grouse', *Ecosphere (Washington, D.C)*, 5: art35-12.

Hunt, L. P., J. G. McIvor, A. C. Grice, and S. G. Bray. 2014. 'Principles and guidelines for managing cattle grazing in the grazing lands of northern Australia: stocking rates, pasture resting, prescribed fire, paddock size and water points – a review', *The Rangeland Journal*, 36.

Huston, Michael A. 1994. *Biological diversity: the coexistence of species on changing landscapes* (Cambridge University Press: Cambridge, [England]).

Isaac, J. L., J. L. De Gabriel, and B. A. Goodman. 2008. 'Microclimate of daytime den sites in a tropical possum: implications for the conservation of tropical arboreal marsupials', *Animal Conservation*, 11: 281-87.

IUCN. 2023. 'The IUCN Red List of Threatened Species', IUCN, Accessed 14/03/23. https://www.iucnredlist.org.

James, Alex I. 2004. 'The creation of fertile patches by four ecosystem engineers in an arid South Australian dunefield', University of New South Wales

James, Alex I., and David J. Eldridge. 2007. 'Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape', *Biological Conservation*, 138: 351-59.

James, Alex I., David J. Eldridge, and Brydie M. Hill. 2009. 'Foraging animals create fertile patches in an Australian desert shrubland', *Ecography*, 32: 723-32.

James, Alex I., David J. Eldridge, and Katherine E. Moseby. 2010. 'Foraging pits, litter and plant germination in an arid shrubland', *Journal of Arid Environments*, 74: 516-20.

James, Craig D., Jill Landsberg, and Stephen R. Morton. 1999. 'Provision of watering points in the Australian arid zone: a review of effects on biota', *Journal of Arid Environments*, 41: 87-121.

Jantz, Samuel M., Brian Barker, Thomas M. Brooks, Louise P. Chini, Qiongyu Huang, Rachel M. Moore, Jacob Noel, and George C. Hurtt. 2015. 'Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation', *Conservation Biology*, 29: 1122-31.

Jari Oksanen, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs, and Helene Wagner. 2020. "Vegan: Community Ecology Package." In.

Jhariya, Manoj Kumar, Ram Swaroop Meena, and Arnab Banerjee. 2021. *Ecological intensification of natural resources for sustainable agriculture* (Springer: Gateway East, Singapore).

Johnson, C. N. 1994a. 'Distribution of Feeding Activity of the Tasmanian Bettong (Bettongia Gaimardi) in Relation to Vegetation Patterns', *Wildlife Research*, 21: 249-55.

———. 1994b. 'Nutritional Ecology of a Mycophagous Marsupial in Relation to Production of Hypogeous Fungi', *Ecology*, 75: 2015-21.

Johnson, C. N., and A. P. McIlwee. 1997. 'Ecology of the Northern Bettong, Bettongia tropica, a Tropical Mycophagist', *Wildlife Research*, 24: 549.

Johnson, Chris. 2006. *Australia's Mammal Extinctions: a 50000 year history* (Cambridge University Press U6 - ctx_ver=Z39.88-2004&ctx_enc=info%3Aofi%2Fenc%3AUTF-8&rfr_id=info%3Asid%2Fsummon.serialssolutions.com&rft_val_fmt=info%3Aofi%2Ffmt%3Akev%3Amtx%3Abook&rft.genre=book&rft.title=Australia%27s+Mammal+Extinctions%3A+a+50000+year+history&rft.au=Johnson%2C+Chris&rft.date=2006&rft.pub=Cambridge+University+Press&rft.externalDBID=7374617475733D707562&rft.externalDocID=oai_researchonline_jcu_edu_au_4635&paramdict=en-US U7 - Book).

Johnson, Christopher N. 1996. "Interactions between mammals and ectomycorrhizal fungi." In, 503-07. England: Elsevier Ltd.

Johnson, P. M. 1978. 'Husbandry of the Rufous rat-kangaroo', *International Zoo Yearbook*, 18: 156-57.

———. 1980a. 'OBSERVATIONS OF THE BEHAVIOR OF THE RUFOUS RAT-KANGAROO, AEPYPRYMNUS-RUFESCENS (GRAY), IN CAPTIVITY', *Australian Wildlife Research*, 7: 347-57.

Johnson, PM. 1980b. 'Observations of the Behaviour of the Rufous Rat-Kangaroo, Aepyprymnus rufescens (Gray), in Capativity', *Wildlife Research*, 7: 347-57.

Jones, Clive G., John H. Lawton, and Moshe Shachak. 1994. 'Organisms as Ecosystem Engineers', *Oikos*, 69: 373-86.

Jones, Menna E., and Leon A. Barmuta. 2000. 'Niche Differentiation Among Sympatric Australian Dasyurid Carnivores', *Journal of Mammalogy*, 81: 434-47.

Kay, F. R., and W. G. Whitford. 1978. 'The burrow environment of the banner-tailed kangaroo rat, Dipodomys spectabilis, in south-central New Mexico', *American Midland Naturalist*, 99: 270-79.

Kearney, Stephen G., Josie Carwardine, April E. Reside, Diana O. Fisher, Martine Maron, Tim S. Doherty, Sarah Legge, Jennifer Silcock, John C. Z. Woinarski, Stephen T. Garnett, Brendan A. Wintle, and James E. M. Watson. 2019. 'The threats to Australia’s imperilled species and implications for a national conservation response', *Pacific Conservation Biology*, 25: 231.

Kerth, G., K. Weissmann, and B. Konig. 2001. 'Day Roost Selection in Female Bechstein's Bats (Myotis bechsteinii): A Field Experiment to Determine the Influence of Roost Temperature', *Oecologia*, 126: 1-9.

Killham, Ken. 1994. *Soil ecology* (Cambridge University Press: Cambridge;New York;).

Lamont, Byron B., Catherine S. Ralph, and Per E. S. Christensen. 1985. 'MYCOPHAGOUS MARSUPIALS AS DISPERSAL AGENTS FOR ECTOMYCORRHIZAL FUNGI ON EUCALYPTUS CALOPHYLLA AND GASTROLOBIUM BILOBUM', *New Phytologist*, 101: 651-56.

Lanz, Bruno, Simon Dietz, and Tim Swanson. 2018. 'The Expansion of Modern Agriculture and Global Biodiversity Decline: An Integrated Assessment', *Ecological Economics*, 144: 260-77.

Lefcheck, Jon, Jarrett Byrnes, and James Grace. 2018. "Piecewise Structural Equation Modeling." In.

Lindenmayer, David B., William F. Laurance, and Jerry F. Franklin. 2012. 'Global Decline in Large Old Trees', *Science*, 338: 1305-06.

Macdonald, David Whyte, and Ruth Feber. 2015. *Wildlife conservation on farmland: Conflict in the countryside* (Oxford University Press, USA).

MacGregor, Christopher I., Ross B. Cunningham, and David B. Lindenmayer. 2015. 'Nest-site selection of the long-nosed bandicoot (Perameles nasuta) in a postfire environment', *Australian Journal of Zoology*, 63: 324-30.

Machovina, Brian, Kenneth J. Feeley, and William J. Ripple. 2015. 'Biodiversity conservation: The key is reducing meat consumption', *The Science of the total environment*, 536: 419-31.

Malajczuk, N., B. Dell, and N. L. Bougher. 1987. 'ECTOMYCORRHIZA FORMATION IN EUCALYPTUS. III. SUPERFICIAL ECTOMYCORRHIZAS INITIATED BY HYSTERANGIUM AND CORTINARIUS SPECIES', *New Phytologist*, 105: 421-28.

Malajczuk, N., J. M. Trappe, and R. Molina. 1987. 'Interrelationships among some ectomycorrhizal trees, hypogeous fungi and small mammals: Western Australian and northwestern American parallels', *Australian Journal of Ecology*, 12: 53-55.

Martin, Greg. 2003. 'The role of small ground-foraging mammals in topsoil health and biodiversity: Implications to management and restoration', *Ecological Management & Restoration*, 4: 114-19.

Maxwell, Sean. 2016. 'The ravages of guns, nets and bulldozers', *Nature (London)*, 536: 143.

McAlpine, C. A., A. Etter, P. M. Fearnside, L. Seabrook, and W. F. Laurance. 2009. 'Increasing world consumption of beef as a driver of regional and global change: A call for policy action based on evidence from Queensland (Australia), Colombia and Brazil', *Global environmental change*, 19: 21-33.

McIlwee, A. P., and C. N. Johnson. 1998. 'The Contribution of Fungus to the Diets of Three Mycophagous Marsupials in Eucalyptus Forests, Revealed by Stable Isotope Analysis', *Functional Ecology*, 12: 223-31.

McKeon, G. M., G. S. Stone, J. I. Syktus, J. O. Carter, N. R. Flood, D. G. Ahrens, D. N. Bruget, C. R. Chilcott, D. H. Cobon, R. A. Cowley, S. J. Crimp, G. W. Fraser, S. M. Howden, P. W. Johnston, J. G. Ryan, C. J. Stokes, and K. A. Day. 2009. 'Climate change impacts on northern Australian rangeland livestock carrying capacity: a review of issues', *The Rangeland Journal*, 31: 1.

Miller, Lisa, Jess Brogden, Southern Farming Systems, Cam Nicholson, Nicon Rural Services, Lisa Warn, and Warn Ag Consulting. 2022. "How do I get perennial grases to thrive and survive? ." In.

Minns, Asher, John Finn, Andy Hector, Maria Caldeira, Jasmin Joshi, Cecillia Palmborg, Bernhard Schmid, Michael Scherer-Lorenzen, and Eva Spehn. 2001. 'The Functioning of European Grassland Ecosystems: Potential Benefits of Biodiversity to Agriculture', *Outlook on agriculture*, 30: 179-85.

Mitchell, Duncan, Edward P. Snelling, Robyn S. Hetem, Shane K. Maloney, Willem Maartin Strauss, Andrea Fuller, and Dehua Wang. 2018. 'Revisiting concepts of thermal physiology: Predicting responses of mammals to climate change', *The Journal of animal ecology*, 87: 956-73.

MLA. 2022. "Global beef industry and trade report." In.: Meat and Livestock Australia.

Munro, Nicola T., Sue McIntyre, Ben Macdonald, Saul A. Cunningham, Iain J. Gordon, Ross B. Cunningham, and Adrian D. Manning. 2019. 'Returning a lost process by reintroducing a locally extinct digging marsupial', *PeerJ*, 7: e6622.

Nash, Maliha S., Erik Jackson, and Walter G. Whitford. 2003. 'Soil microtopography on grazing gradients in Chihuahuan desert grasslands', *Journal of Arid Environments*, 55: 181-92.

Neilly, H. 2017. 'Balancing beef with biodiversity : faunal responses to different cattle grazing strategies', James Cook University.

Neilly, H., and L. Schwarzkopf. 2018. 'Heavy livestock grazing negatively impacts a marsupial ecosystem engineer', *Journal of Zoology*, 305: 35-42.

Neilly, Heather, Peter O'Reagain, Jeremy Vanderwal, and Lin Schwarzkopf. 2018. 'Profitable and Sustainable Cattle Grazing Strategies Support Reptiles in Tropical Savanna Rangeland', *Rangeland Ecology & Management*, 71: 205-12.

Neilly, Heather, and Lin Schwarzkopf. 2017. 'The response of an arboreal mammal to livestock grazing is habitat dependant', *Scientific Reports*, 7: 17382-9.

Nguyen, V. P., A. D. Needham, and J. A. Friend. 2005. 'A quantitative dietary study of the ?Critically Endangered? Gilbert?s potoroo Potorous gilbertii', *Australian Mammalogy*, 27: 1-6.

Noble, J. C. 1993. 'Relict Surface-Soil Features in Semi-Arid Mulga (Acacia Aneura) Woodlands', *The Rangeland Journal*, 15: 48-70.

Noble, James C., Warren J. MÜLler, James K. Detling, and Gilbert H. Pfitzner. 2007. 'Landscape ecology of the burrowing bettong: Warren distribution and patch dynamics in semiarid eastern Australia', *Austral Ecology*, 32: 326-37.

Nuske, S. J., K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger, and S. E. Abell. 2017a. 'Data on the fungal species consumed by mammal species in Australia', *Data in brief*, 12: 251-60.

———. 2017b. 'Redundancy among mammalian fungal dispersers and the importance of declining specialists', *Fungal Ecology*, 27: 1-13.

Nuske, Susan J., Sten Anslan, Leho Tedersoo, Mark T. L. Bonner, Brad C. Congdon, and Sandra E. Abell. 2018. 'The endangered northern bettong, Bettongia tropica, performs a unique and potentially irreplaceable dispersal function for ectomycorrhizal truffle fungi', *Molecular Ecology*, 27: 4960-71.

O'Reagain, P., and J. Bushell. 2015. "Managing for a variable climate: long-term results and management recommendations from the Wambiana grazing trial " In.

O'Reagain, P., J. Bushell, C. Holloway, and A. Reid. 2009. 'Managing for rainfall variability: Effect of grazing strategy on cattle production in a dry tropical savanna', *Animal production science*, 49: 85-99.

O'Reagain, Peter, John Bushell, Lester Pahl, Joe Scanlan, and Department of Agriculture and Fisheries. 2018. "Wambiana Grazing Trial Phase 3: Stocking Strategies for improving Carrying Capacity, Land Condition and Biodiversity Outcomes." In.

O’Reagain, Peter, Joe Scanlan, Leigh Hunt, Robyn Cowley, and Dionne Walsh. 2014. 'Sustainable grazing management for temporal and spatial variability in north Australian rangelands – a synthesis of the latest evidence and recommendations', *The Rangeland Journal*, 36: 223-32.

Orians, Gordon H., and Antoni V. Milewski. 2007. 'Ecology of Australia: the effects of nutrient-poor soils and intense fires', *Biological Reviews*, 82: 393-423.

Pintor, A., E. Graham, J. Engert, and M. Kennard. 2018. "Threatening processes to taxa of conservation concern in Northern Australia." In, edited by Griffith University James Cook University, and Australian Government National Environmental Science Program (NESP), Northern Australia Environmental Resources Hub. dx.doi.org/10.25903/5b72631b2dd70.

Poole, Holly L., Laily Mukaromah, Halina T. Kobryn, and Patricia A. Fleming. 2015. 'Spatial analysis of limiting resources on an island: diet and shelter use reveal sites of conservation importance for the Rottnest Island quokka', *Wildlife research (East Melbourne)*, 41: 510-21.

QGIS.org. %Y. " QGIS Geographic Information System." In.: QGIS Association.

R Core Team. 2019a. "The R Foundation for Statistical Computing Platform." In.

———. 2019b. "R: A Language and Environment for Statistical Computing." In. Vienna, Austria: R Foundation for Statistical Computing.

Rapport, D. J., H. A. Regier, and T. C. Hutchinson. 1985. 'Ecosystem Behavior Under Stress', *The American Naturalist*, 125: 617-40.

Rapport, David J., and Walter G. Whitford. 1999. 'How Ecosystems Respond to Stress: Common properties of arid and aquatic systems', *BioScience*, 49: 193-203.

Reddell, Paul, Alister V. Spain, and Michael Hopkins. 1997. 'Dispersal of Spores of Mycorrhizal Fungi in Scats of Native Mammals in Tropical Forests of Northeastern Australia', *Biotropica*, 29: 184-92.

Ritchie, Hannah, and Max Roser. 2013. ""Land Use"." In. Published online at OurWorldInData.org.

Robley, Alan J. 2001. 'Dietary overlap between the burrowing bettong (Bettongia lesueur) and the European rabbit (Oryctolagus cuniculus) in semi-arid coastal Western Australia', *Wildlife research (East Melbourne)*, 28: 341-49.

Romero, Gustavo Q., Thiago Gonçalves-Souza, Camila Vieira, and Julia Koricheva. 2015. 'Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis', *Biological Reviews*, 90: 877-90.

Rutledge, Kim, Melissa McDaniel, Santani Teng, Hilary Hall, Tara Ramroop, Erin Sprout, Jeff Hunt, Diane Boudreau, and Hilary Costa. 2022. 'Habitat', National Geographic Society https://education.nationalgeographic.org/resource/habitat

Schlager, Felix Erwin. 1982. 'The Distribution, Status and Ecology of the Rufous Rat-Kangaroo, 'Aepyprymnus rufescens', in Northern New South Wales', University of New England

Schmidt-Nielsen, Knut, and Bodil Schmidt-Nielsen. 1952. 'Water Metabolism of Desert Mammals', *Physiological reviews*, 32: 135-66.

Schooley, R. L., B. T. Bestelmeyer, and J. F. Kelly. 2000. 'Influence of Small-Scale Disturbances by Kangaroo Rats on Chihuahuan Desert Ants', *Oecologia*, 125: 142-49.

Sciences, National Academy of. 2021. "The Challenge of Feeding the World Sustainably: Summary of the US-UK Scientific Forum on Sustainable Agriculture." In.: The National Academies Press

Scotts, D.J. 1989. "Ecology of Potorous Longipes (Marsupialia:Potoroidae), and Preliminary Recommendations for Management of Its Habitat in Victoria: A Report to the Australian National Parks and Wildlife Service." In.: The Department.

Seebeck, J.H, and R.W Rose. 1989. "Potoroidae " In *Fauna of Australia* edited by D.W Walton and B.J. Richardson. Canberra AGPS.

Short, Jeff. 1998. 'The extinction of rat-kangaroos (Marsupialia:Potoroidae) in New South Wales, Australia', *Biological Conservation*, 86: 365-77.

Southgate, R.I. 1980. 'Factors affecting the spatial and temporal use of habitat by the rufous rat-kangaroo Aepyprymnus rufescens', University of New England.

Tabeni, S., and R. A. Ojeda. 2003. 'Assessing mammal responses to perturbations in temperate aridlands of Argentina', *Journal of Arid Environments*, 55: 715-26.

Taylor, Robert J. 1991. 'Plants, fungi and bettongs: A fire-dependent co-evolutionary relationship', *Australian Journal of Ecology*, 16: 409-11.

———. 1992. 'Seasonal Changes in the Diet of the Tasmanian Bettong (Bettongia gaimardi), a Mycophagous Marsupial', *Journal of Mammalogy*, 73: 408-14.

Theobald, David M., James R. Miller, and N. Thompson Hobbs. 1997. 'Estimating the cumulative effects of development on wildlife habitat', *Landscape and urban planning*, 39: 25-36.

Thornton, C. M., and K. Shrestha. 2021. 'The Brigalow Catchment Study: V*. Clearing and burning brigalow (<i>Acacia harpophylla</i>) in Queensland, Australia, temporarily increases surface soil fertility prior to nutrient decline under cropping or grazing', *Soil Research*, 59: 146-69.

Thrash, I. 1998. 'Impact of large herbivores at artificial watering points compared to that at natural watering points in Kruger National Park, South Africa', *Journal of Arid Environments*, 38: 315-24.

Tilman, David. 1999. 'The Ecological Consequences of Changes in Biodiversity: A Search for General Principles', *Ecology*, 80: 1455-74.

Tilman, David, Christian Balzer, Jason Hill, and Belinda L. Befort. 2011. 'Global food demand and the sustainable intensification of agriculture', *Proceedings of the National Academy of Sciences - PNAS*, 108: 20260-64.

Tilman, David, and Michael Clark. 2015. 'Food, Agriculture & the Environment: Can We Feed the World & Save the Earth?', *Daedalus (Cambridge, Mass.)*, 144: 8-23.

Tory, M. K., T. W. May, P. J. Keane, and A. F. Bennett. 1997. 'Mycophagy in small mammals: A comparison of the occurrence and diversity of hypogeal fungi in the diet of the long-nosed potoroo Potorous tridactylus and the bush rat Rattus fuscipes from southwestern Victoria, Australia', *Australian Journal of Ecology*, 22: 460-70.

Tuomisto, Hanna L., Ian D. Hodge, Philip Riordan, and David W. Macdonald. 2015. 'Farming for the future: Optimizing farming systems for society and the environment.' in David W. Macdonald and Ruth E. Feber (eds.), *Wildlife Conservation on Farmland Volume 1: Managing for nature on lowland farms* (Oxford University Press).

Valentine, Leonie E., Hannah Anderson, Giles E. StJ Hardy, and Patricia A. Fleming. 2013. 'Foraging activity by the southern brown bandicoot (Isoodon obesulus) as a mechanism for soil turnover', *Australian Journal of Zoology*, 60: 419-23.

Valentine, Leonie E., Michael Bretz, Katinka X. Ruthrof, Rebecca Fisher, Giles E. St J. Hardy, and Patricia A. Fleming. 2017. 'Scratching beneath the surface: Bandicoot bioturbation contributes to ecosystem processes', *Austral Ecology*, 42: 265-76.

Vernes, K. 2010. 'Mycophagy in a community of macropodoid species ' in G. Coulson and M. Eldridge (eds.), *Macropods: the biology of kangaroos, wallabies, and rat-kangaroos* (CSIRO Publishing: Victoria).

Vernes, Karl. 2007. 'Are Diverse Mammal Communities Important for Maintaining Plant-fungal Associations and Ecosystem Health?', *Australasian Plant Conservation: Journal of the Australian Network for Plant Conservation*, 15: 16-18.

Vernes, Karl, Michael Castellano, and Christopher N. Johnson. 2001. 'Effects of Season and Fire on the Diversity of Hypogeous Fungi Consumed by a Tropical Mycophagous Marsupial', *Journal of Animal Ecology*, 70: 945-54.

Vernes, Karl, Tani Cooper, and Stuart Green. 2015. 'Seasonal fungal diets of small mammals in an Australian temperate forest ecosystem', *Fungal Ecology*, 18: 107-14.

Wang, Xinyu, Frank Yonghong Li, Yanan Wang, Xinmin Liu, Jianwei Cheng, Junzhen Zhang, Taogetao Baoyin, and Richard D. Bardgett. 2020. 'High ecosystem multifunctionality under moderate grazing is associated with high plant but low bacterial diversity in a semi-arid steppe grassland', *Plant and Soil*, 448: 265-76.

Whitford, W. G., D. J. Rapport, and A. G. deSoyza. 1999. 'Using resistance and resilience measurements for «fitness» tests in ecosystem health', *Journal of Environmental Management*, 57: 21-29.

Whitford, Walter G., and Fenton R. Kay. 1999. 'Biopedturbation by mammals in deserts: a review', *Journal of Arid Environments*, 41: 203-30.

Wilkinson, Darren A., Gordon C. Grigg, and Lyn A. Beard. 1998. 'Shelter selection and home range of echidnas, Tachyglossus aculeatus, in the highlands of south-east Queensland', *Wildlife research (East Melbourne)*, 25: 219.

Willem Erisman, Jan, Nick van Eekeren, Jan de Wit, Chris Koopmans, Willemijn Cuijpers, Natasja Oerlemans, and Ben J. Koks. 2016. 'Agriculture and biodiversity: a better balance benefits both', *AIMS agriculture and food*, 1: 157-74.

Wintle, Brendan A., Natasha C. R. Cadenhead, Rachel A. Morgain, Sarah M. Legge, Sarah A. Bekessy, Matthew Cantele, Hugh P. Possingham, James E. M. Watson, Martine Maron, David A. Keith, Stephen T. Garnett, John C. Z. Woinarski, and David B. Lindenmayer. 2019. 'Spending to save: What will it cost to halt Australia's extinction crisis?', *Conservation letters*, 12: n/a.

Woinarski, J. C., A. A. Burbidge, and P. L. Harrison. 2015. 'Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement', *Proc Natl Acad Sci U S A*, 112: 4531-40.

Woinarski, J. C. Z., A. A. Burbidge, Peter Harrison, and Damian John Milne. 2014. *The action plan for Australian mammals 2012* (CSIRO Publishing: Melbourne).

Wright, Justin P., and Clive G. Jones. 2004. 'Predicting Effects of Ecosystem Engineers on Patch-Scale Species Richness from Primary Productivity', *Ecology*, 85: 2071-81.

Wright, Justin P., Clive G. Jones, and Alexander S. Flecker. 2002. 'An Ecosystem Engineer, the Beaver, Increases Species Richness at the Landscape Scale', *Oecologia*, 132: 96-101.

Zosky, Kerry L., Adrian F. Wayne, Kate A. Bryant, Michael C. Calver, and Fiona R. Scarff. 2017. 'Diet of the critically endangered woylie (Bettongia penicillata ogilbyi) in south-western Australia', *Australian Journal of Zoology*, 65: 302.