Neilly, Heather Louise (2017) ***Balancing beef with biodiversity: faunal responses to different cattle grazing strategies.*** **PhD Thesis, James Cook University.**

https://doi.org/10.25903/5bc919b6c5274

Balancing Beef with Biodiversity:
Faunal responses to different cattle grazing strategies

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A thesis submitted for the degree of Doctor of Philosophy
College of Science and Engineering
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December 2017

Acknowledgments

This research has been generously funded by Meat and Livestock Australia and the Holsworth Wildlife Endowment, with in-kind support from the DAF QLD. I have been supported by an Australian Postgraduate Award and a top-up scholarship from Meat and Livestock Australia. Many thanks to the JCU Graduate Research School for support and fantastic professional development opportunities.

My fieldwork was only possible with the kind hospitality of Michael and Michelle Lyons of 'Wambiana'. You shared your home and family (Tom, Connor, Sophia and Hugh) with me and my field assistants. You fed us, housed us and taught us a huge amount about the northern beef industry.

I am indebted to Peter O'Reagain and John Bushell for their generous wisdom and provision of logistical support. Many individuals were involved in fieldwork: Richard Duffy, Rachel Duffy, Ben Muller, Stephen Zozaya, Lexie Edwards, Eric Nordberg, Arnaud Gourret, Ken Neal, Roderick Budd and Hannah Jones. Special thanks to Lexie for her help. Hannah spent many hours sorting invertebrates in the lab, I am truly grateful. Eric, thankyou for being a sounding board, the voice of reason and willing participant in many hair-brained schemes (eg. vegetation surveys). Thankyou everyone, it was so much fun!

To my primary supervisor, Lin Schwarzkopf, you are an inspirational academic and personal role model. Pretty much everything you said turned out to be right! Your support has been steadfast and steadying, I feel very lucky to have been your student. Thankyou to my secondary supervisor, Jeremy Vanderwal, for thought provoking conversations, exposing me to great opportunities and introducing me to research areas outside of my comfort zone.

Thankyou to my parents, Gavin and Sue, for always offering support and encouragement, particularly with pursuing higher education. You taught me to always have a go, that there

was always a way and that failure is always an option (and a good learning opportunity). Kerry and Peter, thanks for your moral support and help with babysitting while I was in the field.

This thesis is dedicated to Jason. For your unwavering support and belief in my abilities and your unequivocal optimism. Four years, two babies, a house, a business, a supreme balancing act! Immy and Bea your love has been enormous.

Statement of Contribution of Others

Nature of Assistance	Contribution	Names, Titles and Affiliations of Co-Contributors
Intellectual support	Proposal writing Data Analysis Statistical support Editorial assistance	Prof Lin Schwarzkopf – College Science and Engineering, James Cook University Townsville Prof Jeremy Vanderwal– College Science and Engineering, James Cook University Townsville Dr Peter O'Reagain – QLD Department Agriculture and Fisheries, Charters Towers
Financial support	Field research and travel expenses Stipend Conference attendance grant	Meat and Livestock Australia – Project funding and Top-up scholarship Holsworth Research Endowment Australia Postgraduate award - Australian Government James Cook University - College of Science and Engineering
Data collection	Field assistants	P. O'Reagain, J. Bushell, R. Budd, R. Duffy, L. Edwards, A. Gourret, S. Hart, H. Jones, B. Muller, K. Neal, E. Nordberg, S. Zozaya

Ethics

This research was conducted under the JCU Animal Ethics Committee Approval Number A2037 and under QLD Department of Environment and Heritage Protection, Scientific Purposes permit WISP14499114.

Publication Co-authors

Chapter No.	Details of publication(s) on which chapter is based	Nature and extent of the intellectual input of each author, including the candidate
1	Neilly, H., Vanderwal, J. & Schwarzkopf, L. (2016) Balancing biodiversity and food production: A better understanding of wildlife response to grazing will inform off-reserve conservation on rangelands. *Rangeland Ecology & Management*. 69: 430-436.	The authors co-developed the topic of this essay. HN reviewed the literature and lead the writing of the paper. All authors contributed critically to the drafts and gave final approval for publication.

3	Neilly, H. & Schwarzkopf, L. (accepted; in press) The impact of different cattle grazing regimes on tropical savanna bird assemblages. *Austral Ecology*.	The authors co-developed the research question. HN collected the data, analysed the data and lead the writing of the manuscript. HN developed the figures and tables. Both authors contributed critically to the drafts and gave final approval for publication.
4	Neilly, H. & Schwarzkopf, L. (2017) The response of an arboreal mammal to livestock grazing is habitat dependant. *Scientific Reports* 7(1), 17382.	The authors co-developed the research question. HN collected the data, analysed the data and lead the writing of the manuscript. HN developed the figures and tables. Both authors contributed critically to the drafts and gave final approval for publication.
5	Neilly, H. & Schwarzkopf, L. (2018) Heavy livestock grazing negatively impacts a marsupial ecosystem engineer. *Journal of Zoology* 305(1), 35-42.	The authors co-developed the research question. HN collected the data, analysed the data and lead the writing of the manuscript. HN developed the figures and tables. Both authors contributed critically to the drafts and gave final approval for publication.
6	Neilly, H., Nordberg, E., Vanderwal, J. & Schwarzkopf, L. (2018) Arboreality increases reptile community resistance to disturbance from livestock grazing. *Journal of Applied Ecology* 55(2), 786-799.	The authors co-developed the research question. HN and EN collected the data, and performed all analyses. HN and EN developed the figures and tables. HN lead the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.
7	Neilly, H., O'Reagain, P., Vanderwal, J. & Schwarzkopf, L. (2018) Profitable and sustainable cattle grazing strategies support reptiles in a tropical savanna rangeland. *Rangeland Ecology & Management* 71(2), 205-212.	The authors co-developed the research question. PO collected the profitability and land condition data, HN collected the reptile data, and performed all analyses. HN developed the figures and tables. HN lead the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Abstract

Native wildlife is protected in national parks and reserves, but it is becoming increasing clear that these areas are not large enough to protect biodiversity into the future. There is great potential for rangelands, used for livestock grazing, to be managed in ways that not only provide profits for graziers but also maintain the ecological processes that support native wildlife. This concept is known as ‘off-reserve conservation’. To make recommendations about the best way to achieve off-reserve conservation, we first need to understand how fauna respond to different grazing strategies and how this relates to profitability.

I examined the bird, mammal and reptile communities at an experimental grazing trial (established in 1997) in north Queensland. I aimed to find out how these fauna communities responded to four different grazing strategies and two vegetation types and determine whether a trade-off existed between economic performance, land condition, and biodiversity. Twice a year, over three years, I conducted aural and visual bird surveys, mammal cage trapping and reptile pitfall and funnel trapping. Additionally, I measured terrestrial and arboreal microhabitats at each survey site.

I found that the effect of grazing on wildlife is complex and can be strongly influenced by the vegetation type and seasonal rainfall. I found that abundance and richness can sometimes mask more complex community compositional changes. Overall, reptile abundance responded negatively to heavy grazing. In birds, reptiles and mammals I identified species that benefited from heavy grazing, those negatively influenced by heavy grazing, and species that showed no response to the grazing treatments. In some species, microhabitat selection was a strong driver of grazing response. I found that there was no trade-off between reptiles and profitability: the heavily grazed treatment was the least profitable, and also had the lowest number of reptiles.

My research shows that biodiversity can be maintained in grazing strategies that also have high profitability. As such, economically sustainable red meat production and conservation on rangelands are not necessarily opposing goals. Conserving native wildlife on rangelands is important due to the ecosystem services that wildlife can provide e.g. maintaining soil health, pollination, seed dispersal and insect pest control. For corporate graziers, using sustainable grazing practices and maintaining native wildlife populations suggests excellent stewardship and may be highly valued by consumers.

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Balancing biodiversity and food production: A better understanding of wildlife response to grazing will inform off-reserve conservation on rangelands

Introduction

Protected areas are increasingly considered inadequate, on their own, to conserve biodiversity into the future (Margules and Pressey 2000). ‘Off-reserve’ conservation in areas with an alternative primary land use is a way to complement existing reserve systems (Fischer 2011). Rangelands used for domestic livestock grazing provide an ideal opportunity for off-reserve conservation. For rangelands to serve a dual purpose (i.e., food production and conservation), positive outcomes for the primary land user must be maintained whilst protecting the ecological processes that support biodiversity (Norris 2008). Therefore, it is not only important to understand the impacts of domestic livestock grazing on biodiversity but to combine ecological knowledge with economic and social data (Eyre et al. 2011).

On rangelands, the response of vegetation to grazing has been studied in detail (Díaz et al. 2007; Landsberg et al. 2003) however, the response of vertebrate fauna is complex and less well understood. The research that has been done focuses on high contrast treatments (e.g. Knox et al. 2012; Pafilis et al. 2013; Rickart et al. 2013). Under high intensity grazing regimes, faunal diversity is generally reduced (e.g. Dorrough et al. 2012). However, there are relatively few detailed enquiries into the effects of more moderate levels of grazing. Under moderate intensity grazing, overall faunal diversity may remain relatively constant or may even increase (Lusk and Koper 2013; Martin and McIntyre 2007). The effect of moderate levels of grazing on faunal communities deserves further attention, as this is likely to be where a balance between food production and conservation could be achieved.

Overall measures of biodiversity, such as abundance and species richness, provide insight into faunal response to grazing but may be misleading. These measures can remain constant while the community composition shifts as different species increase or decrease in abundance. Community compositional changes, and the responses of individual species to grazing are, arguably, more important than overall biodiversity measures for informing off-reserve conservation on rangelands (Derner et al. 2009). This is especially true if conservation goals include protecting certain species or encouraging particular assemblages.

So far, research has highlighted the differences between heavy grazing and low or no grazing but we still don't know how *best* to graze rangelands. We need to further understand faunal responses to grazing, however there are challenges involved in collecting the data that will inform off-reserve management strategies. These include: 1) designing experiments at the appropriate scale that will examine faunal responses at moderate levels of grazing, taking into account the complex abiotic and biotic processes that occur on rangelands, and 2) relating this information to food production outcomes, including the economic and social implications of particular management actions. In overcoming these challenges, strategies for off-reserve conservation on rangelands could be developed.

The aim of this review is to broadly synthesize the current global knowledge on the impact of grazing by domestic livestock on terrestrial vertebrate fauna. I highlight the relative lack of research on the impact of grazing between high and low extremes, asserting that this area of moderate grazing intensity is critical for informing off-reserve conservation on rangelands. Finally, I provide direction for future research, arguing that experimental grazing trials could facilitate a multi-disciplinary approach to data collection and inform conservation management strategies on rangelands.

Why are rangelands suitable for off-reserve conservation?

Anthropogenic disturbances such as agriculture, influence biodiversity, often reducing it or changing the assemblage structure (Laurance et al. 2014). Livestock grazing is the most widespread land-use in the world. It occurs on 25% of the global land surface including semi-arid and arid zones, and tropical and temperate regions (Asner et al. 2004). Most livestock grazing takes place on rangelands. Rangelands are defined here as open country that naturally produces forage plants suitable for grazing of domestic livestock or wild animals.

Although rangelands are primarily used for food production, the importance of these vast areas in terms of conservation cannot be overlooked. Indeed, there is fierce debate about the best way to achieve conservation and food production objectives on agricultural land (Hodge et al. 2015; Norris 2008; Phalan et al. 2011). ‘Land sharing’ is where dual land-use occurs over large areas, generally with lower intensity agriculture, whereas ‘land sparing’ refers to higher intensity agriculture over smaller areas, with areas set aside solely for conservation purposes (Phalan et al. 2011).

There is high potential for ‘land sharing’ to be successful on rangelands. In contrast to intensive agricultural practices like cropping, rangelands may be relatively ‘intact’ (McIntyre and Hobbs 1999). Additionally, their sheer size means that management changes could have major biodiversity implications on a large scale.

An understanding of faunal response to various levels of grazing could also help with management of protected areas. While it is implied that protected areas exclude livestock, this is not always the case. In many situations, livestock can exist at relatively high densities inside protected areas, whether managed intentionally (Porter et al. 2014; Williamson et al. 2014) or as feral animals. Removal of feral livestock may be expensive and difficult to achieve, so understanding their impact on fauna could assist with protected area management. The fact that domestic livestock grazing occurs ‘on-reserve’ as well as ‘off-reserve’, suggests that a flexible view of land sharing and/or sparing is required when considering the interface between conservation and agriculture (Kremen 2015).

It is also important to consider that many rangeland systems have an evolutionary history with herbivory and are disturbance–dependent (Fynn et al. 2015; Knapp 1999). Additionally, the presence of domestic livestock alongside native herbivores creates a cumulative grazing pressure (e.g. Ash and Smith 2003). Therefore, the capacity of a rangeland system to tolerate domestic livestock grazing will depend on the evolutionary history of herbivory at that location and the existing native herbivore grazing pressure. Because of these factors, the management strategies required to achieve off-reserve conservation are likely to be system-specific.

Impact of livestock grazing on the landscape

The specific set of agricultural management practices associated with grazing constitute a grazing regime. Stocking rates are managed according to the pre-existing land condition and the system productivity (i.e. rainfall) and can be manipulated by fencing and watering point configurations. Grazing may be continuous, seasonal or rotational with intermittent spelling, and different livestock are sometimes grazed together in mixed flocks. Fire is commonly used in conjunction with grazing to promote new growth and suppress undesirable shrub or woody encroachment in grasslands (Bock et al. 2011; Gregory et al. 2010). Additionally, woody growth may be mechanically or chemically removed. In grasslands this is generally to combat encroachment, whereas in open woodlands, existing trees may be thinned or cleared to promote grass growth and assist with livestock movement through the landscape (Asner et al. 2004). In some areas, forage plant abundance and growth is promoted with the application of fertilizer and the introduction of exotic grasses (Kutt and Fisher 2011). The management practices associated with grazing combine with the effect of grazing itself to create a cumulative impact on the landscape and determine the overall ‘disturbance intensity’. The inherent complexity of grazing regimes is one reason it has been difficult for previous grazing studies to reach clear conclusions and translate these into management recommendations.

Grazing has an effect on the composition, structure and functioning of ecosystems. Heavy grazing can profoundly alter the abiotic and biotic components of a system through: 1) removal of vegetation via herbivory, altering vegetation structure and floristics; 2) trampling, leading to soil compaction and destruction of the soil crust, or, 3) the input of nitrogen (Graetz and Tongway 1986). Indirectly, grazing may change competition and predator/prey dynamics, leading to a change in food web structure (e.g. Knox et al. 2012; Pafilis et al. 2013; Pettigrew and Bull 2014).

The response of vegetation to grazing has been studied in detail (Díaz et al. 2007; Landsberg et al. 2003). Changes in soil nutrients and the soil microbiotic crust due to concentrated grazing have been commonly observed and occur relatively rapidly (Eldridge et al. 2011). The destruction of the microbiotic crust through livestock trampling has implications for water infiltration and seed germination (Eldridge and Greene 1994; Facelli and Springbett 2009; Prasse and Bornkamm 2000). Heavy grazing generally favours annuals over perennials and those plant species that are short and prostrate with a stoloniferous or rosette architecture (Díaz et al. 2007). The resulting vegetation structure is simplified and more open with a higher proportion of bare ground (Landsberg et al. 2003). In some grazing regimes the vegetation structure is further altered by tree clearing or the introduction of exotic grasses (Dorrough et al. 2012; Germano et al. 2012; Martin and McIntyre 2007). This knowledge of plant diversity response to grazing has facilitated the development of generalised models.

Response curves of plant diversity to grazing were proposed a number of decades ago (Milchunas et al. 1988) and built upon in more recent times (Cingolani et al. 2005). It is generally accepted that vegetation heterogeneity is highest under low to moderate levels of grazing but lowest when grazing is very low or high and the extent of the effect depends on the evolutionary history of herbivory and its interactions with other biotic and abiotic factors (Milchunas et al. 1988). Response curves of vertebrate faunal diversity do not exist. It could be assumed they will closely follow plant diversity response, however this has not been tested for vertebrate fauna, and appears not to be the case for invertebrate fauna. In a global review, van Klink *et al* (2014) found that overall, increasing grazing intensity has a negative effect on arthropod diversity. In addition, arthropod diversity responds more negatively to grazing than plant diversity (Rambo and Faeth 1999; van Klink et al. 2014). It is reasonable to suggest that vertebrate fauna diversity responses to grazing will also differ from plant diversity responses.

Effect of grazing on vertebrate fauna

The extent to which species are influenced by grazing will depend on how much they rely on the niches affected by grazing (Milchunas et al. 1988). Grazing can directly alter important structural habitat features at ground level (Brown et al. 2011; Eldridge et al. 2011; Smith et al. 1996). This can positively or negatively affect the ability of fauna to find shelter or thermoregulate, avoid predation, and access food. Community food webs can be altered if changes to vegetation structure alter predator efficiency or abundance and prey availability (Bleho et al. 2014). Additionally, vertebrate responses to grazing interact with their response to the use of non-native grasses (Germano et al. 2012; Kutt and Fisher 2011; Smyth et al. 2009), tree clearing (Brown et al. 2011; Dorrough et al. 2012; Martin and McIntyre 2007) and fire (Fuhlendorf et al. 2006; Kutt and Gordon, 2012). Depending on their niche, some species will be more affected by these additional elements of a grazing regime, instead of livestock grazing itself.

Fire and grazing are inextricably linked in many rangeland systems, and their interaction has an important effect on vertebrate communities (e.g. Fuhlendorf et al. 2006; Kutt and Gordon 2012). Wildfires and grazing by native herbivores both play a role in maintaining the heterogeneity of vegetation structure and supporting the faunal diversity that relies on this heterogeneity (Fuhlendorf and Engle 2001). However, with the introduction of domestic livestock grazing, natural fire and grazing regimes are often altered. Additionally, the interaction between grazing and fire is complex; herbivory can affect fire behaviour and post-fire recovery (Davies et al. 2016) and fire influences grazing patterns. Changes to natural grazing and fire regimes can produce a more homogenous vegetation structure and therefore less habitat variability for fauna (Fuhlendorf and Engle 2001). The effect of the interaction between grazing and fire is often considered more important than either of these factors alone (Fuhlendorf et al. 2009; Kutt and Woinarski 2007).

On a global scale, heavy livestock grazing and associated management actions have been implicated in the decline of vertebrate species richness and abundance (Donald et al. 2001). In many studies, reptile abundance clearly declines at high grazing intensity (Castellano and Valone 2006; Eldridge et al. 2011; Hellgren et al. 2010; James 2003; Kutt and Woinarski 2007; Pafilis et al. 2013; Woinarski and Ash 2002). There is a substantial body of evidence that grazing leads to a reduction in small mammal abundance in North America (Bock et al. 2006; Fleischner 1994; Johnston and Anthony 2008; Rickart et al. 2013; Valone and Sauter 2005), South America (Tabeni and Ojeda 2003), Africa (Keesing 1998; McCauley et al. 2006; Monadjem 1999), New Zealand (Knox et al. 2012) and Australia (Kutt and Gordon 2012; Legge et al. 2011; Read and Cunningham 2010). In the last century a startling decline in birds has been observed in the South and North American grasslands (Azpiroz et al. 2012; Brennan and Kuvlesky 2005; Rahmig et al. 2009) and Australia’s temperate wheat and sheep zone (Attwood et al. 2009). In most cases, such declines are due to the cumulative effects of widespread habitat destruction, intensifying land use, and a lack of refugia; driven at least in part by grazing management practices (Donald et al. 2001).

Conversely, some vertebrate groups show little response or even benefit from heavy grazing. In the arid zones of Australia and North America, reptiles often do not respond to grazing, suggesting resilience (Frank et al. 2013; Germano et al. 2012; Read 2002; Read and Cunningham 2010). Likewise, generalist arboreal reptiles apparently benefit from heavy grazing (Brown et al 2011; Woinarski and Ash 2002; James 2003; Kutt and Fisher 2011; Eyre et al. 2009b). Some mammal species are facilitated by grazing, either through a long evolutionary history with ungulate herbivores, or as an indirect response to associated land management activities, such as increased water availability (Munn et al. 2014). In grazed open woodlands, birds are typically more responsive to tree clearing than grazing (Dorrough et al. 2012; Ludwig et al. 2000; Martin and McIntyre 2007), and in some locations, grazing alone has little effect or may even be beneficial to bird abundance and species richness, provided trees are not cleared (Evans et al. 2006a; Lusk and Koper 2013; Martin and McIntyre 2007).

Relatively few studies examine faunal response at multiple levels of grazing (Table 1.1). Where entire vertebrate groups have been sampled over multiple grazing intensities, species richness can remain unchanged as grazing intensity increases, but the community assemblage generally shifts (Eyre et al. 2009a; Kutt et al. 2012; Martin and McIntyre 2007; Read and Cunningham 2010). The response of birds to moderate levels of grazing has received the most attention (Eyre et al. 2009b; Johnson et al. 2011; Martin and McIntyre 2007; Rahmig et al. 2009; Wallis De Vries et al. 2007). Bird species associated with disturbance increase in abundance as grazing intensity increases (Eyre et al. 2009a; Kutt et al. 2012). While low levels of grazing will affect some sensitive bird species, bird richness can be maintained at moderate levels of grazing (Johnson et al. 2011; Martin and McIntyre 2007). Other studies have examined the response of individual species' abundance to moderate grazing intensities.

For example, ground squirrel (*Spermophilus* spp) and badger (*Taxidea taxus*) abundances had almost linear and opposite responses to increased grazing intensity (Bylo et al. 2014). A lack of holistic data on entire vertebrate faunal communities and how they respond to multiple levels of grazing, impedes our ability to formulate landscape-scale management strategies for rangelands.

Table 1.1 A summary of recent vertebrate response grazing studies, indicating the use of grazing treatments.

Grazing treatments in vertebrate response studies	References
Grazed versus long ungrazed areas: grazing exclosure	Kutt and Woinarski 2007; Blevins and With 2011; Bock et al. 2011; Wasiolka and Blaum 2011; Germano et al. 2012; Rickart et al. 2013; Lusk and Koper 2013; Pafilis et al. 2013
Grazed versus long ungrazed areas: protected land	Woinarski and Ash 2002; Kutt and Gordon 2012
Grazed versus recently ungrazed (e.g. after cattle removal) with sampling at different intervals after grazing removal	Vial et al. 2011; Legge et al. 2011; Kutt et al. 2013; Whitehead et al. 2014
Different levels of grazing	Martin and McIntyre 2007; Eyre et al. 2009a; Hellgren et al. 2010; Read and Cunningham 2010; Kutt et al. 2012; Bylo et al. 2014; Kay et al. 2016

Often, even when grazing studies do include multiple levels of grazing, the focus stays on the changes between the highest contrast treatments. Of course, when no obvious patterns can be seen among other treatment levels, this makes for more clear-cut results and relates directly to land-use differences. But by focusing on extremes we may be missing more nuanced community responses at moderate grazing levels. Where whole vertebrate groups are studied, conservation biologists need to examine compositional changes in more detail. Specific compositional changes, and the responses of individual species to grazing may be more important than overall biodiversity measures for informing off-reserve conservation on rangelands. This is especially important if conservation goals include protecting a certain species or encouraging particular assemblages.

Shifts in community composition are driven by a variety of direct and indirect mechanisms (Figure 1.1). Most grazing response mechanisms are suggested or assumed, and very few have been experimentally tested or examined in detail (but see Rosi et al. 2009; Villar et al. 2013). An understanding of the mechanisms behind community compositional change may make it possible to predict species responses to grazing (Martin and Possingham 2005).

Key challenges

A lot of work has been done at a local scale to describe vertebrate fauna community variability, as well as identifying potential mechanisms. We can now move forward with a focus on data collection that translates directly into practical management advice for off-reserve conservation on rangelands. The first key challenge is to understand vertebrate faunal responses between the extremes, and secondly, to correlate this with food production and profitability. Connecting these different datasets would give us the ability to quantify the cost of achieving specific conservation objectives on rangelands. Previous research has been ineffective at meeting these challenges. This is partly due to the inherent complexity faced with the interacting elements of grazing regimes and the limitations faced when designing grazing studies, but also partly due to a focus of biodiversity studies on maintaining biodiversity, rather than balancing biodiversity and food production outcomes.

	Shelter from environmental extremes	Compete for resources	Avoid predation	Find food
Population increasing	• Reptiles with preference for the open habitats and higher ground temperatures (Read and Cunningham 2010; Read 2002; Frank et al. 2013; James 2003).	• Generalist arboreal reptiles (Brown et al. 2011; Woinarski and Ash 2002; James 2003; Kutt and Fisher 2011; Eyre et al. 2009) • Disturbance-tolerant bird species that can out-compete other species (Woinarski and Ash 2002) • Parasitic cowbirds associated with grazing and parasitizing small passerine nests (Goguen and Mathews 2000)	• Arboreal gecko released from predation pressure (Knox et al. 2001) • Kangaroos have benefited from artificial watering points and the removal of a top predator, the dingo, due to a perceived threat to livestock (Letnic et al. 2012) • Predator avoidance strategy relies on unobstructed visibility (Tabeni and Ojeda 2003; Davidson et al. 2010; Bylo et al. 2014)	• Raptor predation facilitated by lower ground cover (Piana and Marsden 2014) • Reptile predators exploit concentration of prey items around watering points (Curry and Hacker 1990) • Reptile ambush predators can see prey approaching from further away (Pettigrew and Bull 2014)
Population decreasing	• Diurnal reptiles associated with leaf litter (Woinarski and Ash 2002; James 2003) • Burrowing reptiles, where burrow structure is compromised by trampling (Kutt and Woinarski 2007; Kutt et al. 2012; Smith et al. 1996)	• Small passerines outcompeted by aggressive species or nests parasitized (Eyre et al. 2009b; Goguen and Mathews 2000)	• Ground-dwelling mammals that rely on complex ground habitat to avoid predation (Keesing 1998; Rosi et al. 2009	• Fossorial mammals and birds (Smith et al. 1996; Kutt and Woinarski 2007) • Habitat availability of ground-dwelling reptile's invertebrate prey (Pafilis et al. 2013) • Food availability and quality for other herbivorous and granivorous mammals (Keesing 1998)

Figure 1.1: A summary of suggested response mechanisms of vertebrate fauna to livestock grazing. The suggested mechanisms are grouped in four categories: 'shelter from environmental extremes', 'compete for resources', 'avoid predation' and 'find food'. These mechanisms may influence species positively and cause them to increase in abundance ('increasers', listed in the upper row). Or species may respond negatively and decrease in abundance ('decreasers', listed in the lower row

Most grazing studies are designed within an existing grazed landscape where paddocks or properties experiencing differing disturbance intensities are sampled (Dorrough et al. 2012; Germano et al. 2012; Knox et al. 2012; Piana and Marsden 2014). These disturbance intensities may be based on stocking rate, livestock dung counts (indicating their use of the area), distance from watering points (i.e. piosphere trials) or some kind of combination. It is difficult to quantify treatment levels, as there are no standard definitions of ‘high’, ‘moderate’ or ‘low’ grazing. The other elements of a grazing regime are a further complication that influence disturbance intensity and can confound the effect of grazing alone (Brennan and Kuvlesky 2005). Furthermore, prior land use, or historical grazing intensities are usually unknown, and the cumulative effect of native herbivores is often neglected. Without a standard means of quantifying treatment levels, it is difficult to compare different grazing studies and make generalizations about vertebrate responses, even if they occur in similar vegetation types.

In an existing grazed environment, manipulation of grazing regime elements is often out of the researcher’s control, with treatment levels limited to what is already there. Piosphere trials have been used to sample plants (Landsberg et al. 2003) and invertebrates (Hoffmann and James 2011) across grazing gradients as they decrease radially away from watering points. While there is great opportunity in such trials to measure multiple levels of grazing across a gradient, these studies are always confounded by proximity to water, a consideration important to vagile fauna. Cross-fence comparisons (e.g. Read 2002; Read and Cunningham 2010) in existing grazed environments can ensure that landscape features are constant across treatments, however the treatment levels must still be estimated or inferred. Ideally, treatment levels could be controlled or manipulated to avoid uncertainty.

Future directions

A different way to study the response of vertebrate fauna to grazing, is to use a large-scale, plot-based experimental manipulations. Landscape scale grazing trials have been used to study the response of vertebrates in Scotland (Dennis et al. 2007; Evans et al. 2006a; Evans et al. 2006b; Evans et al. 2005; Steen et al. 2005; Villar et al. 2014, 2013; Wheeler 2008), Canada (Bylo et al. 2014; Lusk and Koper 2013) and Australia (Kutt et al. 2012). In this situation, stocking rates and grazing regime elements, such as fire, can be manipulated as required. Many of the confounding factors mentioned above can be eliminated, or at least quantified. Importantly, grazing trials create an opportunity to simultaneously measure biodiversity and the economic performance and livestock productivity of the different treatments (O'Reagain et al. 2009, 2011). Grazing trials are usually established by agricultural research bodies for this purpose anyway. If biodiversity surveys are included as an 'add-on' during the planning phase, the multi-disciplinary data sets collected would be very valuable.

Experimental grazing trials have many benefits but they are expensive to establish and maintain at the appropriate spatial and temporal scale. Ideally, grazing experiments need to be over large spatial and temporal scales so that sites are independent and to sample enough climatic variation (Bylo et al. 2014). Since grazing trials have the potential to yield research outcomes across multiple disciplines, there is also an opportunity to share establishment and maintenance costs. Furthermore, large-scale biodiversity surveys can be made more cost effective by utilising new trapping technologies (Garden et al. 2007; Lindenmayer et al. 2012; Perkins et al. 2013; Swan et al. 2014). Remote sensing (Kilpatrick et al. 2011), landscape scale surveillance techniques (Pimm et al. 2015), camera trapping (Meek et al. 2014), affordable GPS collars (Allan et al. 2013), and acoustic survey of birds and frogs (Lellouch et al. 2014) all have the potential to greatly reduce survey costs.

Collaborations between ecologists, agricultural scientists and land managers may be further supported if we can frame ecological questions in a way that is relevant to food production industries. Taking a functional trait-based approach to assessing the response of fauna to grazing may be useful, particularly as functional traits relate to ecosystem services. While functional traits have been widely applied to plants (e.g. de Bello et al. 2012; Díaz et al. 2007; Lavorel et al. 2007), work is being done to use this approach with invertebrate and vertebrate fauna (Davies et al. 2010; Luck et al. 2012; Martin and Possingham 2005).

Finally, it may be beneficial to focus future research on more detailed investigations of compositional changes and species response mechanisms. Community compositional changes, the responses of individual species to grazing, and the mechanisms driving those responses may be more important than overall biodiversity measures for informing off-reserve conservation on rangelands (Derner et al. 2009). With an understanding of response mechanisms, we can improve our predictive capabilities (Martin and Possingham 2005). Consequently, if the response of wild vertebrates to different grazing intensities can be predicted, land management actions could be manipulated to achieve conservation goals that are targeted towards protecting certain species or encouraging particular assemblages. This allows land managers to prioritize their conservation efforts and make them relevant to their specific rangeland system, rather than aiming to simply maximise fauna abundance or diversity.

Management implications

The grazing of domestic livestock on rangelands is a practice that will continue, if not intensify in the future, particularly considering human population growth and the increasing demand for food. With continuing declines in the major vertebrate fauna groups, it appears that areas set aside for conservation will not be enough, by themselves, to conserve vertebrate biodiversity into the future. Rangelands present an opportunity for ‘off-reserve’ conservation, but our ability to manage vertebrate fauna on rangelands is limited by our understanding of their response to varying levels of grazing. It is particularly important to look at more moderate grazing, as this is where agricultural profitability and the goals of off-reserve conservation are most likely to align.

Large, long-term experimental grazing trials are a potential way forward. Along with their many benefits, grazing trials have the potential to generate economic and food production data alongside biodiversity data. This gives us an ability to quantify the economic cost of conserving a particular fauna species or community assemblage, the kind of information that would help when devising land management incentive strategies or ‘payment for ecosystem service’ style schemes (Wegner 2016). While expense is a major barrier to establishing grazing trials, collaborative partnerships between ecologists, agricultural scientists and land managers could help share the costs and ensure that the most useful research outcomes are achieved.

Thesis aims and structure

In this thesis I investigated the impact of four different cattle grazing regimes on bird, mammal and reptile fauna communities, at a long-term experimental grazing trial in north Queensland. I examined the abundance, richness, community composition and individual vertebrate faunal species responses (where relevant) to the grazing treatments, two different vegetation types and rainfall. Additionally, I aimed to quantify the potential trade-off between profitability and conservation on rangelands, by correlating measures of faunal diversity with long-term economic and land condition metrics that have been measured by the Department Agriculture and Fisheries QLD over the life of the trial.

In chapter two, I describe my study site, the Wambiana Grazing Trial. In chapter three, I examined the bird community, particularly how bird foraging guilds and individual species respond to the grazing treatments and microhabitat variables. In chapters four and five I focused on the impact of the grazing treatments and vegetation types on population dynamics, habitat selection and movement of two mammal species, brushtail possums and rufous bettongs, respectively. In chapter six, I tested the response of the terrestrial and arboreal reptile community to grazing treatment, vegetation and season, and modelled individual reptile species associations with microhabitat variables. In chapter seven, I determined the trade-off between cattle production and reptiles by correlating reptile abundance and species richness with 18-year and 3-year gross margin and different land condition metrics. Finally, in chapter eight, the general discussion, I broadly discuss the management implications of this research and directions for future research (Figure 1.2).

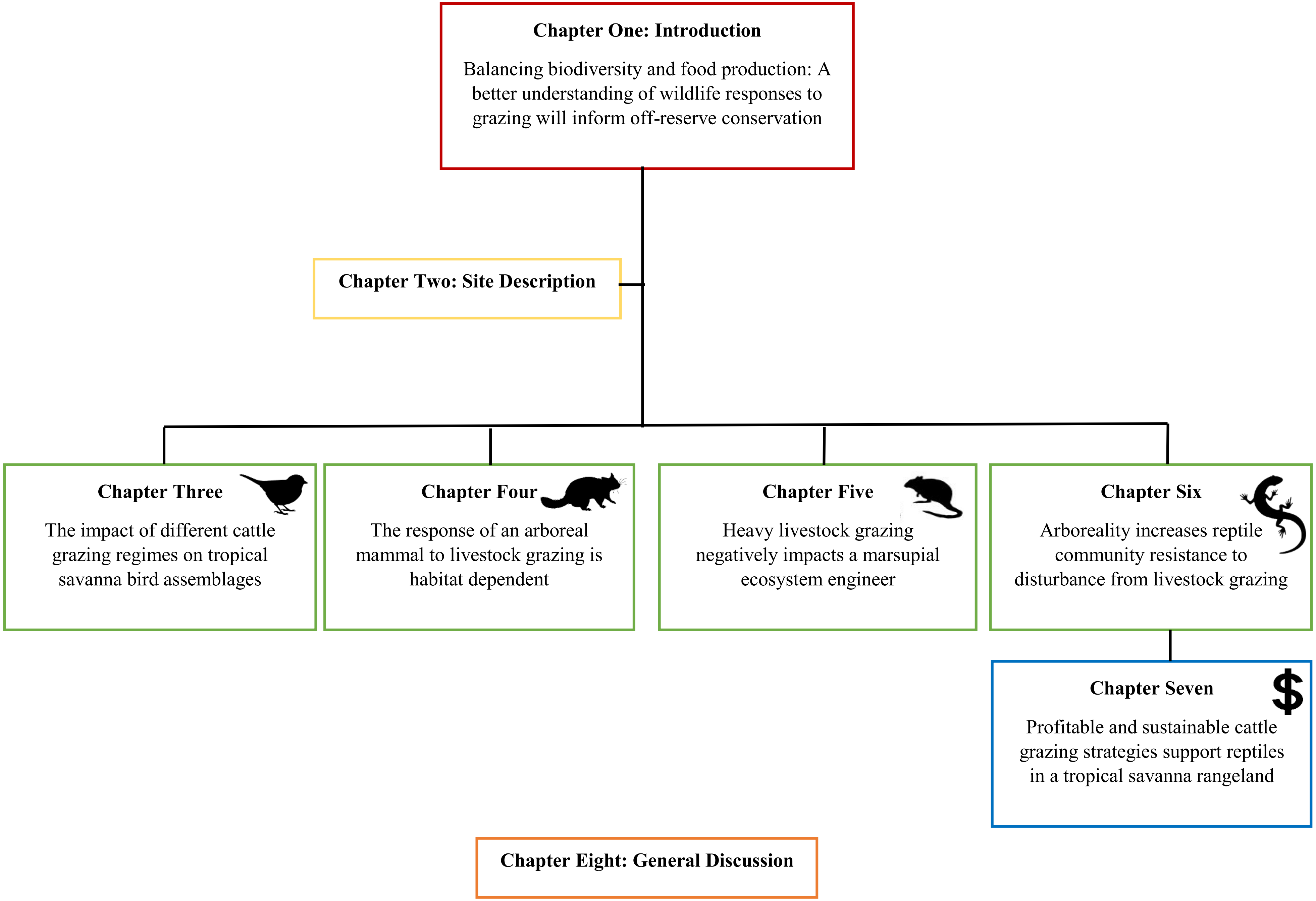


Figure 1.2 Conceptual diagram of thesis structure and chapters

Chapter Two - Site description

The Wambiana grazing trial was established by the Queensland Department of Agriculture and Fisheries in 1997 at ‘Wambiana’, a commercial cattle station (20˚34’S, 146˚07’E), 70 km south of Charters Towers, Queensland, in north-east Australia (Figure 2.1). The property had been grazed by cattle (*Bos indicus*), at relatively moderate stocking rates, since at least the 1870s. The study area was located on relatively flat, low fertility, tertiary sediments within the greater Burdekin River catchment. The region has a distinct summer wet season and winter dry season. Average annual rainfall is 643 mm, but is highly variable (historical range 207-1409 mm) and includes regular droughts.

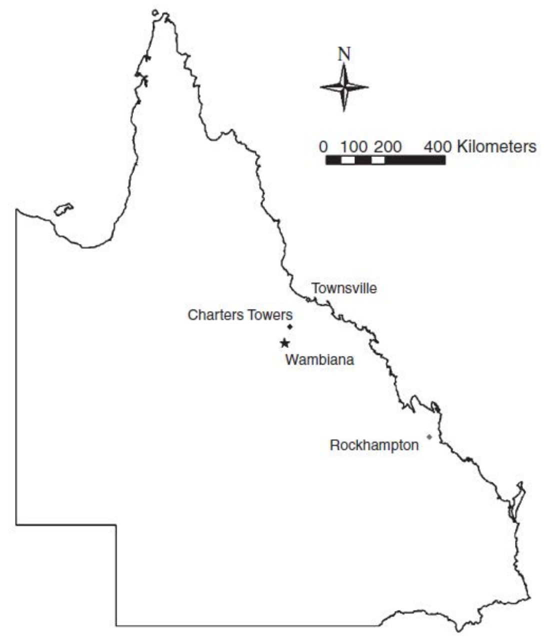


Figure 2.1. Wambiana station is approximately 70 km SW of Charters Towers, QLD (Kutt et al. 2012).

The 1041 ha experimental site consists of 8 paddocks ranging from 93-115 ha in size, with four grazing treatments each replicated twice (Figure 2.2). Twenty-four survey sites were established, six sites within each grazing treatment (survey sites and data collection methods are detailed in specific chapters). Treatments were selected to reflect either typical or recommended management practices in northern Australian rangelands: 1) heavy stocking rate (H) – 4-6 ha · Adult Equivalent-1 (AE, defined as 450 kg steer); 2) moderate stocking rate (M) – 8-10 ha · AE-1; 3) variable stocking rate (V) – stocking rates adjusted annually based on the end of wet season feed availability, range 3-12 ha · AE-1 and; 4) rotational wet season spelling (R) – a third of the paddock spelled each wet season 7-10 ha · AE-1. (O'Reagain et al. 2011). The rationale for each grazing treatment is detailed in Table 2.1. There is no control site at this grazing trial, as the objective is to measure the impacts among different grazing strategies not between grazed and ungrazed areas. Testing different grazing strategies creates an opportunity to make management recommendations about how *best* to graze. Following recommended practice, the entire site was burnt in October 1999 and October 2011 to suppress woody growth. Waterpoints were distributed evenly in each paddock.

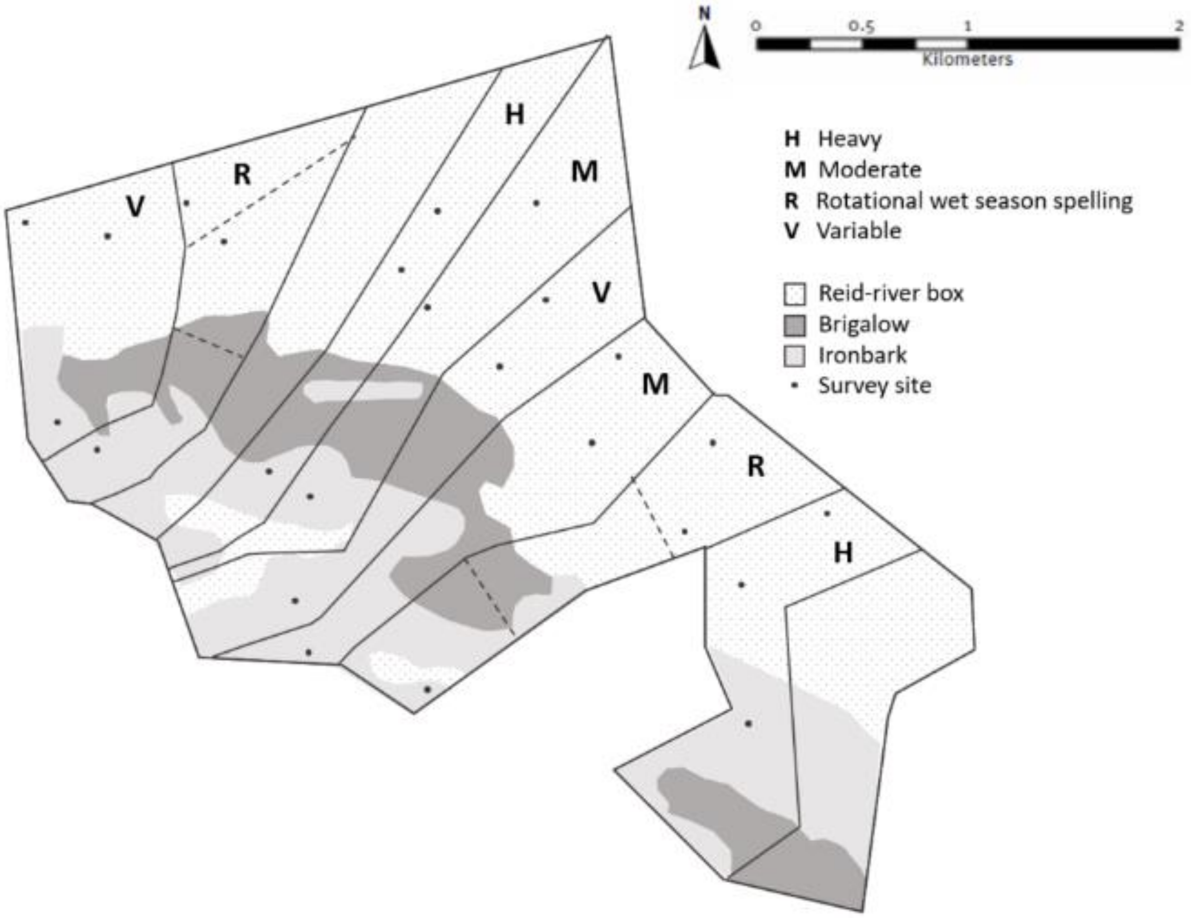


Figure 2.2 The Wambiana grazing trial. Survey sites were located in four different grazing treatments (Heavy, Moderate, Rotational wet-season spelling and Variable) and in two vegetation communities (Reid-river box and Ironbark). A third main vegetation community, characterised by dominant Brigalow, runs in a band through the grazing trial.

Table 2.1 The Wambiana grazing trial grazing treatment stocking rates, and rationale.

Grazing treatment	**Description / stocking rate**	**Rationale**
Moderate (M)	Relatively consistent stocking rate at the Long Term Carrying Capacity (LTCC); 8-10 ha per animal equivalent (AE)	Minimize the risk of over-grazing, maintains land condition
Rotational wet season spelling (R)	Relatively consistent stocking about 50% above the LTCC and ⅓ of the paddock spelled (no grazing) on a rotation basis during the wet season; 7-10 ha per AE	Spelling can buffer against rainfall variability
Variable (V)	Stocking rate adjusted annually at the end of the wet season in accordance with remaining feed availability; 3-12 ha per AE	Stocking rate to match feed availability, which minimize the risk of over-grazing during dry years, but allows heavier stocking rates during wet years
Heavy (H)	Relatively consistent stocking at twice the LTCC; 4-6 ha per AE	Potentially high profitability, especially during wet years

The vegetation consists of open Eucalypt and Acacia savanna woodland underlain by tropical grasses (Figure 2.3). The dominant vegetation communities are: a) Reid River Box (*Eucalyptus brownii*) on texture-contrast soils (sodosols; soil nomenclature follows Isbell & National Committee on Soil and Terrain 1996), with a ground layer of *Bothriochloa ewartiana*, *Dichanthium fecundum*, *Chrysopogon fallax* and various local *Aristida* species; b) Silver Leaf Ironbark (*Eucalyptus melanophloia*) on yellow-brown earths (kandosols) with a ground vegetation of less palatable grass species *Eriachne mucronata* and *Aristida* species but also some areas of *C. fallax* and *Heteropogon contortus*; and c) a small area of Brigalow (*Acacia harpophylla*) woodland on heavy clays (vertosols and grey earths). In the *E. brownii* and *A. harpophylla* vegetation types there is an irregular understory of currant bush (*Carissa ovata*). All paddocks have similar proportions of the main soil types and vegetation communities.

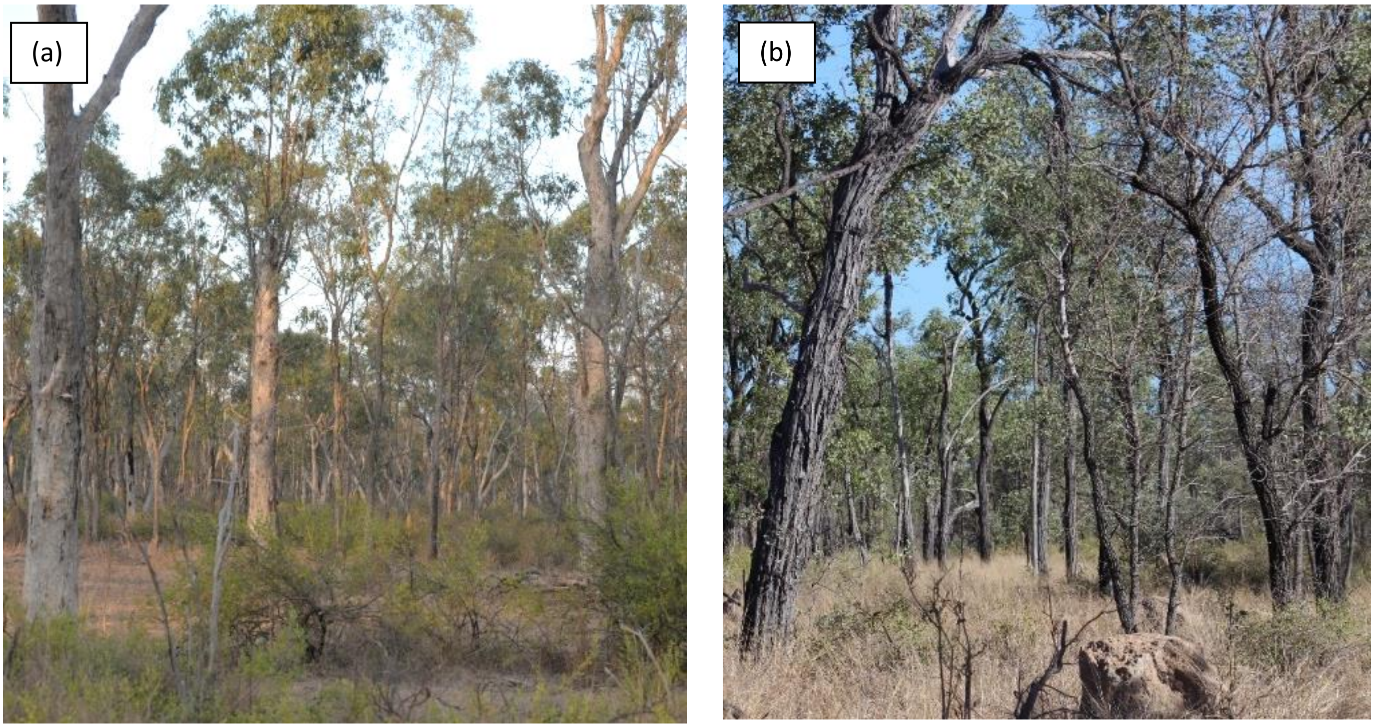


Figure 2.3 a) the Reid River Box (*Eucalyptus brownii*) vegetation community, b) the Silver-leaf Ironbark (*Eucalyptus melanophloia*) vegetation community. The *Acacia harpophylla* vegetation community is not shown as no sites were located within this habitat.

Chapter Three

Adapted from: Neilly, H. & Schwarzkopf, L. (accepted; in press) The impact of different cattle grazing regimes on tropical savanna bird assemblages. *Austral Ecology*.

The impact of different cattle grazing regimes on tropical savanna bird assemblages

Introduction

Avifaunal declines in agricultural areas have been observed globally (Donald et al. 2001; Vickery et al. 2001; Brennan and Kuvlesky 2005; Azpiroz et al. 2012; Rahmig et al. 2009; Attwood et al. 2009). These declines are attributed to the cumulative effect of widespread habitat destruction, intensifying land use and a lack of refugia. In extensive rangelands, used for livestock grazing, birds are typically more responsive to the tree clearing associated with agricultural land use, than grazing itself (Ludwig et al. 2000; Martin and McIntyre 2007; Dorrough et al. 2012). In some locations, grazing alone has little effect or may even be beneficial to bird abundance and species richness provided trees are not cleared (Martin and McIntyre 2007; Evans et al. 2006; Lusk and Koper 2013). Vertebrate responses to grazing are often complex, however, and need to be understood in greater detail to lead to meaningful management recommendations (Chapter 1).

Measures of total bird abundance or assemblage richness may belie community compositional changes, caused by individual species increasing or decreasing in response to grazing. The extent to which individual bird species are affected by grazing depends on how much they rely on the niches affected by grazing (Milchunas et al. 1988). Grazing changes the composition and structure of vegetation, generally producing a simplified, more open ground-layer with a higher proportion of bare ground (Landsberg et al. 2003). This directly changes the structural features available for birds and indirectly influences food availability, for example by altering seed and invertebrate resources (Vickery etal. 2001; van Klink et al. 2014). Species using the ground layer and lower vegetation strata to nest and feed are often less abundant in heavily grazed areas (Kutt et al. 2012; Bock and Bock 1999; Kutt and Fisher 2011; Davies et al. 2010; James 2003; Chapter 6). Conversely, some species benefit from the more open, simplified vegetation structure that heavy grazing tends to promote (Read 2002; Kutt, et al. 2012). Overall, species that use lower habitat strata are likely to be more responsive to grazing (either positively or negatively), than those using higher level habitat strata (Chapter 6). Indeed, the height at which a bird species forages has been used to predict grazing response and response to woody vegetation changes (Martin and Possingham 2005; Kutt and Martin 2010; Tassicker et al. 2006; Shanahan et al. 2011).

Northern Australia is dominated by extensive rangelands used primarily for cattle grazing. Here, tropical savanna bird communities respond to spatial and temporal heterogeneity at multiple scales (Price et al. 2013). Bird community response to livestock grazing is often confounded by vegetation type, local weather patterns and subsequent resource pulses (e.g. flowering or fruiting events). An experimental grazing trial can help to disentangle the effect of livestock grazing and minimise confounding variables (Chapter 1). While the scale of most experimental grazing trials will not capture broad landscape-level responses in bird communities, paddock-level responses to grazing and response mechanisms (such as microhabitat selection) can be investigated.

In this study I examined the impact of four cattle grazing strategies on the savanna bird community at a long-term experimental grazing trial in a northern Australian. I aimed to understand if the bird community composition was shifting in response to the different grazing treatments and predicted that the most responsive bird species would be in the guilds that forage lower to the ground, and are therefore more affected by the livestock grazing disturbance. I examined bird community assemblage responses to the grazing treatments by foraging guilds and also individual species. To examine microhabitat use as a grazing response mechanism, I modelled individual bird species abundance in relation to various measures of terrestrial and arboreal habitat structure.

Materials and methods

This study was conducted at the Wambiana Grazing Trial, see Chapter Two for a detailed site description.

Bird surveys

Twenty-four 1-ha sites were established, i.e. six sites in each grazing treatment. Each site was either in the box or ironbark vegetation community. Over three years (2013, 2014 and 2015) bird surveys were conducted at the end of the wet season (April) and at the end of the dry season (October), for a total of six surveys. At each bird survey, visual and aural observations of bird species' abundance were recorded on eight consecutive mornings. The bird abundance data from the eight consecutive mornings was summed, resulting in a record for each site for each survey (6 surveys at 24 sites, n = 144). On each of the eight consecutive mornings, the observer walked along a fixed 100-m transect through the middle of the site and identified birds seen and heard within the 1-ha site for a period of 5 minutes. This bird survey method has been adapted from a widely used bird survey method for tropical savannas (Perry et al. 2012). The surveys were conducted within four hours after dawn. Differences in bird species detectability among grazing treatments was minimal, in part due to the open structure of savanna woodlands, and also the recording of aural observations as well as visual observations (Kutt and Martin 2010). To minimise observer bias, three observers visited each site an equal number of times during each survey session. Common English and scientific names for birds follow the *WildNet* database (Queensland Government 2015; Table 3.1). Henceforth, bird species will be referred to using common English names.

Microhabitat surveys

Terrestrial and arboreal microhabitat features were measured at each site along 3 x 100 m parallel transects, 50m apart during the 2014 and 2015 surveys. Ground cover was categorised as bare ground, leaf litter >5mm, leaf litter 5-10mm, rock, fine woody debris (<10cm diameter) or coarse woody debris (>10cm diameter). Vegetative cover along the transect was categorised as grass (with grass height also recorded), shrub or tree. Both ground and vegetative cover measures were converted into mean percentages for each site. Additionally, all trees within one metre on either side of the transects were identified, their height and diameter at breast height (DBH) was measured and they were recorded as dead or alive. Mean tree richness and mean number of trees were calculated for each site.

Data analysis

Although it is common to test overall abundance and richness in addition to compositional analyses, I was more interested in the community assemblage and individual species responses to grazing treatments, vegetation type and precipitation. Abundance and species richness may be more relevant to the landscape scale, but for this paddock-scale experiment, it is likely that these metrics are not as useful and detailed analyses are more appropriate (Chapter 1).

Table 3.1: Bird species recorded at the Wambiana grazing trial in the 2013, 2014 and 2015 surveys, categorised in nine foraging guilds (adapted from (Tassicker et al. 2006; Kutt et al. 2004).

Foraging Guild	**Species**
Aerial insectivore (AI)	Black-faced woodswallow *Artamus cinereus* Grey fantail *Rhipidura fuliginosa* Jacky winter *Microeca fascinans* Little woodswallow *Artamus minor* Masked woodswallow *Artamus personatus* Dusky woodswallow *Artamus cyanopterus* Satin flycatcher *Myiagra cyanoleuca* Leaden flycatcher *Myiagra rubecula* Lemon-bellied flycatcher *Microeca flavigaster* White-browed woodswallow *Artamus superciliosus*
Raptor (RA)	Blue-winged kookaburra *Dacelo leachii* Brown falcon *Falco berigora* Torresian crow *Corvus orru* Australian raven *Corvus coronoides* Forest kingfisher *Todiramphus macleayii* Grey butcherbird *Cracticus torquatus* Laughing kookaburra *Dacelo novaeguineae* Pacific baza *Aviceda subcristata* Pied butcherbird *Cracticus nigrogularis* Red-backed kingfisher *Todiramphus pyrrhopygia* Sacred kingfisher *Todiramphus sanctus* Wedge-tailed eagle *Aquila audax* Whistling kite *Haliastur sphenurus*
Foliage insectivore (FI)	Black-faced cuckoo-shrike *Coracina novaehollandiae* Black-eared cuckoo *Chalcites osculans* Brown treecreeper *Climacteris picumnus* Brush cuckoo *Cacomantis variolosus* Cicadabird *Coracina tenuirostris* Pallid cuckoo *Cuculus pallidus* Rufous whistler *Pachycephala rufiventris* Striated pardalote *Pardalotus striatus* Varied sittella *Daphoenositta chrysoptera* Varied triller *Lalage leucomela*

	Weebill *Smicrornis brevirostris* White-throated gerygone *Gerygone olivacea* White-throated treecreeper *Cormobates leucophaeus* White-winged triller *Lalage sueurii* Yellow thornbill Acanthiza lineata Yellow-rumped thornbill *Acanthiza chrysorrhoa*
Foliage insectivore/nectarivore (FIN)	Blue-faced honeyeater *Entomyzon cyanotis* Little friarbird *Philemon citreogularis* Noisy friarbird *Philemon corniculatus* Olive-backed Oriole Oriolus sagittatus Singing honeyeater *Lichenostomus virescens* Striped honeyeater *Plectorhyncha lanceolata* White-throated honeyeater *Melithreptus albogularis* Yellow-throated miner *Manorina flavigula*
Frugivore (FR).	Mistletoebird *Dicaeum hirundinaceum* Spotted bowerbird *Chlamydera maculata*
Nectarivore (NE)	Brown honeyeater *Lichmera indistincta* Rainbow lorikeet *Trichoglossus haematodus*
Ground insectivore (GI)	Grey-crowned babbler *Pomatostomus temporali* Hooded robin *Melanodryas cucullata* Magpie-lark *Grallina cyanoleuca* Red-backed fairy-wren *Malurus melanocephalus* Willie wagtail *Rhipidura leucophrys* Variegated fairy-wren *Malurus lamberti*
Ground insectivore/omnivore (GIO)	Apostlebird *Struthidea cinereal* Australian bustard *Ardeotis australis* Australian magpie *Gymnorhina tibicen* Emu *Dromaius novaehollandiae* Pheasant coucal *Centropus phasianinus*
Granivore (GR)	Bar-shouldered dove *Geopelia humeralis* Budgerigar *Melopsittacus undulatus* Common bronzewing *Phaps chalcoptera* Crested pigeon *Ocyphaps lophotes* Double-barred finch *Taeniopygia bichenovii* Galah *Cacatua roseicapilla* Little button-quail *Turnix velox* Pale-headed rosella *Platycercus adscitus* Peaceful dove *Geopelia striata* Plum-headed finch *Neochmia modesta* Red-tailed black-cockatoo *Calyptorhynchus banksii* Red-winged parrot *Aprosmictus erythropterus* Sulphur-crested cockatoo *Cacatua galerita* Squatter pigeon *Geophaps scripta* Zebra finch *Taeniopygia guttata*

Bird community composition

The abundance of every bird species recorded was collated for each trapping session at each site (n=144). Bird species were categorised into nine foraging guilds (adapted from Tassicker et al. 2006; Kutt et al. 2004; Table 3.1). I constructed a site-by-species table populated by the abundance of each species, and then summed these according to foraging guilds. The differences in bird foraging guild assemblages were examined using a multivariate extension of a generalised linear model (GLM), using the function *manyglm* in the package *mvabund* (Wang et al. 2012). A *manyglm* with negative binomial distribution was applied, with grazing treatment, vegetation type, precipitation and their interactions as the explanatory variables. Precipitation is defined here as the total rainfall (from the Wambiana Grazing Trial weather station) from the 6-month period prior to each survey session. This measure of precipitation is used to account for the response of savanna birds to short-term weather patterns (Reside et al. 2010) and the well-known impact that recent preceding rainfall can have on birds' food resources (Price et al. 2013). The *manyGLM* analysis is an alternative to distance-based multivariate analyses. Multiple GLMs are fitted to many variables simultaneously and an *anova.manyglm* function can be used for hypothesis testing. Univariate test statistics and p-values were calculated for each foraging guild included in the community model to indicate their relative contribution to the overall variance among the communities. Pairwise comparisons were made among the grazing treatments in the significant foraging guilds using the Tukey test in *lsmeans* (Lenth 2016).

This test was then repeated to examine the differences in the bird community species assemblages, using the 15 most abundant bird species. The final models were validated by examining the deviance residuals. To visualise the overall community response to grazing I plotted the standardised model co-efficients from a GLM with LASOO penalties to create a ‘heat-map’ (Brown et al. 2014). Pairwise comparisons were made among the grazing treatments in the significant individual species using the Tukey test in *lsmeans* (Lenth 2016).

Individual species microhabitat associations

Generalised linear models, with either a poisson or negative binomial distribution, were used to analyse the microhabitat associations of individual bird species, using abundance and microhabitat data collected in 2014 and 2015. I chose to model only those species with a significant response to grazing, as identified in the *manyglm* analysis. The optimal models were selected using the Akaike Information Criterion (AICc) from the *dredge* function in *MuMIn* (Bartoń 2015). The optimal models were validated by examining the deviance residuals.

Results

Over the six bird surveys, 6251 birds were observed in diurnal surveys, comprising 78 different species. Precipitation (6-months prior to survey) varied throughout the three-year period: April 2013 – 438 mm, October 2013 – 131 mm, April 2014 – 477 mm, October 2014 – 67 mm, April 2015 – 208 mm, October 2015 – 3 mm. In April 2014, after the wettest preceding 6 months, *Carissa ovata* was fruiting but this was uniform across all sites and no mass flowering events were observed during any of the survey periods.

The differences in bird foraging guild assemblage were explained by grazing treatment, precipitation and vegetation type (Table 3.2). None of the interactions between the variables were significant. The significant grazing treatment response was driven by the ground insectivore and ground insectivore/omnivore guilds (Figure 3.1). Ground insectivores were highest in the moderate and rotational wet season spelling treatments and significantly lower in the variable and heavy treatments. Ground insectivores/omnivores were highest in the heavy treatment, significantly lower in the moderate and variable treatments and there was no significant difference between the heavy and rotational wet season spelling treatments. Foliage insectivore/nectarivores and frugivores were the only guilds to be significantly affected by precipitation. Foliage insectivores, foliage insectivore/nectarivores, granivores and nectarivores drove the significant response to vegetation type. The two guilds that forage at the highest vegetation strata (aerial insectivores and raptors), did not influence the significant response of any of the explanatory variables.

Similarly, the fifteen most abundant bird species were analysed in a multivariate GLM. Grazing treatment, vegetation type, precipitation and the vegetation type precipitation interaction were significant explainers of compositional change (Table 3.3). Four species contributed significantly to the grazing treatment response: the Australian magpie, double-barred finch, grey-crowned babbler, and red-backed fairy-wren, and the black-faced cuckoo-shrike was approaching significance (Table 3.3). Other species showed varying responses to vegetation type, precipitation and their interaction. As grazing treatment did not interact with vegetation type or precipitation we can visualise the bird species' grazing treatment responses in a 'heat-map', plotting standardised model co-efficients from the *manyGLM* model (Figure 3.2). The species were grouped by foraging guild with the ground-feeding guilds at the bottom, followed by foliage-feeding guilds and then aerial-feeding guilds. The strongest associations are visible in the ground-feeding guilds.

Table 3.2: The ManyGLM analysis testing the relationship between bird foraging height assemblages and grazing treatment, vegetation type and precipitation (total in the 6 months prior to survey) and their interactions. The p values of the variables in the optimal model are given, first for the multivariate community analysis, and then broken down by individual foraging guild contribution. AI – aerial insectivore, FI- foliage insectivore, FIN – foliage insectivore/nectarivore, FR- frugivore, GI – ground insectivore, GIO – ground insectivore/omnivore, GR – granivore, NE – nectarivore, RA – raptor.

		Individual foraging guild contributions (p-value)								
Optimal model	Overall p-value	AI	FI	FIN	FR	GI	GIO	GR	NE	RA
Grazing treatment	0.014*	0.553	0.135	0.198	0.778	0.001*	0.021*	0.493	0.311	0.895
Precipitation	0.039*	0.570	0.105	0.050*	0.004*	0.820	0.968	0.429	0.130	0.668
Vegetation type	0.001*	0.821	0.008*	0.045*	0.061	0.346	0.354	0.001*	0.031*	0.659

Table 3.3: The ManyGLM analysis testing the relationship between bird species assemblages and grazing treatment, vegetation type and precipitation (total in the 6 months prior to survey) and their interactions. The p values of the variables in the optimal model are given, first for the multivariate community analysis, and then broken down by individual species contribution.

Optimal model	Overall p-value	Apostle bird	Australian magpie	Black-faced cuckoo-shrike	Double-barred finch	Grey-crowned babbler	Jacky winter	Little friarbird	Noisy friarbird	Pied butcherbird	Red-backed fairy-wren	Rufous whistler	Striated pardalote	Weebill	White-throated gerygone
Grazing treatment	0.002*	0.457	0.008*	0.063	0.013*	0.043*	0.719	0.515	0.736	0.594	0.001*	0.690	0.482	0.548	0.936
Vegetation type	0.001*	0.385	0.558	0.033*	0.623	0.893	0.036*	0.026*	0.245	0.523	0.074	0.004*	0.647	0.004*	0.041*
Precipitation	0.001*	0.408	0.112	0.672	0.092	0.347	0.001*	0.007*	0.454	0.951	0.256	0.771	0.004*	0.001*	0.001*
Precipitation * Vegetation type	0.017*	0.229	0.427	0.139	0.466	0.128	0.029*	0.383	0.037*	0.122	0.035*	0.194	0.038*	0.349	0.698

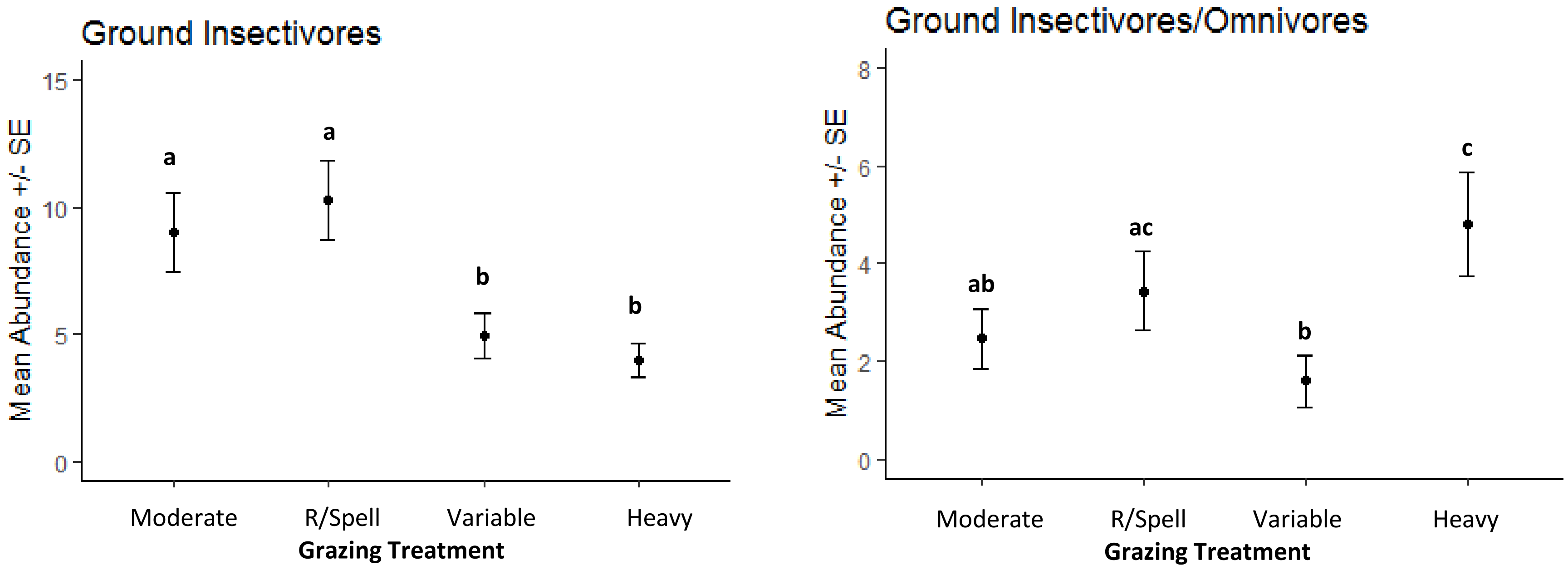


Figure 3.1: Mean bird abundance ± S.E for Ground Insectivores and Ground Insectivore/Omnivores among the four grazing treatments. Post hoc Tukey tests were used to examine the effect of each factor level and significant differences ($p<0.05$) are reported.

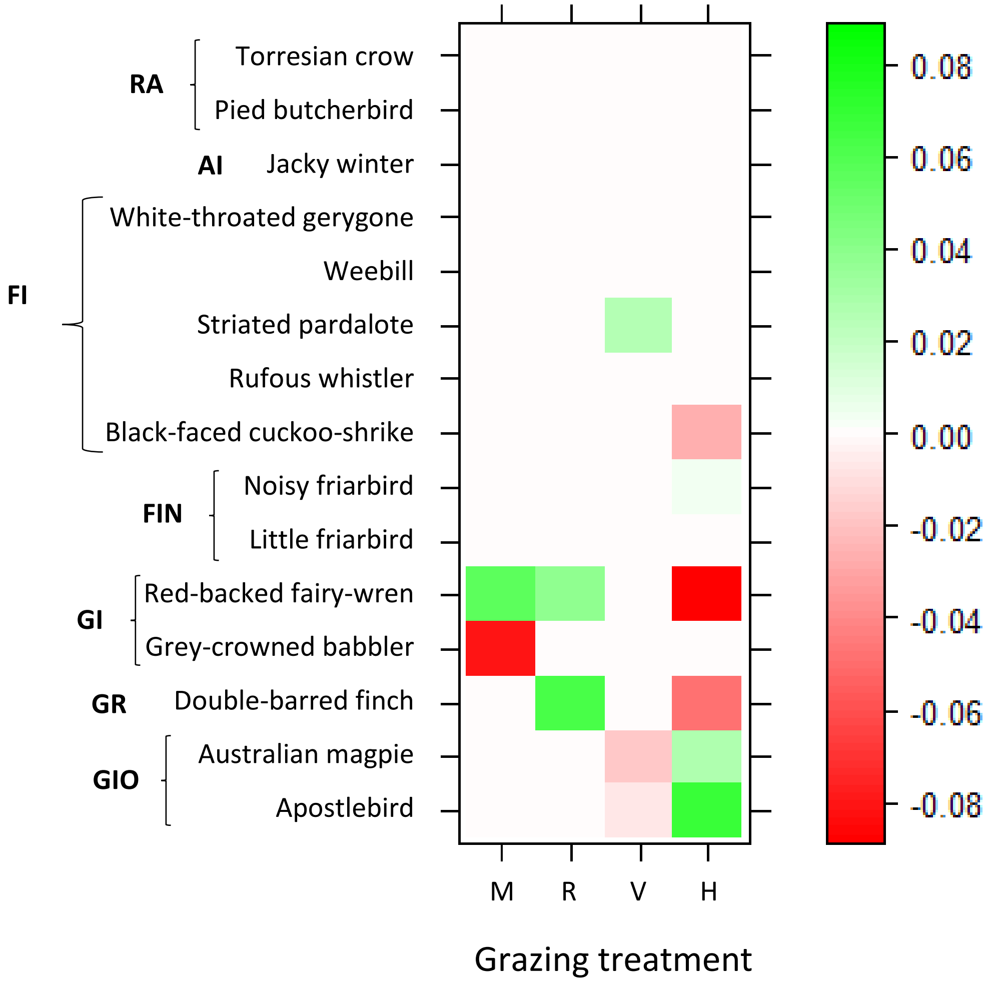


Figure 3.2: The response of bird community to grazing treatments (M-moderate, R-rotational wet season spelling, V-variable, H-heavy), as visualised using the standardised model co-efficients from a generalised linear model- LASOO model. In this type of model, terms which do not explain any variation in species response are set to zero. The stronger the association, the brighter the square, positive associations are in green and negative associations are in red. Species have been arranged by forgaging guild AI – aerial insectivore, FI- foliage insectivore, FIN – foliage insectivore/nectarivore, FR- frugivore, GI – ground insectivore, GIO – ground insectivore/omnivore, GR – granivore, NE – nectarivore, RA – raptor

The red-backed fairy-wren showed a typical ‘decreaser’ species response (i.e. decreasing in abundance with increasing grazing pressure), however the mean abundance of the Australian magpie, double-barred finch, grey-crowned babbler and the black-faced cuckoo-shrike showed various patterns of grazing treatment response (Figure 3.3). Australian magpie abundance was significantly lower in the variable treatment compared to the other treatments, double-barred finches were significantly more abundant in the rotational wet season spelling treatment and grey-crowned babblers were least abundant in the moderate grazing treatment. In addition to grazing treatment responses, individual species responded to vegetation type, precipitation and their interaction, most notably species from the foliage insectivore (striated pardalote, white-throated gerygone, weebill) and aerial insectivore (jacky winter) foraging guilds.

The four species that showed a significant response to grazing treatment in the manyGLM analysis (and black-faced cuckoo-shrikes), responded positively and negatively to different combinations of microhabitat variables (Table 3.4). Australian magpies and grey-crowned babblers were positively associated with termite mounds, double-barred finches were negatively associated with grass cover but positively with grass height and red-backed fairy-wrens were positively associated with grass cover and *Carissa ovata* cover.

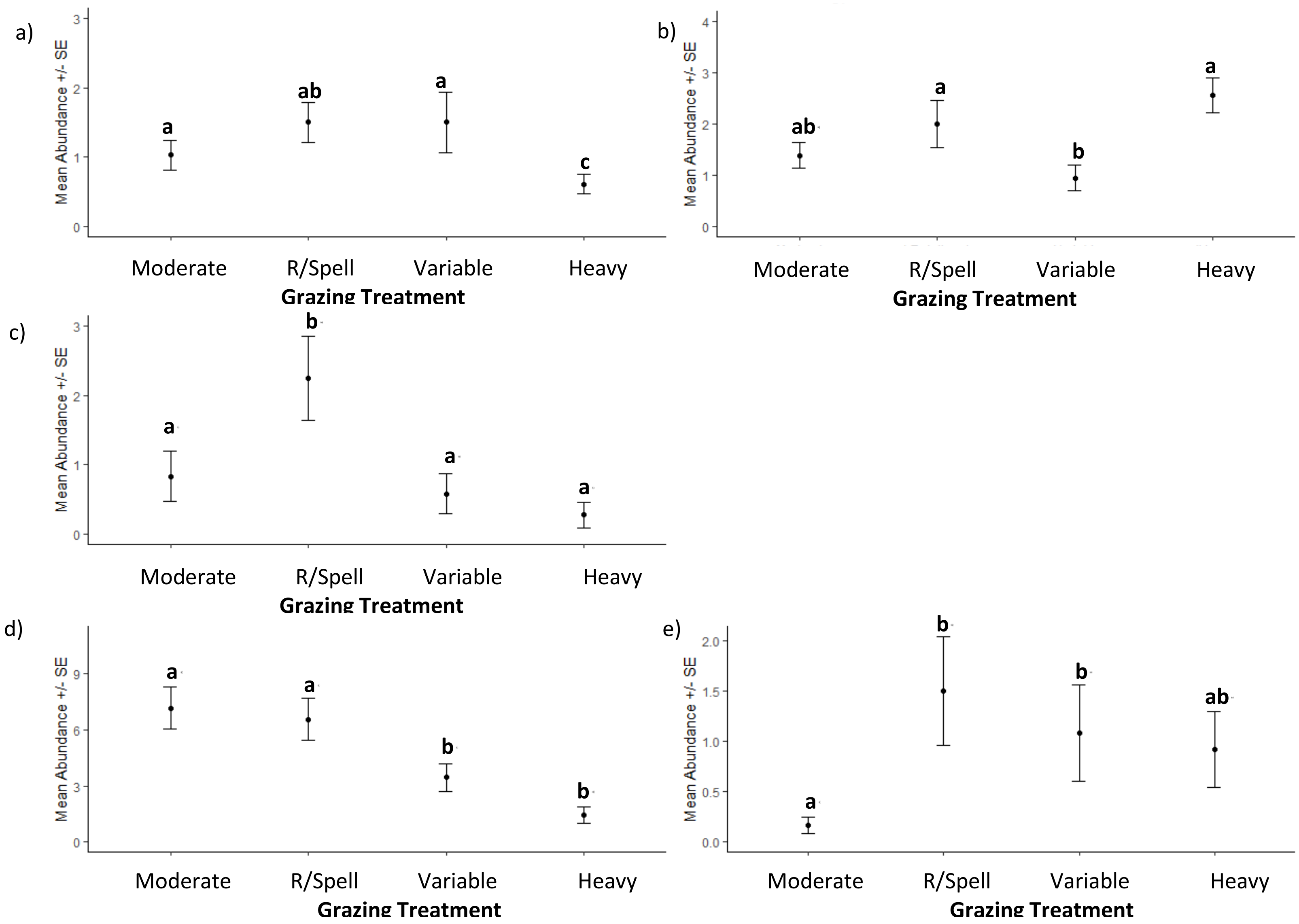


Figure 3.3: Mean abundance ± S.E of individual bird species among the four grazing treatments: a) Black-faced cuckoo-shrike; b) Australian magpie; c) Double-barred finch; d) Red-backed fairy-wren, and; e) Grey-crowned babbler. Post hoc Tukey tests were used to examine the effect of each factor level and significant differences ($p<0.05$) are reported.

Table 3.4: Generalised linear models (GLM) of the response of individual bird species to microhabitat variables. The full model terms are listed in the table. The optimal model includes all significant term, '+' indicates a positive association and '-', a negative association. GLM distributions are indicated (P = poisson, NB = negative binomial).

	Microhabitat Full Model: GLM Grass + Grass height + Fine Woody Debris + Coarse Woody Debris + *Carissa ovata* + Leaf Litter>5mm + Termite Mound + Bare Ground+ Dead Trees+ Trees<5cm Diameter at Breast Height (DBH) +Trees 5-10cm DBH + Trees 10-20cm DBH + Trees 20-30cm DBH + Trees>30cm DBH+ Tree Richness + Number of Trees	
	Terms in optimal model	**P value**
Australian magpie (NB)	Termite Mound (+)	<0.01
Black-faced cuckoo-shrike (P)	Fine Woody Debris (-)	0.01
	Trees 10-20cm DBH (+)	0.02
	Number Trees (-)	<0.01
	Tree Richness (+)	<0.01
Double-barred finch (NB)	Grass (-)	<0.01
	Grass Height (+)	<0.01
	Fine Woody Debris (+)	<0.01
	Coarse Woody Debris (-)	0.04
	Trees 5-10cm DBH (-)	0.01
	Trees 20-30cm DBH (-)	<0.01
Grey-crowned babbler (NB)	Grass (-)	<0.01
	Coarse Woody Debris (+)	0.02
	Termite Mound (+)	0.02
	Trees Dead (-)	<0.01
	Trees>30cm DBH (-)	0.04
	Number Trees (+)	<0.01
	Tree Richness (-)	0.01
Red-backed fairy-wren (NB)	Grass (+)	<0.01
	Coarse Woody Debris (-)	0.05
	Carissa ovata (+)	<0.01

Discussion

My results show that ground-foraging guilds were more responsive to different cattle grazing strategies. However, within these guilds, the individual species driving compositional change responded to the grazing treatments in various ways. For example, although double-barred finches responded significantly to the grazing treatment, this was not reflected in the overall response of granivores. This confirms the idea that wildlife responses to grazing are often complex and species specific (Chapter 1). We found that those species negatively associated with heavy grazing had a relatively small body size (red-backed fairy-wren, double-barred finch), in comparison to the larger-bodied species that were positively associated with heavy grazing (Australian magpie, apostlebird). This supports global meta-analyses that have found bird species with smaller body mass are more sensitive to disturbance than heavier species (Samia et al. 2015, Blumstein et al. 2005).

The red-backed fairy-wren was negatively impacted by the heavy grazing treatment, showing a 'decreaser' pattern of abundance. Kutt et al. 2012, also observed decreasing abundance patterns with grazing, when they conducted bird surveys at the same location in 1998 and 2003, suggesting that these birds responded to the Wambiana grazing trial treatments quickly, and maintained similar responses over time. Red-backed fairy-wrens were positively associated with grass and shrub (*Carissa ovata*) cover and, suggesting that these structures are important to a species that is an understorey specialist (Murphy et al. 2009). *C. ovata* cover was relatively high in the heavy grazing treatment, as it is unpalatable to cattle (Chapter 6). Presumably, in the absence of this shrub species, the impact of heavy grazing on red-backed fairy-wrens could have been much more pronounced.

The Australian magpie is a disturbance-tolerant species (Kutt and Fisher 2011), and was resistant to the impact of heavy grazing. However, this species' patterns of abundance may have been strongly driven by food availability, as suggested by a positive association with termite mounds. Yellow-throated miners are also associated with disturbance, and have received a lot of attention due to their increases in abundance in heavily grazed areas (Kutt et al. 2012; Eyre et al. 2009; Woinarski and Ash 2002). This species was not analysed separately due to a low number of observations, but I did not find relatively higher numbers of yellow-throated miners in the heavy grazing treatment. They were least abundant in the moderate grazing treatment and similar in abundance in the other grazing treatments (HN pers obs; unpublished data). This may indicate the heavy grazing treatment is less disturbed than areas further south where miners (*Manorina* sp.) move into heavily disturbed environments and aggressively exclude passerines from resources (Eyre et al. 2009).

Although the focus of this study was bird responses to different grazing strategies, I also found that nectarivores were responsive to vegetation type and frugivores to precipitation. A number of individual species responded to vegetation type, precipitation, or responded to precipitation in a manner dependent on the vegetation type (i.e., there was an interaction between these terms). Recent preceding rainfall and subsequent resource pulses can have big effects on birds in highly seasonal savanna environs (Price et al. 2013; Reside et al. 2010; Kutt et al. 2012), making it difficult to study savanna birds that are often nomadic and move in response to resource availability (Kutt et al. 2012). Similarly, the changes to microhabitat (in response to different grazing strategies) may influence food availability, indirectly driving foraging guild and bird species response to grazing treatments. Heavy grazing can reduce seed production (Vickery et al. 2001) and deplete the soil seed bank (Pol et al. 2014). Additionally, foliar arthropod abundance generally decreases where grass is less structurally diverse (Vickery et al. 2001; van Klink et al. 2014; Wallis De Vries et al. 2007; Dennis et al. 2007). It would be interesting to measure or experimentally test exactly how rainfall and changes in vegetation structure (in response to different grazing strategies) influence food availability for birds.

Savanna birds respond to spatial and temporal heterogeneity at both a landscape scale and at fine scale (Price et al. 2013), and our ability to detect bird responses to grazing is scale dependent (Dumbrell et al. 2008). Experimental grazing trials are often criticized for not being of an appropriate spatial scale for highly vagile fauna such as birds (Kutt et al. 2012; Wallis De Vries et al. 2007). This study design has provided insight into bird responses at a paddock scale (i.e., their rate of use of various paddocks), but cannot tell us about bird responses at landscape scale, which, even for the same species, may be quite different (James 2003). Similarly, savanna birds may respond differently on different temporal scales (Reside et al. 2010; Kutt et al. 2012). While this study took place over the short-term (three years), some of my findings were consistent with patterns described among the grazing treatments 10-17 years prior (Kutt et al. 2012). Ideally, to effectually inform landscape-scale rangeland management strategies, studies should be designed at multiple scales (Fischer et al. 2004).

Management implications

Here I have experimentally tested grazing strategies without the confounding effect of other land management practices. In reality, vertebrate grazing response interacts with their response to fire (Kutt and Gordon 2012), non-native pasture (Germano et al. 2012; Smyth et al. 2009; Kutt and Fisher 2011), and tree clearing (Dorrough et al. 2012; Brown et al. 2011; Martin and McIntyre 2007). Pastoral land in tropical savannas is subject to a suite of disturbances that must be considered holistically when forming grazing management strategies.

Globally, agricultural land use is implicated in the decline of many bird species (Donald et al. 2001). The use of land for food production is likely to increase, considering the growth of human populations. Therefore, it is essential to understand how different land management strategies will impact bird communities and then use this information to inform off-reserve conservation (Chapter 1). While some of the patterns observed in this study seem straightforward to interpret, e.g. lower foraging guilds are more responsive to grazing and the red-backed fairy-wren as a ‘decreaser’ species, other bird community dynamics are harder to explain and translate into management recommendations. Universally, grazing conservatively or not clearing trees may result in the best outcomes for the most species (Chapter 6). However, where land managers have specific conservation goals relating to certain species, a more nuanced approach will be required.

Summary

Globally, agricultural land-use is implicated in the decline of avifauna. In rangelands, used for livestock grazing, bird community responses to grazing can be complex, species-specific and scale dependent. I tested the hypothesis that bird foraging height predicts bird species responses to grazing, such that species using lower vegetation strata are most likely to be responsive to the impacts of livestock grazing. I examined the response of a tropical savanna bird community to four different grazing strategies at a long-term grazing trial in northern Australia. I predicted that responses would be species-specific, and ground-foraging guilds more responsive to grazing treatment than foliage- or aerial-foraging guilds. I analysed the

bird community assemblage using multivariate generalised linear models and examined individual species in relation to microhabitat variables. I found that while ground-foraging guilds were more responsive to grazing treatment, individual species dynamics within a foraging guild could be contradictory. Individual species, such as the red-backed fairy-wren, decreased in abundance with increased grazing, and were positively associated with grass and shrub (*Carissa ovata)* cover, whereas Australian magpies increased in abundance in the most heavily grazed paddocks. In general, the responses of bird species to grazing were more pronounced closer to the ground, but whether the responses were positive or negative was driven by bird species ecology. Measures examining the responses of individual species are more useful than assemblage measures (such as richness) to describe the impacts of anthropogenic disturbance such as grazing.

Chapter Four

Adapted from: Neilly, H. & Schwarzkopf, L. (2017) The response of an arboreal mammal to livestock grazing is habitat dependent. *Scientific Reports* 7(1), 17382.

The response of an arboreal mammal to livestock grazing is habitat dependent

Introduction

The impact of livestock grazing on biodiversity is important, not only due to the vast extent of global rangelands, but to the diversity of biomes in which grazing occurs (Asner et al. 2004). Grazing alters ground-level structures directly, e.g. by soil compaction from trampling, the removal of vegetation through herbivory and the addition of nutrients (Fleischner 1994). The indirect effects of grazing may further impact lower habitat strata, but can also negatively impact arboreal structures (Chapter 6).

While vegetation responses to grazing have been studied in detail, the response of the vertebrate fauna that use these habitats is complex, and has received less attention (Chapter 1). Vertebrate fauna can increase in abundance with increasing grazing disturbance, decrease in abundance, or remain unchanged (e.g. (Martin and McIntyre 2007; Dorrough et al. 2012; Lusk and Koper 2013). These responses depend on the way that grazing alters microhabitat and the specific habitat requirements of fauna species (Milchunas et al. 1988). Vegetation type, the use of fire, the introduction of non-native grasses and tree clearing, can interact with species' responses to grazing, often exacerbating negative impacts (Fuhlendorf et al. 2009; Kutt and Fisher 2011; Germano et al. 2012; Kutt and Gordon 2012). The complexity and species-specific responses of vertebrates in rangelands, can make it difficult to translate research results into clear management recommendations.

Although grazing is broadly considered a factor contributing to vertebrate species' declines (Donald et al. 2001), arboreal species may be somewhat resistant to grazing disturbance, because they can mostly avoid ground-level impacts, as seen in birds (Martin and Possingham 2005; Kutt and Martin 2010) and arboreal reptiles (Chapter 6). Arboreal mammals are present in agroecosystems globally, but mammal community grazing studies usually focus on small terrestrial mammals (e.g. Germano et al. 2012; Kutt and Gordon 2012; Bösing et al. 2014), with arboreal mammals receiving less attention (but see (Woinarski and Ash 2002; Beever and Brussard 2004; Kinnaird and O'Brien 2012; Butynski and Jong 2014; Radford et al. 2015). Due to their prevalence on rangelands, the response of arboreal mammals to grazing needs further attention, so that these species can be considered when devising grazing management strategies.

The common brushtail possum (*Trichosurus vulpecula vulpecula* Kerr 1792, henceforth 'brushtail possum'), is a medium-sized, arboreal marsupial found in a range of disturbed environments, including tropical savanna rangelands grazed by cattle (Van Dyck and Strahan 2008). They thrive in Australian urban areas, are considered a pest in some agricultural areas in Australia, and are a serious introduced pest species in New Zealand (Kerle et al. 1992; Statham and Statham 1997; Russell et al. 2013; Cowan 2016). Their adaptability is due to their use of a variety of habitat types, their ability to breed continually and to exploit a variety of seasonal food sources (Kerle et al. 1992; How and Hillcox 2000; Kerle 2001; Cowan 2014).

Aside from stable populations in urban areas, brushtail possum populations have declined in many parts of their native range, most markedly in arid central Australia (Kerle et al. 1992; Kerle 2004; Woinarski 2004; Russell et al. 2013). These declines are attributed to a variety of factors including habitat loss, drought, introduced feral predators and hunting (How and Hillcox 2000; Kerle 2001). Consequently, reintroduction programs have been successful in areas where feral cats and foxes have been excluded (e.g. Short and Hide 2014). Whilst brushtail possums are an arboreal species heavily utilising trees, they use rock-holes, caves and burrows for nesting and also frequently walk along the ground to move between trees in areas where the tree canopy is not connected (Kerle et al. 1992; How and Hillcox 2000). The ability of brushtail possums to persist in disturbed areas if vertical structures are present (Carthew et al. 2015), combined with their use of the ground to move between trees, suggest that they may benefit from cattle grazing disturbance, where trees are retained, and grass cover is reduced. Since most of the brushtail possum range coincides with rangelands, it is important to understand their response to grazing, and investigate if microhabitat selection is driving this response.

I examined population dynamics, habitat selection and movement of brushtail possum individuals, in response to four different grazing strategies (all without any associated tree clearing), and between two vegetation types, using mark-recapture data. This study took place on a long-term cattle-grazing trial in tropical savanna woodland in northern Australia. I aimed to identify if brushtail possum abundance was influenced by different grazing strategies and vegetation types, and then if individuals were selecting or avoiding certain microhabitat features. Due to this species' adaptability to disturbance and the lack of tree clearing associated with the grazing treatments, I expected brushtail possums to be resistant to the impact of heavy grazing. As such, I predicted that brushtail possums would select ground microhabitat features that were consistent with relatively disturbed areas, but select more complex arboreal microhabitats.

Materials and methods

This study was conducted at the Wambiana Grazing Trial, see Chapter Two for a detailed site description.

Mammal surveys

Twenty-four 1-ha sites (100m x 100m) were established, with six sites located in each of the four grazing treatments (See Chapter Two, Figure 2.2). Each site was in either the Box or the Ironbark vegetation community.

Four surveys were conducted; these took place in 2014 and 2015, in both April (end of the wet season) and October (end of the dry season). Along the centre line of each 1-ha site, a rectangular, wire cage trap (710 x 305 x 305mm) was set at 0m, and another half-way along, at 50m. Each cage trap was baited with a ball of peanut butter, rolled oats, and vanilla essence. Cage traps were checked before dawn and closed for the remainder of the day (with bait removed), before being re-opened and re-baited in the late afternoon. Each trapping session ran for a 10-night period. Captured animals were removed from traps, identified, weighed, measured, marked with a unique ear clip combination and then released at the site of capture. Species nomenclature followed Dyck and Strahan (2015).

Microhabitat surveys

Microhabitat features were measured at each site during each survey session (Table 4.1). Within a 1-ha site, 3 x 100 m parallel transects, 50m apart, were established. Along the transect, ground cover was categorised as bare ground, leaf litter >5mm, leaf litter 5-10mm, rock, fine woody debris (<10cm diameter) or coarse woody debris (>10cm diameter). Vegetative cover along the transect was categorised as grass (with grass height also recorded), shrub or tree. Both ground and vegetative cover measures were converted into mean percentages. Additionally, all trees within one metre on either side of the transects were identified and their height and diameter at breast height (DBH) was measured. I also measured mean percentage canopy cover, mean distance to nearest tree (m) >2m tall, mean percentage canopy connectivity, mean percentage trees with hollows (further detail in table 4.1).

Data Analysis

A range of analyses were performed in R (R Core Team 2016), with specific packages cited where relevant.

Population dynamics

Brushtail possum population dynamics for the entire grazing trial were examined by analysing the mark-recapture data in *Rcapture* (Rivest and Baillargeon 2015). Population dynamics could not be modelled among treatments or between vegetation types as individuals could move between sites. Due to the hierarchical nature of the trapping data, I used a robust design analysis, i.e., within a trapping session (10 consecutive days of capture) the population is assumed to be closed (not experiencing immigration or mortality), but between each trapping session the population is considered open. A robust design can generate estimated abundances for each trapping session and survival rates between periods.

Table 4.1: A description of the microhabitat variables surveyed at each site.

Microhabitat characteristics	**Description**
Ground cover	A tape measure was laid on the ground along a 100m transect. The amount of bare ground (BG), rock, leaf litter (LL) and leaf litter depth (mm), fine woody debris (<10cm diameter) (FWD), coarse woody debris (>10cm diameter) (CWD) was recorded in cms and converted into a percentage.
Vegetative cover	Along the 100m transect, the amount of grass (and grass height), shrub and other vegetative cover was recorded and converted into a percentage.
Other features	Other ground features were measured along the 100m transect including termite mounds (TM), and burrows.
Trees	Any tree that fell 1-m either side of the 100m transect was identified and measured for diameter at breast height (DBH) (cm) and height category (m)
Canopy Cover (%)	Estimated canopy cover *via* spherical densiometer.
Canopy connectivity (%)	The percentage of overstory trees sampled that had overlapping canopy or branches.
Tree hollows (%)	The percentage of overstory trees sampled that had hollows or cavities visible from the ground.

Grazing treatments, vegetation type and microhabitat use

A generalised linear mixed model, with poisson distribution, was used to analyse the response of brushtail possum abundance to grazing treatment and vegetation type (fixed effects), with year and season included in the model as random effects. To analyse the response of brushtail possum abundance to the microhabitat variables at each site, I used a generalised linear model with negative binomial distribution (to account for overdispersion). Both analyses were performed using *lme4* (Bates et al. 2015). The optimal models were selected using the Akaike Information Criterion (AICc) from the *dredge* function in *MuMIn* (Bartoń 2015). The optimal models were validated by examining the deviance residuals. Pairwise comparisons among grazing treatment and between vegetation type were made using the Tukey test in *lsmeans* (Lenth 2016).

Additionally, I performed habitat selection analyses on the variables in the optimal models, using *adehabitatHS* (Calenge 2016). The data was structured as a ‘design II study’, i.e., each trapped individual was identified and habitat use was recorded for each individual. Since microhabitat variables were collected at a site level, when an individual was trapped at a site, it was considered to be using the microhabitat variables at that site. The habitat availability was measured at a population scale, i.e., habitat units were considered equally available to all individuals. I used Manly selection ratios (Manly et al. 2002) to calculate habitat availability to habitat use, for each animal, for each habitat type and then averaged over all animals.

Individual home-ranges and movement

Although not the focus of this study, home range size was calculated, in *adehabitatHR* (Calenge 2006), for individuals with at least five recaptures. First, I estimated the kernel utilisation distribution (KUD) and then extracted the 95% and 50% home range contours. KUD contours are used here to visualise individuals use of grazing treatments and vegetation types.

Results

Population dynamics

Across four surveys and 1920 trap nights, 63 unique individuals were captured and 38 were subsequently recaptured (Table 4.2). Overall, it was estimated that 79 ± 21.7 (S.E.) individuals inhabited the survey area over the two year period, with high capture probabilities in the last three surveys and survival probabilities between surveys around 50% (Figure 4.1). Breeding occurred multiple times per year, as unfurred joeys were recorded in all surveys.

Grazing treatments, vegetation type and microhabitat use

The optimal generalised linear mixed model included grazing treatment and vegetation type and the interaction between these two variables (AICc = 317.7). The next best model only contained grazing treatment, however the AICc value was sufficiently lower (ΔAICc = 2.49) to accept the more complex, optimal model. The highest mean abundance of brushtail possums was found in the Heavy grazed Box sites (Figure 4.2). Within the Box vegetation community, the Heavy and Variable treatments had a significantly higher abundance than the Moderate and Rotational treatments. There was no significant difference among grazing treatments within the Ironbark vegetation community. On average, individuals selected Heavy (Manly selection ratio = 1.42 ± 0.29 SE) and Variable treatments (1.11 ± 0.21 SE) and avoided Moderate (0.95 ± 0.20 SE) and Rotational treatments (0.52 ± 0.13 SE). Of 63 individuals marked, 20 individuals used multiple grazing treatments (31.7%), and 43 only used 1 of the grazing treatments: 16 only used Heavy (25.4%), 16 only used Variable (25.4%), 5 only used Moderate (7.94%) and the remaining 6 individuals only used the Rotational treatment (9.52%). On average, individuals selected the Box vegetation type (Manly selection ratio= 1.13 ± 0.11 SE) and avoided the Ironbark vegetation community (0.74 ± 0.22 SE). Of 63 individuals marked, 4 individuals used both vegetation types (6.35%), 44 only used the Box (69.8%) and 15 only used the Ironbark vegetation type (23.8%).

When modelling brushtail possum response to microhabitat variables, the optimal model contained the terms Canopy Cover, *Carissa ovata* cover, Number Dead Trees, Number Trees >10m, Tree Richness and Grass Cover (AICc 298.5, ΔAICc = 2.21). All terms were ecologically relevant to brushtail possum microhabitat use, so these variables were used to test habitat selection using Manly selection ratios. On average, brushtail possums selected the highest category of Trees >10m, Number of trees, Tree Richness, Canopy Cover and Hollows (mean Manly selection ration >1), however due to high variability, only the selection of high Canopy Cover was significant (Figure 4.3 a-h). Brushtail possums selected low Grass cover (Figure 4.3g), and significantly avoided Number of Trees 0-10 (Figure 4.3b) and low and medium Canopy Cover (Figure 4.3e).

Table 4.2: Trap success, recapture rates, sex ratios and population size of *Trichosurus vulpecula vupecula* captures at each trapping session

Survey session	Trap nights	Trap success %	No. animals trapped	Density/ha	No. unique trapped females	No. unique trapped males	Recapture rate all %	Sex ratio F:M	Females with pouch young (%)
April 2014	480	2.50	12	0.01	5	5	0	1:1	40.0
October 2014	480	10.6	51	0.03	8	26	60.8	1:3.25	50.0
April 2015	480	19.2	92	0.05	14	33	69.6	1:2.36	35.7
October 2015	480	19.8	95	0.04	12	33	86.3	1:2.75	50.0
Overall	1920	13.0	250		17	46	72.4	1:2.71	47.1

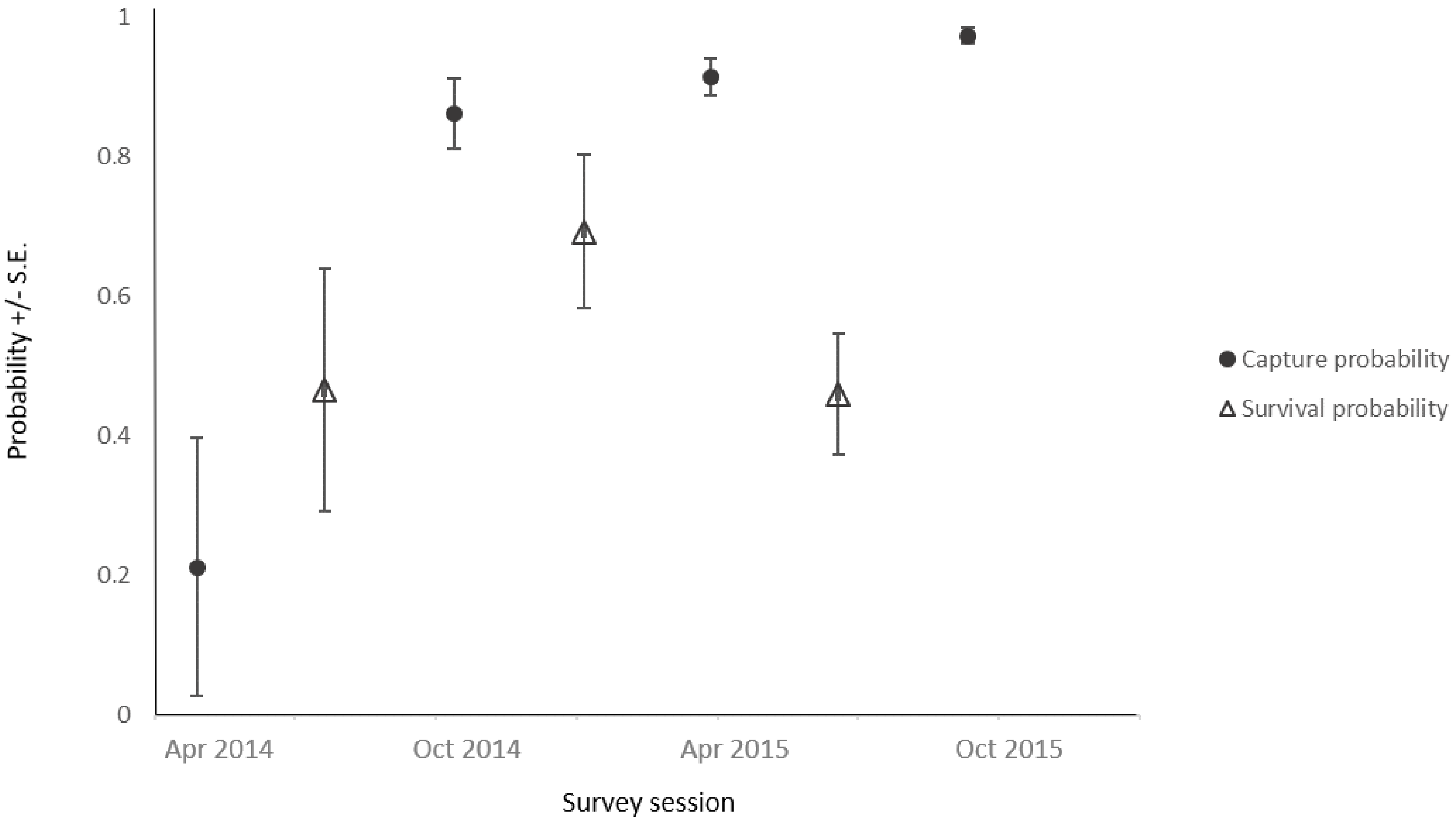


Figure 4.1: Estimated capture probability at each survey session and survival probability between survey sessions +/- S.E., for *Trichosurus vulpecula vulpecula* population.

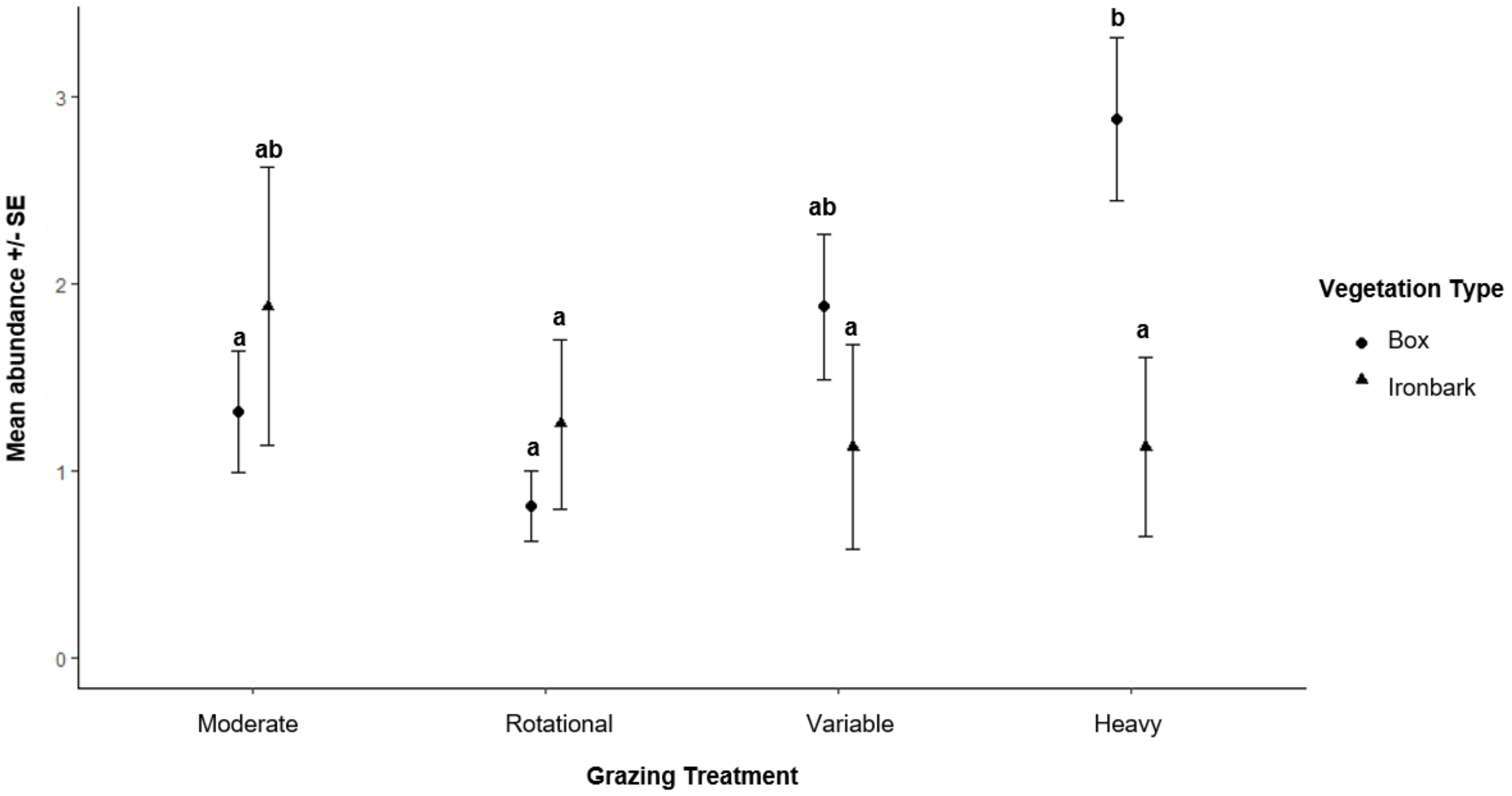
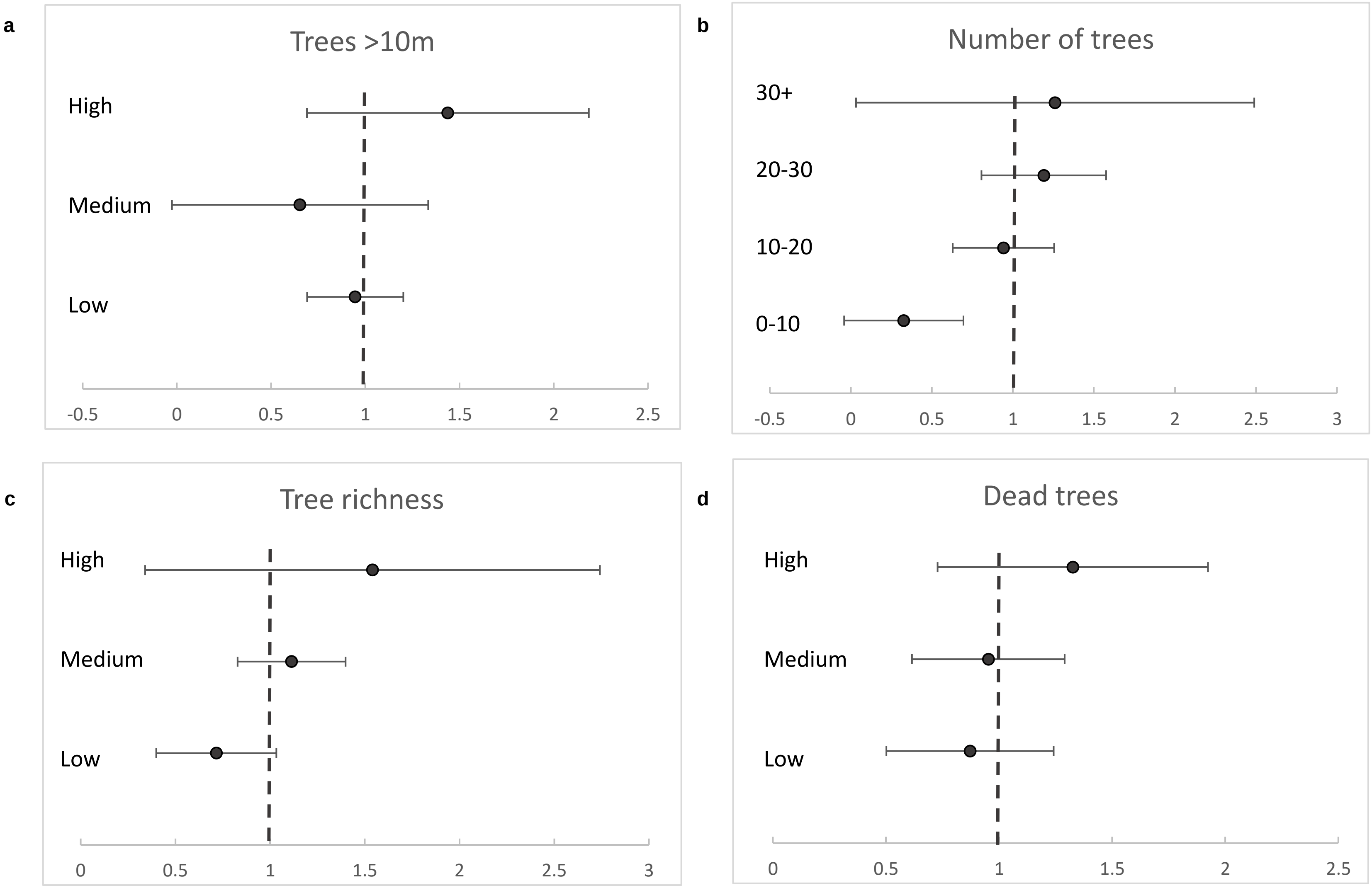


Figure 4.2: Mean *Trichosurus vulpecula vulpecula* abundance +/- SE, significantly different terms indicated by different letters (Tukey posthoc α=0.05).


a
Trees >10m
High
Medium
Low
-0.5
0
0.5
1
1.5
2
2.5
b
Number of trees
30+
20-30
10-20
0-10
-0.5
0
0.5
1
1.5
2
2.5
3
c
Tree richness
High
Medium
Low
0
0.5
1
1.5
2
2.5
3
d
Dead trees
High
Medium
Low
0
0.5
1
1.5
2
2.5

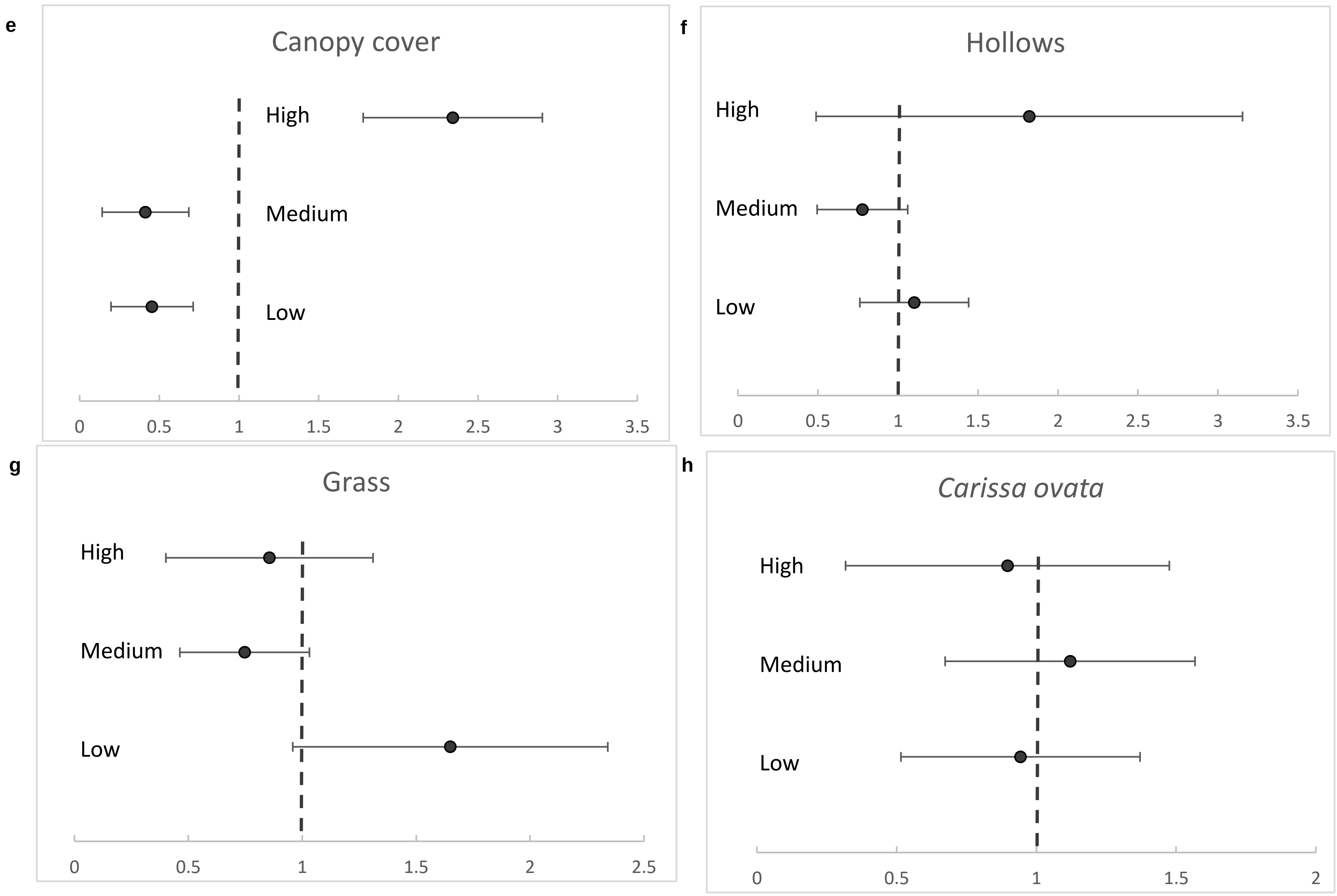


Figure 4.3: Mean Manly selection ratios with 95% confidence interval for *Trichosurus vulpecula vulpecula* use of microhabitat variables. Microhabitat variables are 'selected' where Manly selection ratio is >1, and 'avoided' where Manly selection ratio is >1. Results are considered significant were the 95% confidence intervals do not cross 1.

Individual home-ranges and movement

Twelve individuals had sufficient recapture data (at least five recaptures) to calculate kernel utilization densities (KUDs). Two individuals were recaptured more than five times (ID 28 and 42), but were only ever recaptured at the same location, therefore home range analysis could not be done. One individual (7.14%), used both vegetation types, two individuals used Ironbark only (14.28%), and the remaining 11 individuals only used the Box vegetation type (78.6%) (Table 4.3, Figure 4.4). Most individuals used more than one grazing treatment, the greatest percentage of relocations overall was in the Heavy, followed by Variable, then Moderate, and finally Rotational wet-season spelling (Table 4.3, Figure 4.5). Home range sizes were variable; the mean 95% KUD was 181.44 ha ± 62.95 SE and the mean 50% KUD was 22.91ha ± 7.66 SE. Individual 20 was identified as an outlier and was omitted from the mean KUD contour calculations (Table 4.3).

Table 4.3: The number of relocations, the vegetation type used, the percentage of relocations in four grazing treatments, the kernel utilisation densities (KUD) at 95% and 50% and the sex of *Trichosurus vulpecula vulpecula* individuals captured at least five times.

ID	**No. relocations**	**Vegetation type used**	**% Relocation in each grazing treatment**				**95% KUD (ha)**	**50% KUD (ha)**	**Sex**
			Heavy	**Variable**	**Rotational**	**Moderate**			
20	6	Box & Ironbark	66.6	33.3	0	0	3161.7	785.9	M
3	11	Box	81.8	0	0	18.2	762.3	92.9	F
4	16	Box	93.8	0	6.2	0	66.7	5.9	M
22	5	Box	100	0	0	0	45.9	7.2	M
23	9	Box	11.1	55.6	0	22.2	164.7	23.6	M
24	10	Box	100	0	0	0	35.6	5.2	F
26	9	Box	88.9	0	0	11.1	253.1	22.5	M
41	6	Box	16.7	33.3	50	0	268.2	37.2	M
44	15	Box	0	33.3	0	66.7	56.2	7.2	M
60	15	Box	12.5	37.5	0	50	85.6	10.6	M
42	12	Box	0	100	0	0	n/a	n/a	M
28	6	Box	0	100	0	0	n/a	n/a	M
71	16	Ironbark	12.5	37.5	0	50	93.6	13.7	M
2	11	Ironbark	0	18.2	18.2	63.6	163.9	26.1	M

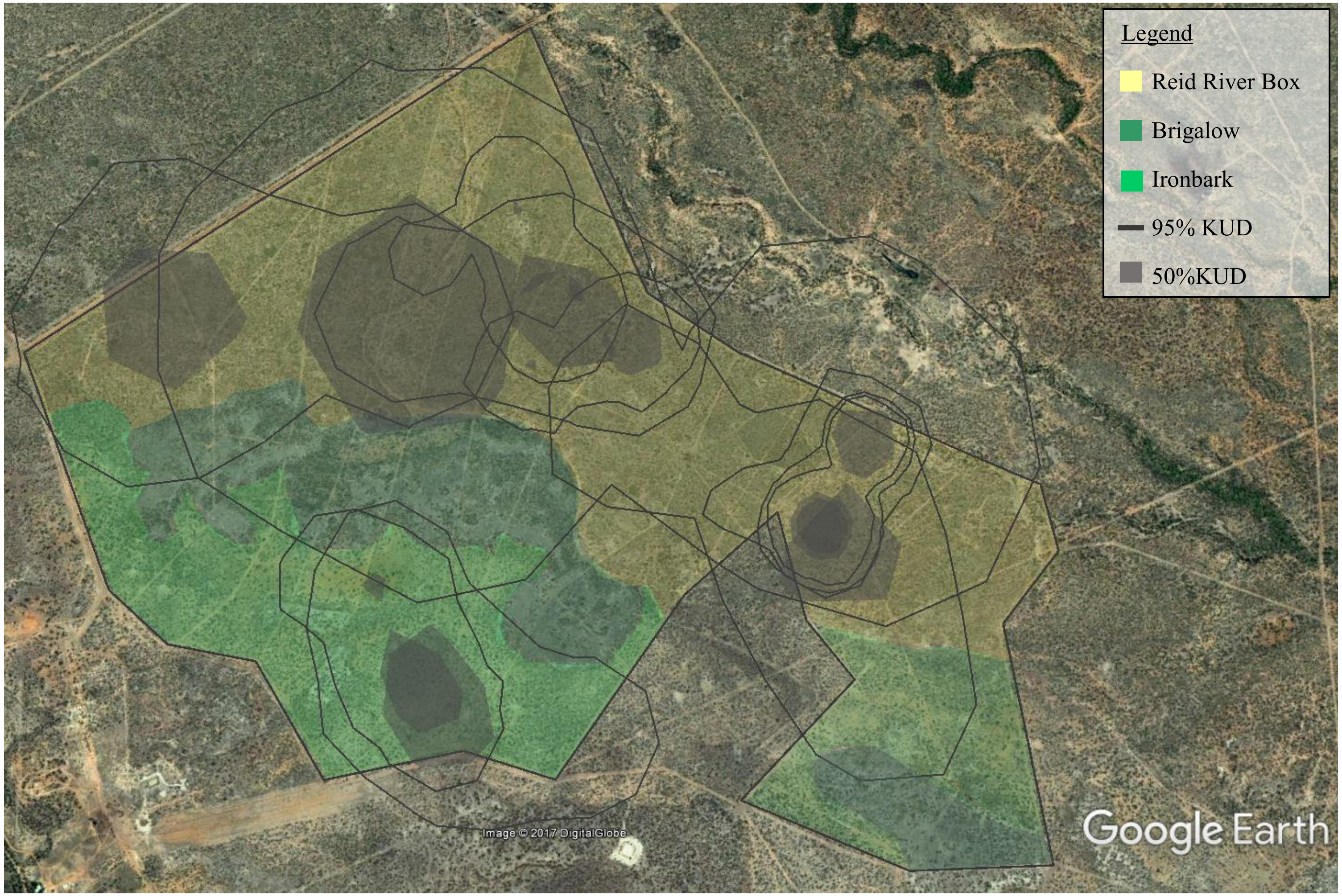


Figure 4.4: The 95% and 50% kernel utilisation densities (KUD) of *Trichosurus vulpecula vulpecula* individuals in relation to the Wambiana grazing trial vegetation communities.

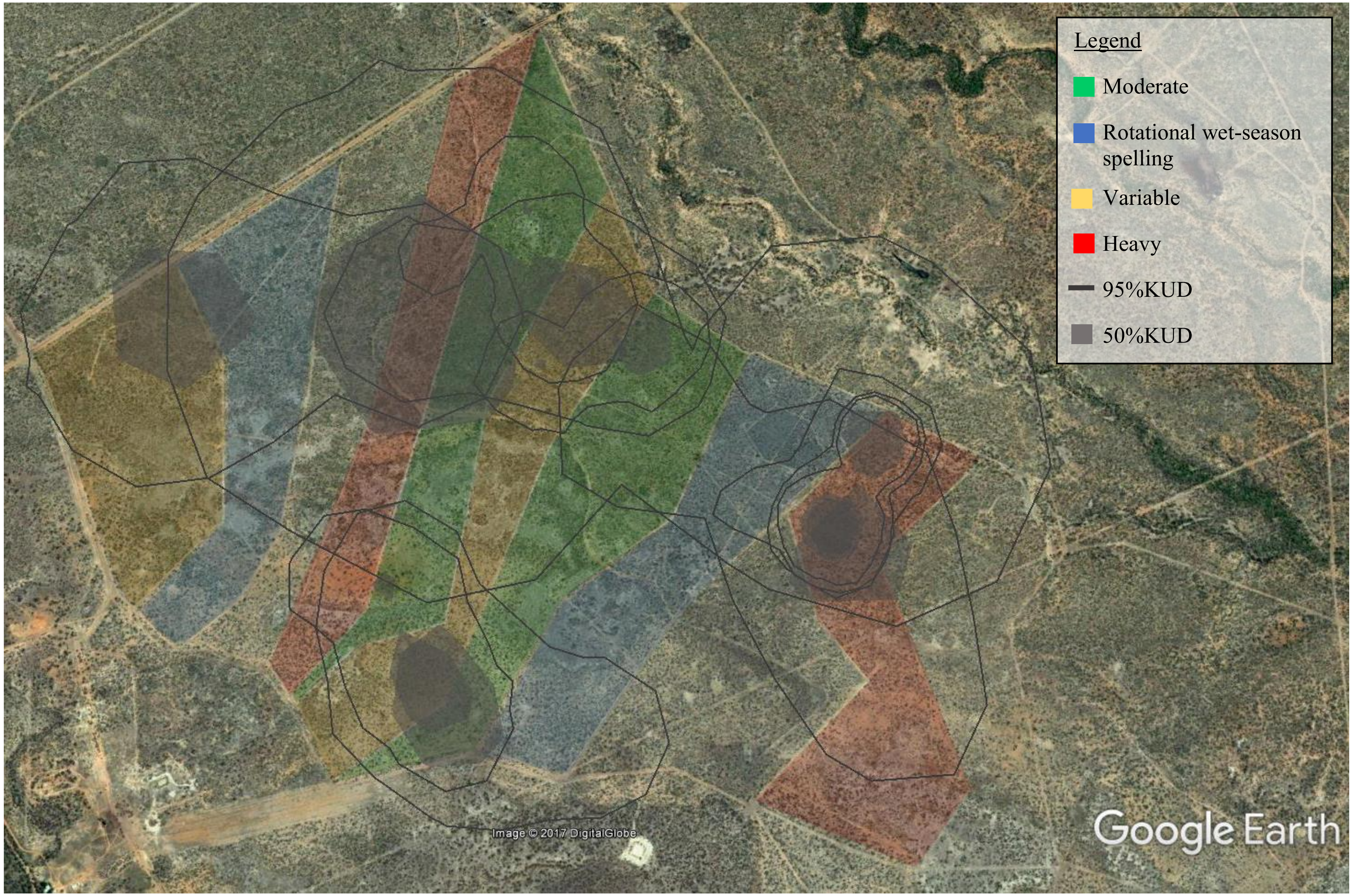


Figure 4.5: The 95% and 50% kernel utilisation densities (KUD) of *Trichosurus vulpecula vulpecula* individuals in relation to the Wambiana grazing trial grazing treatments.

Discussion

High capture probabilities suggested my brushtail possum population estimates were reliable, despite being much lower than recorded densities in wetter areas of Australia (Kerle 1998; How and Hillcox 2000; Isaac et al. 2008). The individuals on the grazing trial had sufficient food quantity and quality to reproduce, even in 2015, when rainfall was low and food availability would likely have been lower than in the other years of the study (Cowan 2014). Brushtail possums primarily eat *Eucalyptus sp.* leaves, present in both vegetation types, but will exploit seasonal food sources during fruiting or flowering events (DeGabriel et al. 2009). Seasonal differences in resource use could potentially affect detectability, however, while spotlighting I never saw groups of individuals congregating to feed on specific trees (unpublished data; HN pers obs). Additionally, the use of a standardised trapping methodology minimised differences in detectability, compared with subjective survey methods such as spotlighting.

In this study, brushtail possums clearly preferred the Box vegetation. This vegetation type was characterised by a higher total number of trees and a higher tree species richness than the Ironbark. High canopy cover was also more common in the Box vegetation, which was the microhabitat feature most strongly selected by brushtail possums. Overall, individuals selected the most complex arboreal habitat available, as has been observed in other locations where this species select rainforest and forest communities over woodland (Lindenmayer et al. 2008). Although not tested here, the preference for Box may be linked to a preference for particular *Eucalyptus* species. Brushtail possums avoid species containing certain secondary plant metabolites, particularly tannins (Marsh et al. 2003), so it is possible the Box supports preferred food sources compared to the Ironbark vegetation type.

Overwhelmingly, individuals only used one habitat type or the other. If recapture rates were very low, a chance observation of such a pattern would be more likely, but recapture rates were relatively high in this study. If one looks only at the individuals captured five or more times, the exclusive use of a certain vegetation type is still evident. Sex, body weight or reproductive traits did not explain why certain individuals were using certain vegetation types. The lack of relationship between breeding status and habitat is typical of brushtail possums: reproductive success of this species is not sensitive to habitat type or disturbance, because they are highly physiologically resilient (Flynn et al. 2011). Furthermore, it is unlikely that territorial individuals were excluding others, as many of the estimated home ranges overlapped, suggesting some level of social tolerance, as has been observed elsewhere (Kerle 1998). It is possible that individuals remained in a particular vegetation type because they were restricted from moving between the two habitats (Forman 1995). The band of Brigalow vegetation that divides the Box and Ironbark on my study site, may be acting as matrix habitat between two suitable habitats, affecting movement. Although this vegetation type has canopy cover comparable to the Box, tree richness is relatively low and the dominance of *Acacia harpophylla* may limit suitable food resources (HN pers obs). Indeed, the majority of individuals that used both vegetation types did so at the far south-eastern side of the trial where the Box and Ironbark intrograde directly, with no division by Brigalow. Indeed, the majority of individuals that used both vegetation types did so at the far south-eastern side of the trial where the Box and Ironbark intrograde directly, with no division by Brigalow. Conversely, in a highly fragmented agricultural landscape, *Trichosurus vupecula hypoleucus* have been observed moving hundreds of metres through treeless gaps between vegetation patches (Molly and Davis 2016). In this case, matrix habitat did not impede *T. v. hypoleucus* movement. *T. v. hypoleucus* are a geographically isolated subspecies of the common brushtail possum, and are smaller, have denser fur and a more omnivorous diet than other subspecies (Kerle et al. 1991). The diet and morphological differences may explain the behavioural differences between these subspecies.

In addition to a preference for specific arboreal microhabitat features, brushtail possum individuals also preferred low percentage cover of grass, which occurred most commonly at sites in the Heavy grazed treatment. The Rotational wet-season spelling treatment has the highest grass cover, and was avoided. The preference for the Heavy treatment occurred only in the Box vegetation. Different responses to grazing in different vegetation communities has been observed in other taxa (Chapter 5; Woinarski and Ash 2002). In this case, it was the combination of the complex arboreal microhabitat (found in the Box), and a more open ground layer (found in the Heavy grazing treatment), that brushtail possums preferred. In this study, where trees are not cleared and frequent fire is not part of the management regime, brushtail possums are not only resistant to heavy grazing but in the Box, they prefer it.

While brushtail possums spend the majority of their time in the trees, they come to the ground to move between trees where canopy is not connected (Kerle 2001). Grass cover and height is important for some species to facilitate movement through agricultural matrices (Kay et al. 2016) and this may be the case for brushtail possums, although it is not known how much they rely on visual cues for navigation. In northern parts of Australia, low ground cover, caused by over grazing, fire, or both, increases small terrestrial mammals' risk of predation from introduced predators (McGregor et al. 2014). The combination of low ground cover and predation has been implicated in the decline of many tropical marsupials (Fisher et al. 2014). The relatively high numbers of brushtail possums in the Heavy grazed sites and individual recaptures, suggests that it is unlikely that predation rates are increased by low ground cover in this instance. Presumably this is because an arboreal mammal spends much less time on the ground than a terrestrial mammal, and in addition, dingo and feral cats were observed in very low numbers due to sustained control efforts on and around the grazing trial (HN pers obs). Future research could deploy GPS collars to investigate the mechanism behind the brushtail possum's preference for low grass cover, including quantifying the amount of time this species spends on the ground.

There are obvious limitations when using mark-recapture data only, as opposed to GPS tracking data, or a combination of both, to analyse habitat selection, movement and home ranges. GPS collars can track individuals' habitat use over their entire range, instead I only have data on their habitat selection at a site level. I have, however, collected very detailed microhabitat data at each site, and this can provide insight into habitat use at scales relevant to brushtail possums. It would likely not be feasible to collect microhabitat data with this level of detail across an individual's entire range. Additionally, I have collected data from 63 unique individuals over two years, which may not have been possible with a GPS tracking study, in which the cost of GPS collars can be a limiting factor to the number of individuals tracked (Thomas et al. 2011). One particular limitation of these results is the calculation of kernel utilisation densities based only on mark-recapture data. As such, I was unable to interpret home range sizes in detail, but rather, I used this analysis to help visualise the patterns of individuals' use of the vegetation types and grazing treatments.

One benefit of using a large-scale, experimental grazing trial is that I can isolate the impact of different grazing strategies on vertebrate fauna, which can be very difficult in areas where grazing also interacts with disturbance from fire and tree clearing (Chapter 1). However, it is important to acknowledge that species' declines in rangelands are most likely to be the result of cumulative impacts from multiple threats, including events that occurred historically (Eyre et al. 2011). The brushtail possum is an example of a species, despite being highly adaptable and resilient, has been unable to cope with pressure exerted by multiple threats including grazing. In urban environments, brushtail possums can thrive as long as there are trees or anthropogenic structure they can use (Carthew et al. 2015). Likewise, in this study the brushtail possum thrives in the Heavy grazing treatment where arboreal habitat is essentially intact. Other studies have also shown that retaining trees is more important for arboreal fauna than the grazing intensity (Woinarski and Ash 2002; Beever and Brussard 2004; Martin and McIntyre 2007). Presumably, if heavy grazing was combined with a practice directly impacting trees (e.g., tree clearance), brushtail possums would respond differently (Michael et al. 2016). This study suggests that heavy grazing by itself is not impacting the brushtail possum negatively, however, it is clearly essential to consider all grazing-related disturbances holistically, when making rangeland management decisions.

Management Implications

This insight into habitat selection may assist with optimising reintroduction programs for the brushtail possum. Identifying locations with high tree richness, high canopy cover and low grass cover may enhance reintroduction success. Additionally, certain matrix habitats may act as movement barriers, potentially limiting access to seasonal food resources.

More generally, this study confirms that species responses to grazing are complex. The different response of the same species in two vegetation types I observed here, suggests that grazing management recommendations need not only be species-specific, but also vegetation-community-specific. A future focus on the vegetation-grazing interaction may help to identify where grazing pressure is more, or is less, impactful on fauna populations and provide important context to determine the benefits of ‘land-sharing’ versus ‘land-sparing’ decisions (Law and Wilson 2015; Kremen 2015; Michael et al. 2016).

For arboreal mammals, reptiles and birds to persist in grazed landscapes, tree retention is essential. Global rangelands vary in their extent of arboreal habitat and therefore arboreal fauna (Asner et al. 2004, Chapter 1), however it is widely accepted that tree retention generally increases species richness (Benton et al. 2003). Therefore, compared to intensive agriculture (where trees are routinely cleared), extensive rangelands (where trees are retained) have the potential to support higher faunal diversity. Rangelands, under specific management, may be areas where agriculture and conservation can successfully co-exist.

Summary

Inappropriate livestock grazing is implicated in the decline of vertebrate fauna species globally. Faunal responses to grazing can interact with the vegetation community in which they occur. I measured the response of an arboreal marsupial, the common brushtail possum (*Trichosurus vulpecula vulpecula*) to different cattle grazing strategies and vegetation types, and examined whether microhabitat selection is driving this response. I hypothesised that where arboreal habitat is intact, brushtail possums would be resistant to the impacts of heavy grazing. I conducted a mark-recapture survey among four grazing treatments and in two vegetation types (Box and Ironbark), at a long-term grazing trial in northern Australia. I found that brushtail possums were resistant to the impact of heavy grazing in both vegetation

types, but preferred the heavy grazing treatment in the Box vegetation type. Complex arboreal habitat and low ground cover was preferred, and high grass cover and low tree species richness avoided. Most individuals exclusively used one vegetation type, with few using both, suggesting a ‘matrix’ vegetation between the Box and Ironbark may be creating a movement barrier. Vegetation type should provide a context for determining the benefits to arboreal wildlife of adopting a particular grazing management strategy.

Chapter Five

Adapted from: Neilly, H. & Schwarzkopf, L. (2018) Heavy livestock grazing negatively impacts a marsupial ecosystem engineer. *Journal of Zoology*. 305(1), 35-42.

Heavy livestock grazing negatively impacts a marsupial ecosystem engineer

Introduction

Ecosystem engineers are species that modify their environment, directly or indirectly changing the resources available to other species (Jones et al. 1994). They influence habitat heterogeneity, ecological functions and ultimately shape the composition and diversity of plant and animal communities (Jones et al. 1997; Wright et al. 2002). The decline of ecosystem engineers can have major effects on the surrounding biota and the health of an ecosystem (Fleming et al. 2014). Anthropogenic disturbances, such as agriculture, can reduce the abundance and diversity of vertebrate fauna species, including those with an ecosystem-engineering role (Fleischner 1994). In these instances, the impact of the anthropogenic disturbance is compounded by the loss of habitat modifying species (Crain and Bertness 2006).

Grazing by domestic livestock is a widespread disturbance, occurring on 25% of Earth's land surface (Asner et al. 2004). Grazing alters ground-level habitat structures, e.g., by reducing vegetation and compacting soil (Fleischner 1994). Floristic grazing response has been well studied, however the effect of grazing on vertebrate fauna is more complex and has received less attention (Chapter 1). The extent that fauna species are impacted by livestock grazing depends on whether they rely on the niches affected by grazing (Milchunas et al. 1988).

While grazing can impact species through a variety of direct and indirect mechanisms, species' habitat preference may be useful in predicting their grazing response (Martin and Possingham 2005).

Digging and burrowing mammals are present on many rangelands (areas grazed by domestic livestock) and are important ecosystem engineers. Through their activities, digging mammals aerate soil, incorporate nutrients, create litter traps and disperse seeds and fungal spores (Eldridge and James 2009). These activities, can, in turn, influence hydrology, nutrient cycling, the structure of vegetation communities and the habitat structures available to other vertebrate fauna (Davidson et al. 2012; Valentine et al. 2017).

Most digging and burrowing mammals rely on ground-level habitat, therefore, may be strongly impacted by ground-level grazing disturbance. The responses of several burrowing species to grazing have been investigated, and can be positive (e.g., prairie dogs and ground squirrels in North America; (Davidson et al. 2010; Bylo et al. 2014)) or negative (e.g., marmots in central Asia; (Poudel et al. 2016), tuco-tucos in South America; (Rosi et al. 2009)), and some species have no response to grazing (e.g. giant mole-rats in Africa (Vial et al. 2011)). Across the extensive rangelands of Australia, the cumulative impacts of livestock grazing in association with drought, altered fire regimes and introduced predators, are responsible for the decline and extinction of many digging mammals (Legge et al. 2011; Woinarski et al. 2011). These mammal species play a critical role in maintaining healthy soils, and their loss further exacerbates the impact of ongoing anthropogenic disturbances (Eldridge and James 2009; Fleming et al. 2014).

Rufous bettongs (*Aepyprymnus rufescens*; Gray, 1837) are medium-sized marsupials (1.3-3 kg) found on Australian rangelands; and are the largest and most widely-distributed member of the family Potoroidae (Van Dyck and Strahan 2008). This nocturnal species lives in grassy woodlands and feeds on herbs, grasses, and invertebrates. They do not dig burrows, instead sheltering in grass 'nests', but dig for root tubers and underground fruiting fungi (Claridge et al. 2007). Fruiting fungal bodies, or 'truffles', form a beneficial symbiosis with tree roots, and rufous bettongs facilitate truffle spore dispersal through their faeces (Reddell et al. 1997; Nuske et al. 2017). While microhabitat use by rufous bettongs has not been explicitly examined, similar species require access to foraging areas to dig for fungi and grassy shelter sites where they can build nests (Claridge et al. 2007).

Rufous bettongs were historically widespread, but have declined in the southern and western extents of their distribution, partly attributed to predation by the introduced red fox (*Vulpes vulpes*) and the impact of agriculture (Claridge et al. 2007). However, the response of rufous bettongs to grazing is unknown and has not been tested experimentally. The Tasmanian bettong (*Bettongia gaimardi,* Potoroidae), responded to increasing grazing intensity by foraging less in those areas where native grasses where removed by livestock (Driessen et al. 1990). The authors speculated that grazing-related soil compaction may impede fungal growth and the Tasmanian bettongs' ability to dig and access this food resource.

In this study, I quantified rufous bettong population dynamics and habitat selection, among four different grazing treatments and between two different vegetation at a long-term cattle-grazing trial in tropical savanna woodland in northern Australia. To measure habitat selection, individuals were marked and recaptured over 4 trapping sessions in two years. I aimed to identify if rufous bettong abundance was responding to different grazing treatments and vegetation types, and then if individuals were selecting or avoiding certain microhabitat features. Due to this species' use of ground-level habit structures for shelter and food, I predicted that rufous bettongs would avoid the most disturbed areas, with reduced ground cover, and prefer areas with high grass cover and more complex terrestrial structures.

Materials and methods

This study was conducted at the Wambiana Grazing Trial, see Chapter Two for a detailed site description.

Mammal surveys

In each grazing treatment, six 1-ha sites were established; a total of 24 sites across the grazing trial (Chapter 2, Figure 2.2). Sites were either in the ironbark or box vegetation communities. In total, four surveys were conducted: twice a year (April and October), over two years (2014 and 2015). To trap rufous bettongs we used wire cage traps (710 x 305 x 305 mm) baited daily with balls of peanut butter, rolled oats and vanilla essence. Two cage traps were set at each site, 50 m apart. The cage traps were operated for a 10-night period. They were opened at dusk, checked in the morning just before dawn, and then closed during the day. Any animals captured were removed from the traps, identified, measured and marked with a unique ear clip combination and released at the site of capture. Species nomenclature followed Dyck and Strahan (2015).

Microhabitat surveys

Within each 1-ha site, terrestrial microhabitat variables were recorded along 3 x 100 m parallel transects. Ground cover was categorised as bare ground, leaf litter >5mm, leaf litter 5-10mm, rock, fine woody debris (<10cm diameter) or coarse woody debris (>10cm diameter). Vegetative cover along the transect was categorised as grass (with grass height also recorded), shrub or tree. Other features were measured along the transects including termite mounds and burrows. The cover values were converted to mean percentages. Microhabitat variables were measured during each of the trapping surveys.

Data Analysis

Population dynamics

To investigate rufous bettong population dynamics, mark-recapture data was analysed in Rcapture (Rivest and Baillargeon 2015). I used a robust design analysis, due to the hierarchical nature of the trapping data, i.e., within a trapping session (10 consecutive days of capture) the population is assumed to be closed (not experiencing immigration or mortality), but between each trapping session the population is considered open. A robust design can generate estimated abundances for each trapping session and survival rates between periods.

Grazing treatments, vegetation type and microhabitat use

Rufous bettong response to grazing treatment and vegetation type was examined using a generalised linear mixed model, with a negative binomial distribution. Grazing treatment and vegetation type were fixed effects and year and season were included in the model as random effects (*lme4*; Bates et al. 2015). Model selection was performed using the Akaike

Information Criterion (AICc) from the dredge function in *MuMIn* (Bartoń 2015). The optimal model was validated by examining the deviance residuals.

Rufous bettongs can move over large areas and between sites, therefore abundance modelling was complemented by analysing how individuals (identified through mark-recapture) chose habitat compared to what was available. To investigate rufous bettong use of grazing treatment, vegetation type and microhabitat variables, I performed habitat selection analyses using *adehabitatHS* (Calenge 2016). The microhabitat variables (mean percentage cover) were categorised as low, medium or high depending on their available range. Each trapped individual was identified and habitat use was recorded for each individual, therefore the data was structured as a ‘design II study’. Due to the vagile nature of the study species, habitat units were considered equally available to all individuals. Manly selection ratios (Manly et al. 2002) were used calculate habitat availability to habitat use, for each animal, for each habitat type and then averaged over all individuals.

Results

Population dynamics

Across four surveys and 1920 trap nights, 46 unique individuals were captured and 16 were subsequently recaptured (Table 5.1). Overall, I estimated that 55.8 ± 4.6 (S.E.) individuals inhabited the survey area, with estimated density peaking in April 2014 and declining to the lowest density in October 2015 (Figure 5.1). Capture probabilities remained high throughout the four surveys, but survival probabilities between surveys more than halved between survey three and four (Figure 5.1). In April 2014, four joeys were recorded from four females, and in

October 2014 one joey was recorded from a different female. No joeys were recorded in 2015.

Table 5.1: Trap success, recapture rates, sex ratios and population size of rufous bettong *(Aepyprymnus rufescens*) captures at each trapping session

Survey session	Trap nights	Trap success %	No. animals trapped	Estimated Density (estimated number/ha)	No. unique trapped females	No. unique trapped males	Sex ratio F:M	Recapture rate all %
April 2014	480	7.71	37	0.03	9	15	1:1.7	0
October 2014	480	5.83	28	0.02	8	8	1:1	75.0
April 2015	480	8.33	40	0.02	7	14	1:2	70.0
October 2015	480	4.17	20	0.01	7	5	1:0.71	60.0

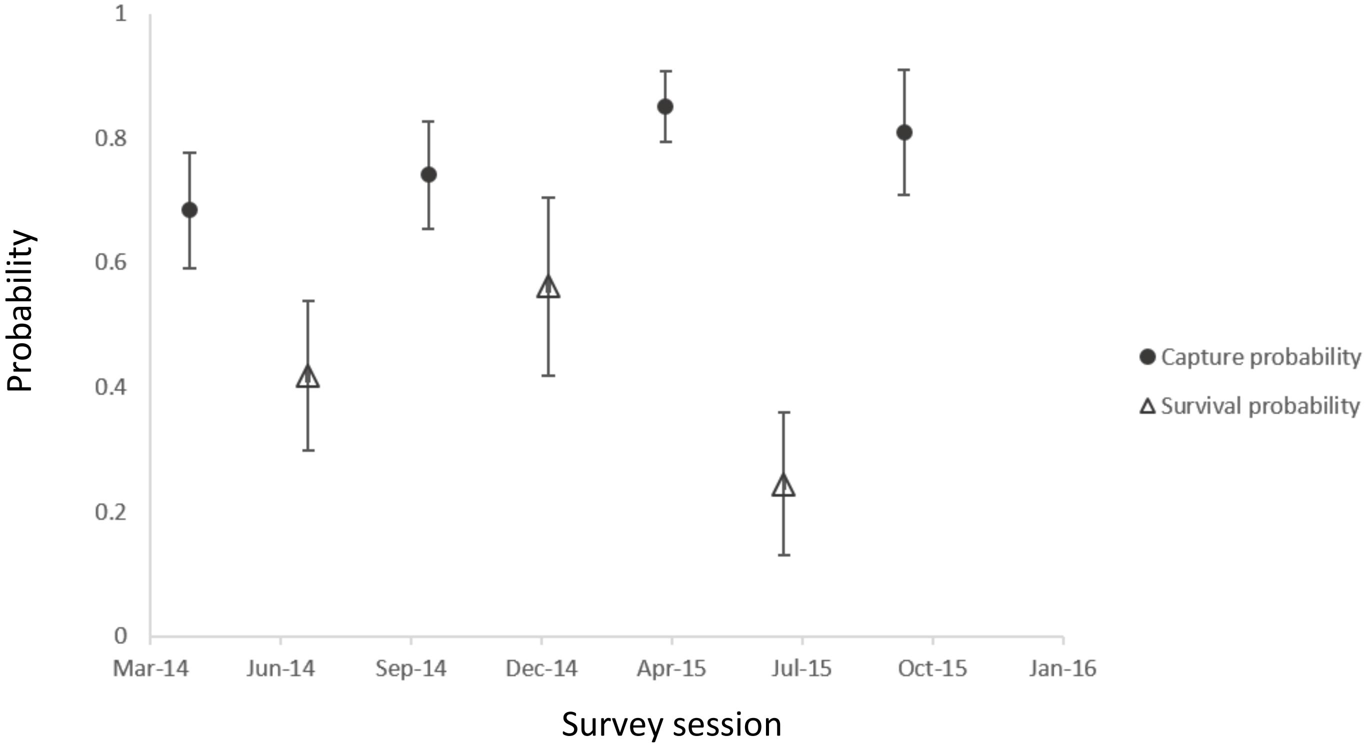


Figure 5.1: Estimated capture probability at each survey session and survival probability between survey sessions +/- S.E., for rufous bettong (*Aepyprymnus rufescens)* population.

Grazing treatments, vegetation type and microhabitat use

Rufous bettong abundance responded to the interaction between grazing treatment and vegetation (grazing*vegetation, p=0.05; Figure 5.2). Within box, abundance was similar among grazing treatments, however in the ironbark, the heavy grazing treatment was much lower than the moderate, rotational and variable grazing treatments. Although the interaction term was significant, when using AICc for model selection the top generalised linear mixed model included vegetation type only (ΔAICc = 0). This was followed by the null model (ΔAICc = 1.50) and then the model containing the grazing * vegetation term (ΔAICc = 6.37).

On average, individuals selected ironbark (Manly selection ratio = 2.04 ± 0.95 SE) and avoided box (0.48 ± 0.47 SE; Figure 5.3a). Rufous bettong individuals avoided the heavy grazing treatment (0.49 ± 0.49 SE) but had no significant selection for the other grazing treatments (Figure 5.3b).

The microhabitat category ranges were assigned based on the availability of that variable within the grazing trial (Table 5.2). The mean percentage cover of leaf litter >5 mm, coarse woody debris, fine woody debris and termite mounds was relatively low, never reaching more than 5% at any of the sites. On average, rufous bettongs had a significant preference for sites with medium leaf litter < 5 mm, high grass height and low *Carissa ovata* cover. They avoided sites with high bare ground, low grass, low leaf litter <5 mm, high coarse woody debris, high fine woody debris, low or medium grass height, and medium *Carissa ovata* (Figure 5.4a-i).

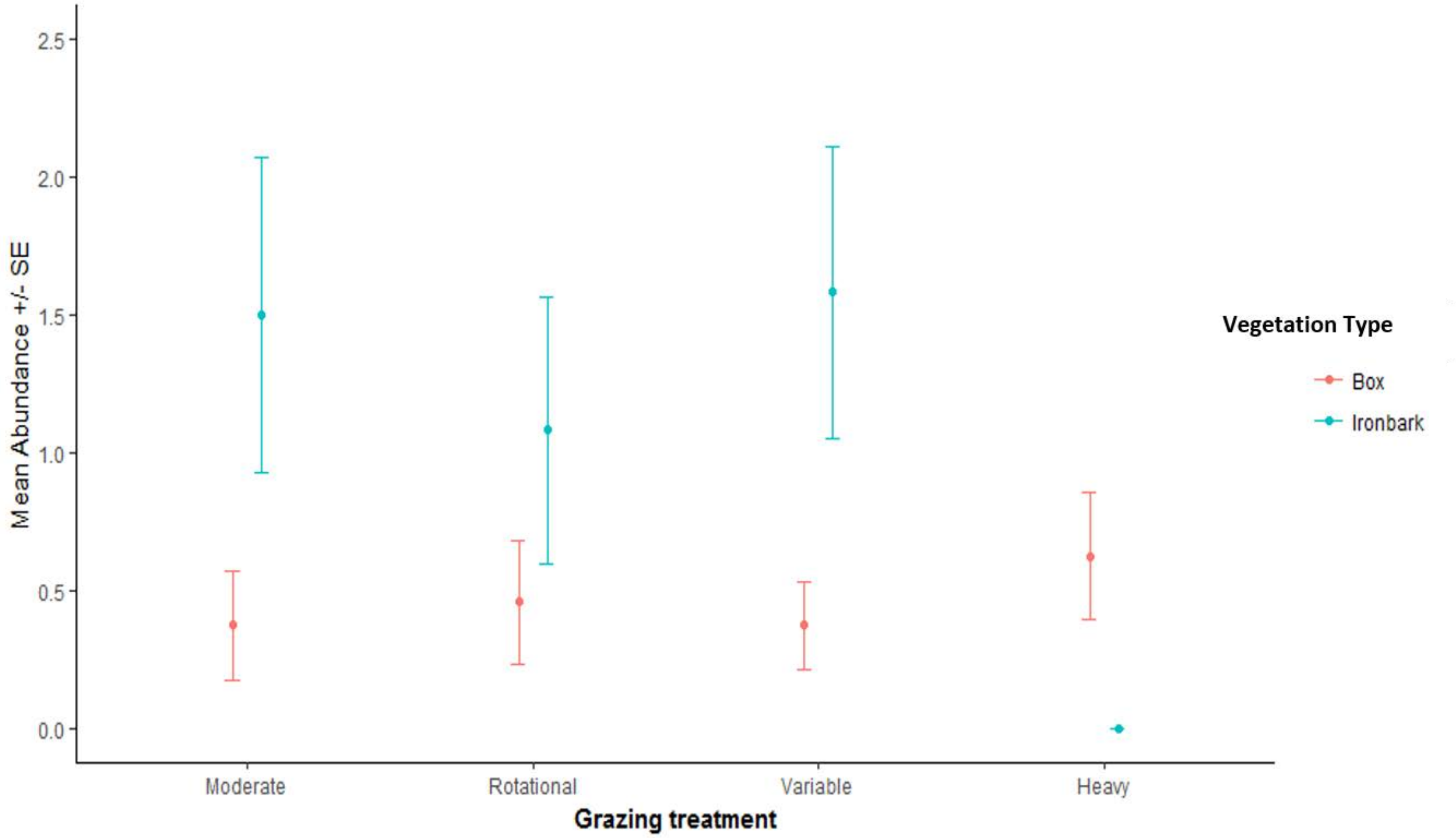


Figure 5.2: The mean abundance +/- standard error of Rufous Bettong (*Aepyprymnus rufescens*) across four grazing treatments and two vegetation types.

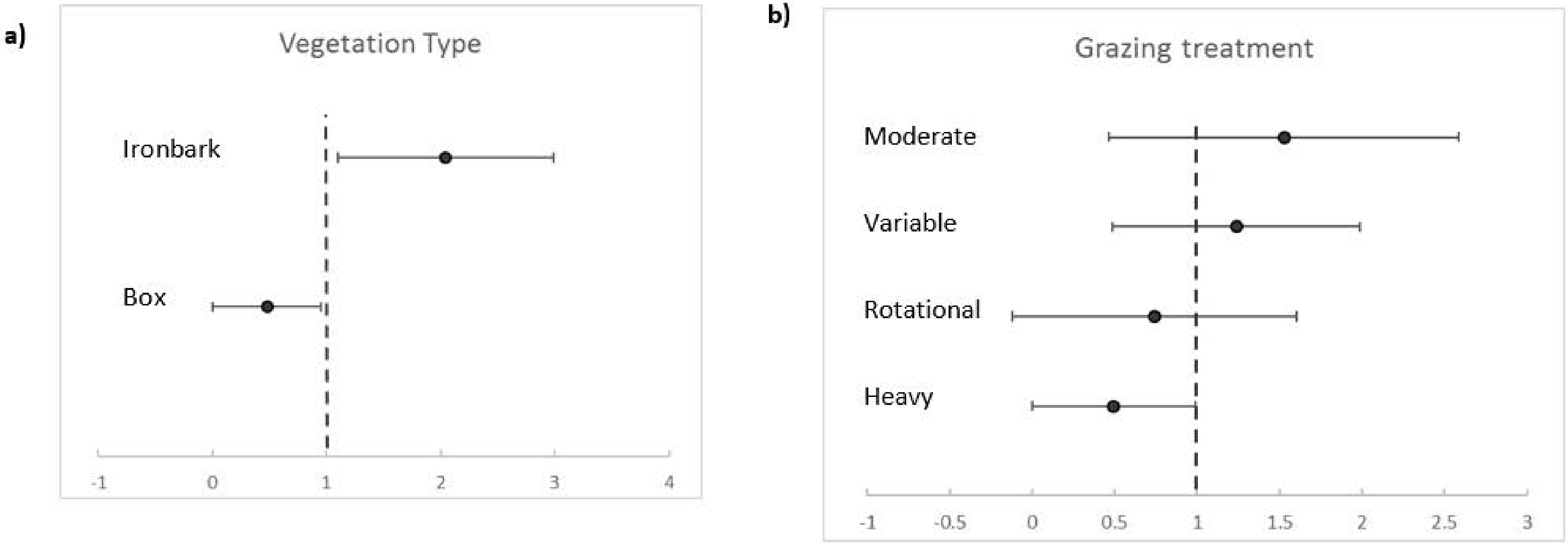


Figure 5.3: Mean Manly selection ratios with 95% confidence interval for rufous bettong (*Aepyprymnus rufescens*) use of: a) vegetation type; and b) grazing treatment. Variables are 'selected' where Manly selection ratio is >1, and 'avoided' where Manly selection ratio is >1. Results are considered significant were the 95% confidence intervals do not cross one.

Table 5.2: The range of different microhabitat variable categories (low, medium and high) and the relative availability of each microhabitat category at the study location, used in habitat selection analyses.

Microhabitat variable	**Microhabitat category range**			**Relative availability**		
	Low	**Medium**	**High**	**Low**	**Medium**	**High**
Bare ground (mean % cover)	0-20	20-50	50+	0.54	0.40	0.10
Grass (mean % cover)	0-15	15-30	30+	0.50	0.25	0.50
Leaf litter < 5mm (mean % cover)	0-30	30-60	60+	0.17	0.75	0.17
Leaf litter > 5 mm (mean % cover)	0-1	1-2	2+	0.75	0.13	0.13
Coarse woody debris (mean % cover)	0-0.75	0.75-1.5	1.5+	0.58	0.33	0.10
Fine woody debris (mean % cover)	0-0.75	0.75-1.5	1.5+	0.75	0.13	0.75
Termite mound (mean % cover)	0-0.75	0.75-1.5	1.5+	0.54	0.42	0.04
Grass height (mean height cm)	0-25	25-50	50+	0.25	0.33	0.42
Carissa ovata (mean % cover)	0-10	10-20	20+	0.42	0.40	0.21

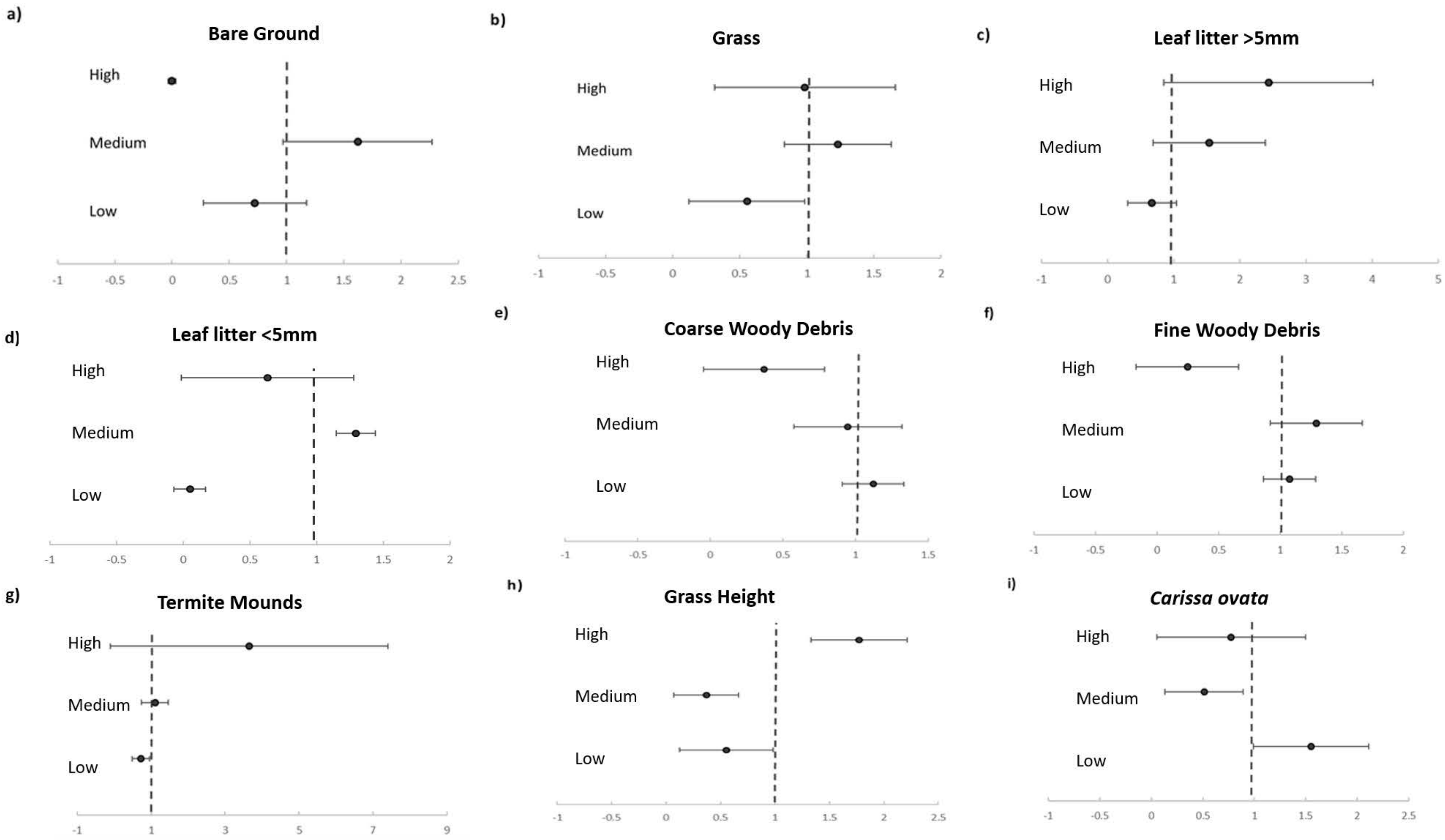


Figure 5.4: Mean Manly selection ratios with 95% confidence interval for rufous bettong (*Aepyprymnus rufescens*) use of microhabitat variables. Microhabitat variables are 'selected' where Manly selection ratio is >1, and 'avoided' where Manly selection ratio is >1. Results are considered significant were the 95% confidence intervals do not cross one.

Discussion

I have shown that rufous bettongs were impacted negatively by heavy grazing, and this is partly attributable to microhabitat selection. However, they showed no difference in their preference for the other, more conservative, grazing treatments. This may indicate that rufous bettongs can tolerate moderate levels of grazing, as supported by their persistence in northern Australia, where livestock grazing is extensive and rufous bettong populations are secure (Van Dyck and Strahan 2008). In their southern and western extent, where they have declined, more intensive agriculture is coupled with high fox densities (Johnson et al. 1989). While low densities of cats and dingos were present in the study area, most of northern Australia is free from foxes (HN pers. obs.; Van Dyck and Strahan 2008). Less intense grazing regimes in northern Australia, the absence of foxes and the comparatively broad diet of rufous bettongs (Nuske 2016), may explain why, as a species, rufous bettongs have fared better than many digging mammals in the ‘critical weight range’ (Fleming et al. 2014).

In my study, rufous bettongs clearly selected the ironbark vegetation, and within the ironbark they avoided the heavy grazing treatment. Further, their preference for ironbark was negatively associated with cattle utilisation rates. Cattle preferentially grazed the box, where there were more palatable grasses, but when stocking rates were high, they also consumed less palatable species found in the ironbark, i.e. in the heavy grazing treatment in ironbark (O’Reagain and Bushell 2011). Therefore, by selecting the moderate, rotational wet-season spelling and variable ironbark sites, rufous bettongs avoided the highest cattle densities. The areas with lower cattle densities were associated with high grass, which rufous bettongs preferred over low or medium grass height. The presence of long grass is important to rufous bettongs, who shelter during the day in cone-shaped grass nests (Van Dyck and Strahan

2008). Rufous bettongs preferences for other variables were mixed; and did not always favour more complex ground features as predicted. This is perhaps due to a requirements for a mosaic of microhabitats, as has been found in other potoroid species (Norton et al. 2010).

High capture probabilities suggested the rufous bettong population estimates were reliable. These estimated densities were much lower than those recorded in wetter areas, east of the great dividing range in the Townsville region, but huge variation in densities have been recorded in relation to soil fertility (Johnson et al. 2005). The home range of rufous bettongs is also highly variable, from 15ha – 107ha, suggesting that at this 1041 ha study location there was likely home range overlap between the 46 individuals I marked (Frederick and Johnson 1996; Johnson et al. 2005). In 2015, the driest year of the study, breeding was not observed, and estimated survival rates were low. In northern NSW, rufous bettongs declined in drought conditions and sought water in dried stream beds (Claridge et al. 2007). It is possible that rufous bettongs seeking free water moved out of the grazing trial during 2015 to nearby permanent water storage dams.

Rufous bettong individuals could move freely between sites, therefore, abundance modelling provided limited insight into this species' responses to grazing and vegetation. However, spotlighting data recorded over the trapping sessions did support the abundance trends observed from trapping data (HN unpublished data). While the grazing and vegetation interaction term was a weak predictor of rufous bettong abundance, there was discord between the model significance and model selection results. Consequently, the habitat selection analyses (from mark-recapture data) provided a better description of use of grazing treatments by rufous bettongs in relation to vegetation types and microhabitat features. There are limitations in using mark-recapture data, compared to GPS tracking data, to analyse habitat selection. While I have not tracked individuals across their entire range (as would be possible with GPS tracking data), my site level microhabitat data is very detailed, providing insight into habitat use at scales relevant to rufous bettongs.

Although microhabitat selection is often investigated as a mechanism likely driving grazing responses (e.g. Chapter 1, 3, 4, 6), rufous bettongs could be responding to other direct and indirect grazing impacts, as observed in other fossorial mammals in rangelands (Rosi et al. 2009; Poudel et al. 2016). High cattle densities may increase the chance of nest trampling and could be a reason for bettongs to avoid the heavy grazing treatment. Furthermore, soil compaction may reduce the ability of rufous bettongs to dig in the soil and access below-ground food resources (Driessen et al. 1990). It is likely that rufous bettongs are responding to a combination of direct and indirect grazing impacts and it would be beneficial to experimentally test these potential mechanisms.

Along with the impact of feral predators, it is likely that fire has an important effect on rufous bettong abundance, particularly considering that fire can promote truffle growth (McMullan-Fisher et al. 2011). Increased access to below-ground food resources may explain the positive response of rufous bettongs to fire in tropical savannas (Abom et al. 2016). While this study design is useful because it isolates the impact of grazing, it is clear that many other threats occur and interact with grazing on rangelands, and need to be considered holistically when devising management recommendations (Eyre et al. 2011).

Management implications

The management of digging mammals in rangelands deserves attention due to their role as ecosystem engineers and the benefits of their activities on soil health (Eldridge and James 2009; Eldridge et al. 2016). As such, ecosystem engineers should be a focus for conservation, as their presence can positively impact a suite of species (Crain and Bertness 2006). Digging and burrowing animals not only enhance habitat heterogeneity (Parsons et al. 2016), thus creating habitat for other small mammals, reptiles and invertebrates (Davidson et al. 2008; Ewacha et al. 2016), but can influence ecosystems through non-engineering pathways such as predation and competition (Prugh and Brashares 2012). Therefore, maintaining ecosystem engineer populations may be a cost-effective tool to lessen the negative impacts of grazing on soil health, restore degraded habitats and assist in the recovery of other species of conservation concern (Eldridge and James 2009; Eldridge et al. 2016; McCullough Hennessy et al. 2016).

Summary

Ecosystem engineers play an important role in resource availability and can be negatively impacted by anthropogenic disturbances, such as livestock grazing. The decline of digging and burrowing mammals in Australia is partly attributed to agriculture, however little is known about their use of microhabitats, and thus, how they respond to different cattle grazing regimes. Here, I examine the response of a marsupial ecosystem engineer, the rufous bettong (*Aepyprymnus rufescencs*) to cattle grazing strategies and vegetation types, and examine whether microhabitat selection is driving this response. I hypothesised that rufous bettongs would be negatively impacted by heavy cattle grazing due to their use of ground-level microhabitat features. I conducted a mark-recapture trapping survey among four grazing treatments and in two vegetation types (box and ironbark woodlands), at a long-term grazing trial in northern Australia. I modelled rufous bettong abundance in response to grazing treatment and vegetation type and determined microhabitat preference using Manly selection ratios. I found that rufous bettongs preferred ironbark and avoided heavy grazing. Thus, they avoided the areas of highest cattle utilisation. On average, individuals preferred high grass and other terrestrial microhabitat variables of moderate complexity. My results indicate that habitat selection is contributing to the response of a marsupial ecosystem engineer to different grazing strategies. Mammalian digging and burrowing ecosystem engineers should be a conservation focus on rangelands due to their positive influence on a suite of species and their ability to potentially mitigate some of the negative impacts of cattle grazing on soil health.

Chapter Six

Adapted from: Neilly, H., Nordberg, E., Vanderwal, J. & Schwarzkopf, L. (2018) Arboreality increases reptile community resistance to disturbance from livestock grazing. *Journal of Applied Ecology* 55(2), 786-799.

Arboreality increases reptile community resistance to disturbance from livestock grazing

Introduction

Grazing by domestic livestock occurs across 25% of the Earth's land surface (Asner et al. 2004) and is implicated as a contributing factor in the decline of vertebrate species' richness and abundance (Donald et al. 2001). The extent of grazing impact will depend on how much that species relies on the niches that are affected by grazing (Milchunas et al. 1988). Grazing alters ground-level habitat structures such as vegetation, woody debris and leaf litter (Eldridge et al. 2011; Brown et al. 2011). It is, however, unclear exactly how grazing effects arboreal habitat. Alterations in habitat structure affect the vertebrate fauna that live in grazed environments, potentially impacting on their ability to access food, avoid predation, and thermoregulate (Chapter 1). Grazing impacts can have a positive effect on species, causing them to increase in abundance ('increasers'), have a negative effect ('decreasers'), or have no effect.

Within a fauna community, the presence of increaser species, or a lack of decreaser species, suggests a degree of resistance to grazing. Here, 'resistance' means the ability to tolerate (i.e. not be negatively impacted by) livestock grazing (Carpenter et al. 2001). Resistance may be represented by an increase in abundance, or no detectable response to grazing. In arid

Australia and North America, some reptiles show no response to grazing, due to their preference for the open habitats and higher ground temperatures promoted by heavy grazing (Read 2002; Read and Cunningham 2010; Germano et al. 2012). Likewise, bird communities can remain unaffected by grazing or even show an increase in diversity, provided trees are not cleared (Martin and McIntyre 2007; Lusk and Koper 2013). At a functional group or species level, heavy grazing may facilitate predation (Curry and Hacker 1990; Kutt et al. 2013; Piana and Marsden 2014) or affect predator avoidance strategies (Pettigrew and Bull 2014; Bylo et al. 2014). Overall, those species resistant to grazing either benefit directly or indirectly from the structural changes at ground level, or avoid these areas by using other habitat strata, for example arboreal niches.

The degree to which ‘arboreality’ influences a species’ response to grazing impacts, has been explored for birds, where bird foraging height has been used to predict species response to grazing (Martin and Possingham 2005; Kutt and Martin 2010), but has yet to be explicitly addressed in reptiles. Arboreal reptiles are abundant in disturbed areas, including areas grazed by domestic livestock (Woinarski and Ash 2002; Knox et al. 2012) and generally use upper-strata microhabitats such as tree hollows, cracks and fissures in dead branches, and loose bark (Gibbons and Lindenmayer 2002). Therefore, they may be unaffected by ground-level disturbances because they spend little time in the altered habitat layer. They may also benefit where other species have declined due to reduced competition for food and other resources.

The effect of grazing on arboreal habitat has received less attention compared to the obvious, ground-based impacts. However, livestock may indirectly affect trees through soil compaction (Fleischner 1994), consuming or trampling saplings (Pitt et al. 1998), breaking low branches or consuming palatable shrubs (Jones 1981). Furthermore, soil compaction leads to excess run-off, erosion, and ultimately a decrease in water infiltration to root systems (Castellano and Valone 2007). Bare ground, created by a lack of herbaceous foliage, grasses, or even leaf litter, can lead to increased soil temperatures, resulting in high evaporative water loss (Yates et al. 2000). A decrease in water and nutrient absorption begins to change the vegetation community and structure, including trees, leading to desertification (Fleischner 1994; Blesky and Blumenthal 1997). Arboreal species may also respond to grazing-related land management techniques, such as tree clearing. Tree clearing is used in conjunction with livestock grazing to promote grass growth, directly impacting arboreal fauna by removing habitat (Gibbons and Lindenmayer 2000; Martin and McIntyre 2007).

Here I investigate the response of arboreal and terrestrial reptile communities to four different cattle grazing strategies at a long-running, experimental grazing trial in a northern Australian, tropical savanna woodland. The reptile community at this location is diverse and abundant and, importantly, operates at scales appropriate to the size of this grazing trial, as opposed to more vagile avian and mammalian fauna. I measured the effect of different grazing treatments on ground and arboreal habitat, hypothesising that ground-level habitat would be more impacted than arboreal habitat. I aimed to identify how arboreal and terrestrial reptiles responded to the grazing treatments as a community, as functional groups and individual species. I predicted that those species that relied on ground-level heterogeneity (e.g., ground-dwelling litter skinks) would likely respond negatively to higher levels of grazing. Conversely, I predicted that arboreal reptile species may be more likely to exhibit resistance to the effects of grazing.

Materials and methods

This study was conducted at the Wambiana Grazing Trial, see Chapter Two for a detailed site description.

Reptile surveys

Twenty-four 1-ha sites were established, with six sites located in each of the four grazing treatments. Additionally, sites were located in different vegetation types; 16 in Reid River Box and eight in Silver-leaf Ironbark. The different number of sites in the vegetation communities reflects their relative area within each paddock. The sites were located at least 100m from vegetation boundaries and 200m from cattle watering points. Within a treatment and vegetation type, adjacent sites were at least 400m apart. Species detectability was assumed to be equal as standardised survey methods were used at each site and my primary aim was to compare among treatments.

Terrestrial reptile survey

Four surveys were conducted to assess the terrestrial reptile community. These occurred in 2014 and 2015, in April (end of the wet season) and October (end of the dry season). At each site, a trap array was set-up and comprised: 4 x 30cm diameter pitfall buckets at 10m intervals in a ‘T’ configuration, intersected by drift fence (one 20m length and one 10m length); and 6 x funnel traps (18cm x 18cm x 79cm), two placed either side of the drift fence at each of the 3 ends of the fence. Pitfall and funnel traps were opened for 10 nights and checked twice daily. Captured animals were removed from traps, identified, weighed, measured and then released at the site of capture.

Arboreal reptile survey

Timed nocturnal spotlighting was conducted at each site, twice per trapping session, where observers searched the ground, bushes and trees for arboreal reptiles. I conducted 16 spotlight surveys (5.3 person-hours) per site between 2014 and 2015. In addition, 24 arboreal cover boards (ACBs; Nordberg and Schwarzkopf 2015) were used to monitor populations of both diurnal and nocturnal arboreal lizards in April and October of 2015 only (total of 2304 trap nights). ACBs were set up a day prior to the surveys, allowing animals time to utilize the shelters and then checked each morning (0700 - 1100 h). Due to variation in trapping methods and survey dates, capture data of *Cryptoblepharus australis,* was excluded from community analysis, but was used for individual species analyses.

Microhabitat surveys

Structural complexity of microhabitat features was measured during each of the four reptile surveys. At each site, 3 x 100 m parallel transects, 50m apart, were established. Terrestrial features such as ground cover (e.g., bare ground, leaf litter, grass cover, etc.) were categorized along each transect (Table 6.1). All trees within one metre on either side of the transects were identified and their height and diameter at breast height (DBH) was measured. Arboreal habitat characteristics were measured in overstory trees throughout the site, including canopy cover, number of dead trees and hollows (Table 6.1).

Table 6.1 The microhabitat characteristics that were surveyed with a description of methodology.

Habitat characteristics	**Description**
Terrestrial	
Ground cover	A tape measure was laid on the ground along the 100m transect. The amount of bare ground (BG), rock, leaf litter (LL) and leaf litter depth (mm), fine woody debris (<10cm diameter) (FWD), coarse woody debris (>10cm diameter) (CWD) was recorded and converted into a percentage.
Vegetative cover	Along the 100m transect, the amount of grass (and grass height), shrub and other vegetative cover was recorded and converted into a percentage.
Other features	Other ground features were noted along the 100m transect including termite mounds, and burrows.
Arboreal	
Trees	Any tree that fell 1-m either side of the 100m transect was identified and measured for diameter at breast height (DBH) (cm) and height category (m)
Canopy Cover (%)	Estimated canopy cover *via* spherical densitometer.
Distance to nearest tree (m)	Distance (m) between adjacent trees >2 m tall.
Bark Index (1-3)	An index of bark roughness/flakiness ranging from 1-3; 1 representing little or no flaking bark, and often little no known refuge options for sheltering lizards; 3 represents very flaky and loose bark with ample refuge microhabitats available for sheltering lizards.
Canopy connectivity (%)	The percentage of overstory trees sampled that had overlapping canopy or branches.
Tree hollows (%)	The percentage of overstory trees sampled that had hollows or cavities visible from the ground.

Data Analysis

I used a range of complementary univariate and multivariate analyses in R (R Core Team 2016). Where relevant, optimal models were determined by comparing models based on the Akaike Information Criterion (AICc) using the *dredge* function in *MuMIn* (Bartoń 2015), pairwise comparisons were made of the terms in the optimal model using the Tukey test in *lsmeans* (Lenth 2016) and the final models were validated by examining the deviance residuals.

Habitat characteristics

Structural habitat features were analyzed using two-way analysis of variance to investigate the effects of vegetation type and grazing treatment on the mean cover of structural variables in the lower strata (ground level) as well as mean values for arboreal habitat characteristics. Pairwise comparisons were made using Tukey's tests.

Reptile abundance and richness

Abundance and species richness were collated for a trapping session (n=96) for arboreal and terrestrial species. Generalised linear mixed models (GLMM) with a negative binomial distribution (accounting for overdispersion) were used to examine abundance and species richness in relation to grazing treatments and vegetation type (fixed effects), with year and season as random effects (*lme4*; Bates et al. 2015). Variables were explored for collinearity before including them in the model.

Reptile community composition

Arboreal and terrestrial community compositional differences were explored using a multivariate extension of a generalised linear model (GLM), using the function *manyglm* in *mvabund* (Wang et al. 2012). This analysis is an alternative to distance-based multivariate analyses. Multiple GLMs are fitted to many variables simultaneously and an *anova.manyglm* function can be used for hypothesis testing. Univariate test statistics and p-values were calculated for each species in the model to indicate their relative contribution to the overall variance among the communities. I constructed a site-by-species table populated by the abundance of species that were present in at least five sites. This function does not allow for mixed effects models and so each year was analysed separately. Multivariate GLMs with a negative binomial distribution were applied, with grazing treatment, vegetation type, season and year (and their interactions) as the explanatory variables. Arboreal and terrestrial reptile communities were modelled separately. To visualise the overall community response to grazing I plotted the standardised model co-efficients from a GLM with LASOO penalties to create a ‘heat-map’ (Brown et al. 2014). Reptile species taxonomy followed Wilson (2015).

Individual species and functional group responses

GLMs, with a negative binomial distribution, were used to analyse the responses of the most abundant arboreal and terrestrial species, and functional groups, to the relevant arboreal and terrestrial microhabitat variables (Table 6.1). I analysed two terrestrial functional groups: diurnal litter skinks and terrestrial geckos, and one arboreal functional group: arboreal geckos (Appendix 1). Their responses to grazing treatment and vegetation type (landscape-scale variables) were analysed with GLMMs using year and season as random effects (*lme4*; Bates et al. 2015). A poisson or negative binomial distribution was applied where appropriate.

Results

Microhabitat Characteristics

Grazing treatment had a major effect on the structural complexity available to terrestrial reptiles. Six of eight terrestrial habitat features were significantly affected by grazing treatment (Figure 6.1). Grass cover, grass height, leaf litter, and coarse woody debris were all greatly reduced in areas with high stocking rates. In the heavy grazing treatment (H), the consumption of grasses and leaf litter by cattle lead to large areas with bare ground and low structural complexity. Conversely, only two of 10 arboreal habitat characteristics (% Canopy connectivity and # Trees > 30 cm DBH) were significantly different among the grazing treatments (Figure 6.2, Appendix 2, Table 1).

Reptile abundance and species richness

Over 3840 pitfall and 5760 funnel trap nights, 684 terrestrial reptiles of 18 species were observed. Over 57.6 hours of spotlighting and 288 ACB trap nights, 624 arboreal reptiles of 8 species were observed. The optimal GLMM for terrestrial reptile abundance included grazing treatment and vegetation type (Table 6.2, Figure 6.3a). The moderate (M), rotational wet-season spelling (R) and variable (V) treatments, all had significantly higher terrestrial reptile abundance than in H, but were not different from each other. Overall, the H sites in Ironbark had significantly lower terrestrial reptile abundance than all the other grazing treatment and vegetation type combinations. The Box vegetation type had higher terrestrial reptile abundance than the Ironbark.

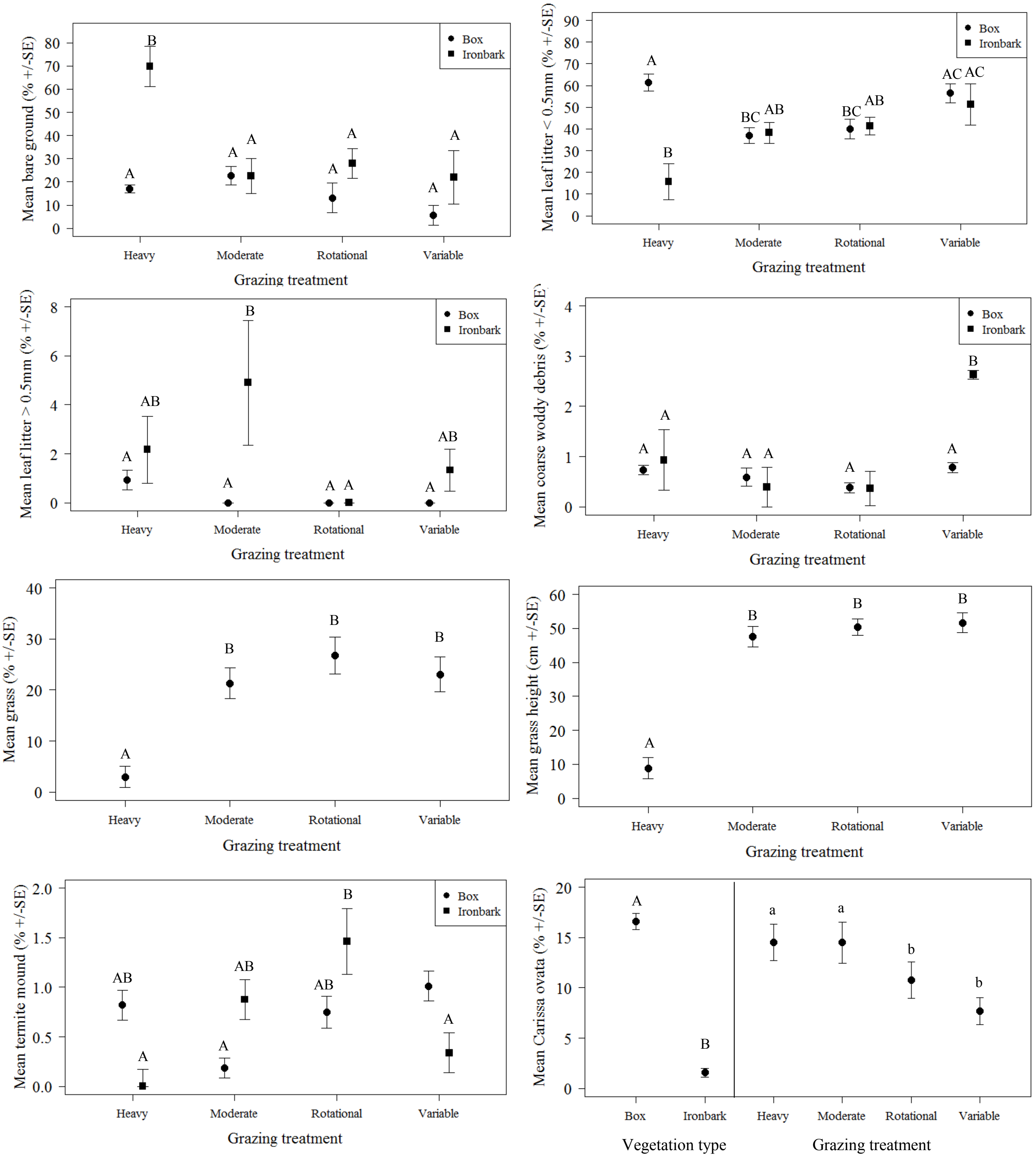


Figure 6.1 Mean ± SE measures of terrestrial habitat characteristics. Only terms with a significant difference are presented, indicated by different letters (2-way ANOVA; Tukey posthoc test; α = 0.05)

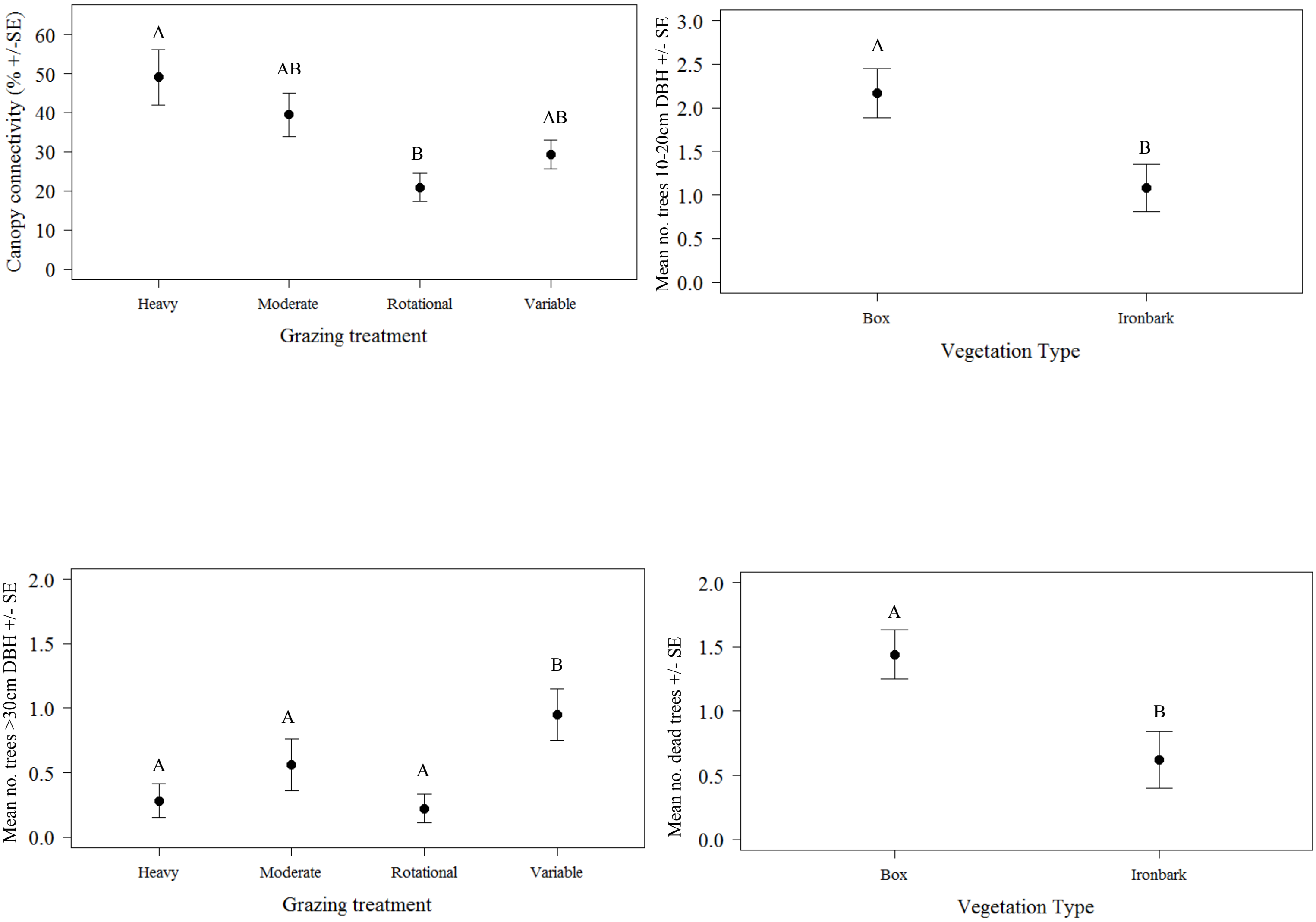


Figure 6.2 Mean ± SE measures of arboreal habitat characteristics. Only terms with a significant difference are presented, indicated by different letters (2-way ANOVA; Tukey posthoc test; $\alpha = 0.05$)

Table 6.2 The relationship between reptile abundance and reptile species richness and grazing treatment, vegetation type and season as described by a generalized linear mixed model (GLMM) with negative binomial distribution. Grazing treatment, vegetation type are fixed effects and year and season are random effects. The top model is reported based on AIC values. *Response variable ~1* indicates the null model. Post hoc Tukey tests were used to examine the effect of each factor level and significant differences (p<0.05) are reported.

Response Variable	**Model**	**df**	**Log Likelihood**	**AIC**	**ΔAICc**	**AICc weight**	**Post hoc test**
Terrestrial Reptile Abundance	Grazing + Vegetation	8	-262.837	543.3	0	0.521	Grazing Moderate>Heavy Rotational>Heavy Variable>Heavy Vegetation Box>Ironbark
	Grazing*Vegetation	11	-259.424	544.0	0.66	0.374	Grazing * Vegetation Moderate Box> Heavy Box Moderate Box> Heavy Ironbark Rotational Box> Heavy Ironbark Variable Box> Heavy Ironbark Moderate Ironbark>Heavy Ironbark Rotational Ironbark>Heavy Ironbark
	Grazing	7	-265.634	546.5	3.21	0.105	As above
Terrestrial Reptile Richness	~Vegetation	5	-168.561	347.8	0	0.252	Not significant
	~1	4	-169.737	347.9	0.12	0.237	
	Grazing	7	-166.359	348.0	0.20	0.228	
Arboreal Reptile Abundance	Grazing + Vegetation	8	-214.477	446.6	0	0.856	Grazing Heavy>Moderate Variable>Moderate Vegetation Ironbark>Box
	Vegetation	5	-220.585	451.8	5.23	0.063	As above
	Grazing * Vegetation	11	-213.398	451.9	5.33	0.060	Not significant
Arboreal Reptile Richness	~1	4	-100.222	208.9	0	0.669	Not significant
	Vegetation	5	-100.042	210.8	1.87	0.263	
	Grazing	7	-99.406	214.1	5.2	0.050	

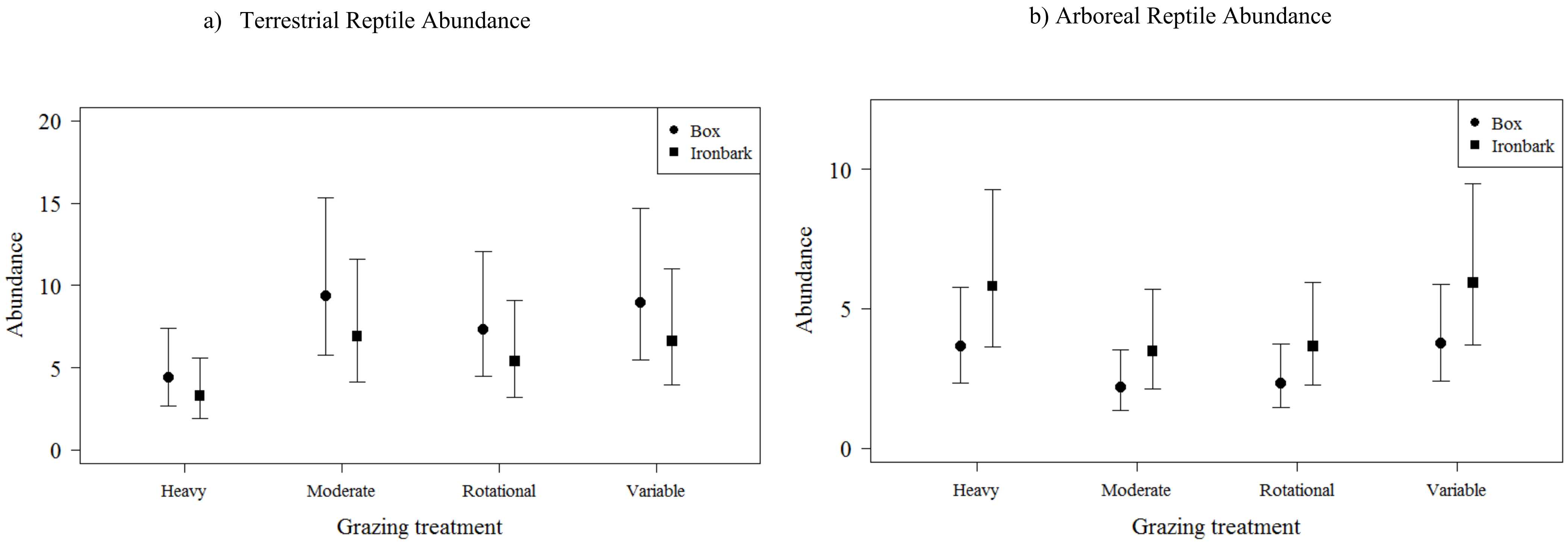


Figure 6.3 The mean fitted values with 95% confidence intervals of the negative binomial GLMMs for: a) Terrestrial Reptile Abundance ~ Grazing + Vegetation, and b) Arboreal Reptile Abundance ~ Grazing + Vegetation.

Arboreal reptile abundance was also significantly affected by grazing treatment and vegetation type, however, in this case, H and V supported higher abundances (Table 6.2, Figure 6.3b). Furthermore, reptile abundance was higher in Ironbark than in Box. The interaction of these two variables, although included in the second best model, was not statistically significant. The optimal model for terrestrial reptile richness included vegetation, although it was not statistically distinguishable from the null model (ΔAICc=0.12). The best arboreal reptile richness model was the null model. Model coefficients for the optimal abundance models are included in Appendix 3 (Table 1, 2).

Reptile Community

Eight species were included in the terrestrial community analysis: three small, litter-dwelling, diurnal skinks (*Carlia munda, Menetia greyii* and *Morethia taeniopleura*), a larger, surface active, diurnal striped skink (*Ctenotus robustus*), a diurnal dragon (*Diporiphora nobbi*), and a group of nocturnal, ground-dwelling geckos, including the fat-tailed gecko (*Diplodactylus conspiculatus*), Bynoe's gecko (*Heternotia binoei*), and the box-patterned gecko (*Lucasium steindachneri*). Overall, the response of the terrestrial reptile community to grazing was more negative than the response of the arboreal reptile community (Figure 6.4). In 2014 and 2015, terrestrial reptile community composition was explained by season and an interaction between grazing and vegetation (Table 6.3). The seasonal responses were driven by the same individual species (*C. munda, M. greyii, C. robustus, M. taeniopleura*), however the individual species driving the interaction of grazing and vegetation changed from 2014 to 2015. Only *H. binoei* consistently influenced this interaction term. The H Ironbark community was most different from the other communities, with a lower abundance of all species, except at the end of the dry season in 2015. During this trapping session, abundance of all species was much lower than at any other time in any other year, so detecting differences among treatments was difficult (Appendix 4; Figure 1).

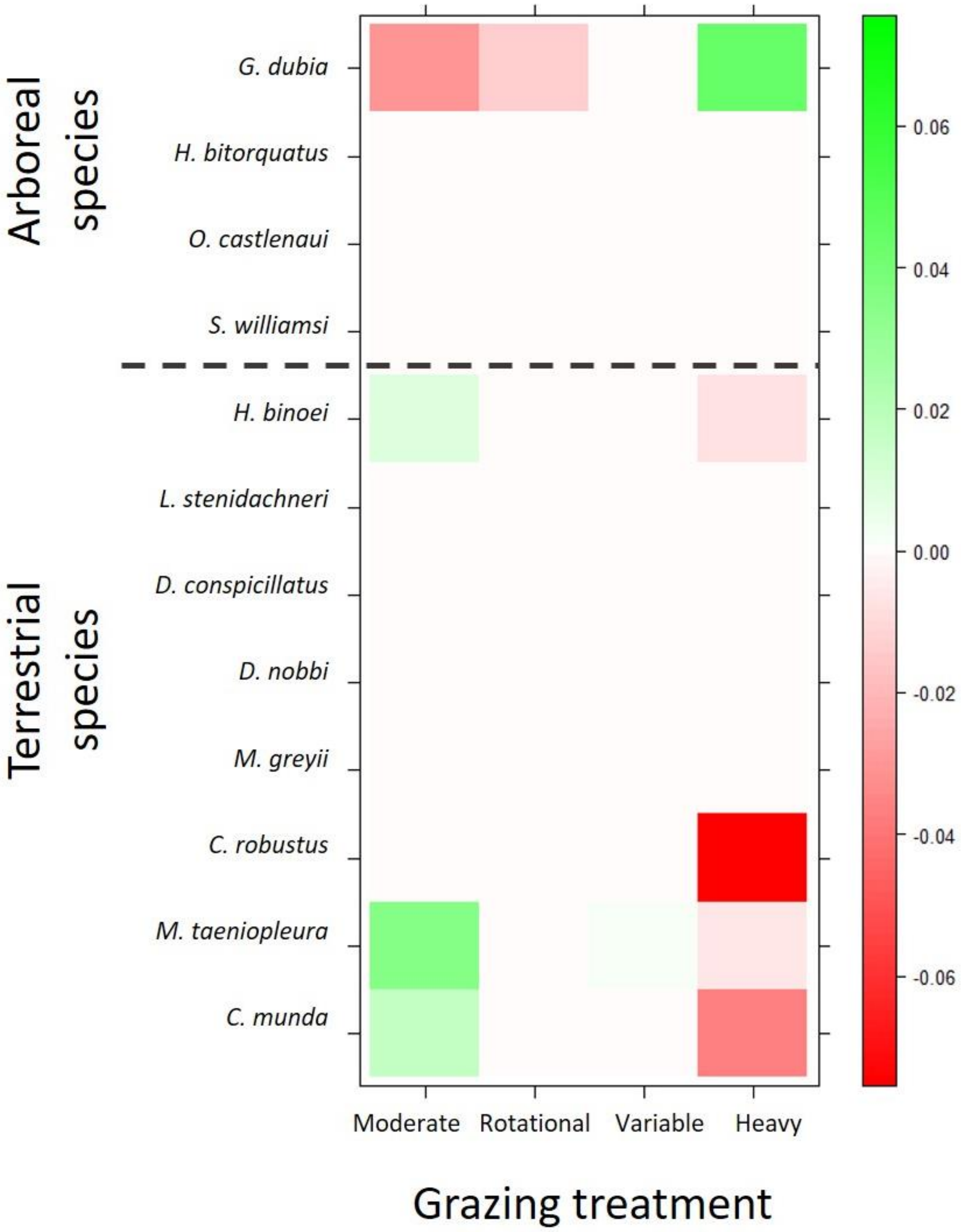


Figure 6.4 The response of arboreal and terrestrial reptile communities to grazing, as visualised using the standardised model co-efficients from a generalised linear model-LASOO model. In this type of model, terms which do not explain any variation in species response are set to zero. The stronger the association, the brighter the square, positive associations are in green and negative associations are in red.

Table 6.3 The ManyGLM analysis testing the relationship between reptile assemblages (arboreal and terrestrial) and grazing treatment, vegetation type and season (and their interactions) for 2014 and 2015. The p values of the variables in the optimal model are given, first for the multivariate community analysis, and then broken down by individual species contribution.

Terrestrial Reptile Community									
Optimal Model	**Community (P value)**	**Individual Species Contributions (P value)**							
		Carlia munda	*Diplodactylus conspiculatus*	*Menetia greyii*	*Ctenotus robustus*	*Diporiphora nobbi*	*Heteronotia binoei*	*Lucasium steindachnerri*	*Morethia taeniopleura*
2014									
Grazing*Vegetation	<0.01	0.38	0.52	0.05	0.01	0.05	0.07	0.79	0.54
Season	<0.01	0.06	0.31	0.06	<0.01	0.06	0.14	0.14	0.06
2015									
Grazing*Vegetation	0.02	0.31	0.91	0.65	0.24	0.27	<0.01	0.15	0.60
Season	<0.01	<0.01	0.58	0.01	0.04	0.34	0.19	0.25	<0.01

Arboreal Reptile Community					
Optimal model	**Community (P value)**	**Individual Species contribution (P value)**			
		Gehyra dubia	*Hoplocephalus bitorquatus*	*Oedura castlenaui*	*Strophurus williamsi*
2014					
Season	<0.01	0.01	0.113	1.00	1.00
2015					
Vegetation	<0.01	<0.01	1.00	0.68	0.23

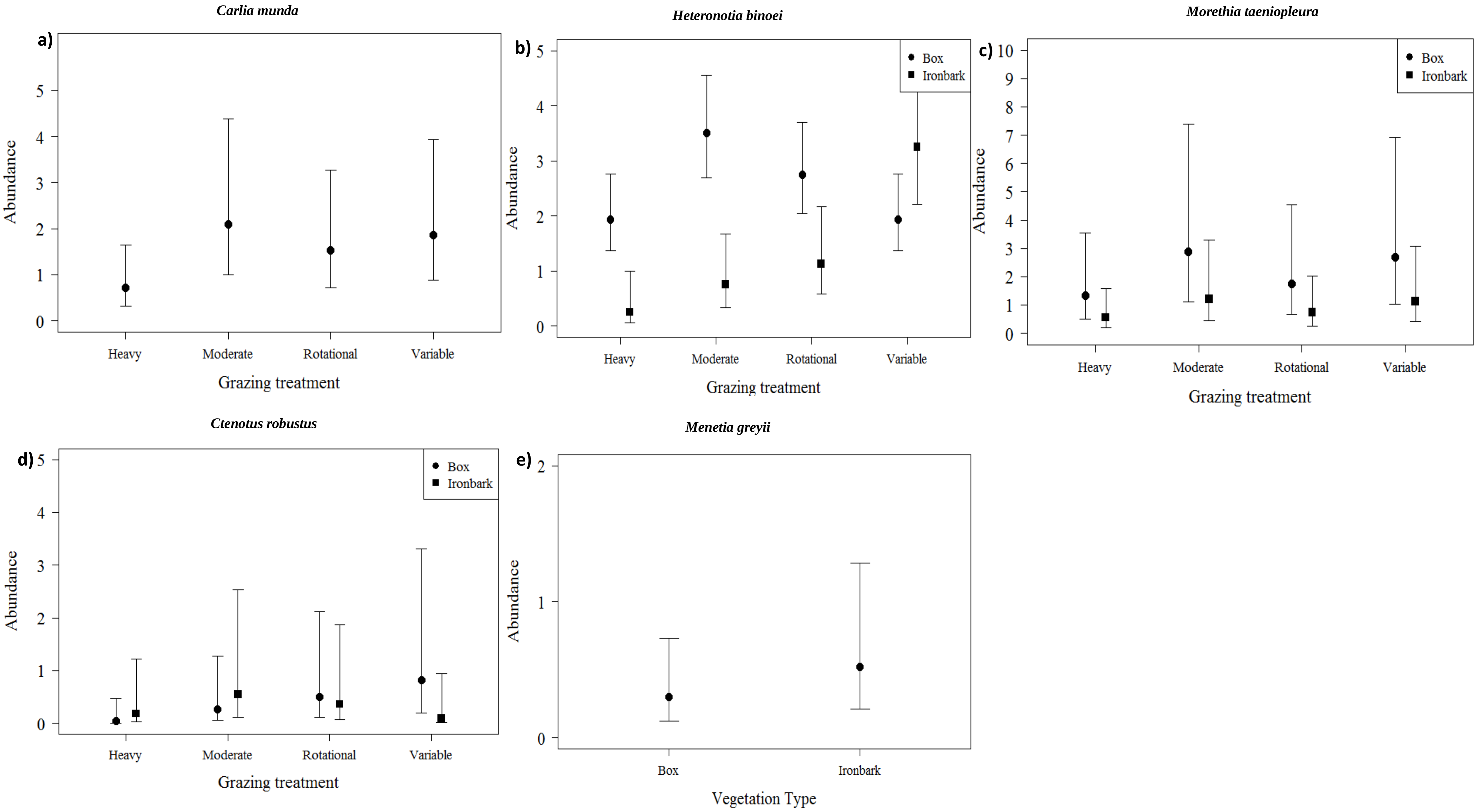
Four arboreal species were included in the community analysis: house geckos (*Gehyra dubia*), pale-headed snakes (*Hoplocephalus bitorquatus*), northern velvet geckos (*Oedura castlenaui*), and eastern spiny-tailed geckos (*Strophurus williamsi*). *Gehyra dubia* was the most abundant species in this community subset. In the arboreal reptile community there was a significant effect of season in 2014 and of vegetation type in 2015, strongly driven by *G. dubia* (Table 6.3). Fitted value plots for *H. bitorquatus, O. castlenaui and S. williamsi* could not be drawn due to their relatively low abundance. Due to the overwhelming influence of *G. dubia*, individual species analysis may be more appropriate than community analysis. *Cryptoblepharus australis* was not included in the arboreal community analysis due to a difference in trapping method and effort (ACBs), as well as the limitation that surveys were only conducted in 2015, however this species is examined individually.

Individual species and functional group responses

The five most abundant terrestrial species and the terrestrial functional groups (Appendix 1) were analysed separately (Table 6.4). There was a significant effect of grazing on four of the five species, and in the litter skink and terrestrial gecko functional groups (Table 6.4, Figure 6.5a-g). *Carlia munda* (Figure 6.5a) and *M. taeniopleura* (Figure 6.5c) both had highest abundance in M and were lowest in H. The interaction between grazing and vegetation is evident for *H. binoei* (Figure 6.5b), where abundance was higher in Box in H, M and R but not in V. Overall, litter skinks were less abundant in H, whereas terrestrial geckos typically showed different responses to grazing in different vegetation types. Individual species responded to various microhabitat features (Table 6.4). Litter skinks were negatively associated with bare ground and positively associated with grass cover, whereas terrestrial gecko abundance was influenced by fine-woody debris and *C. ovata* cover.

Table 6.4: The response of individual reptile species and functional groups to landscape scale and microhabitat using generalised linear mixed models (GLMM) and generalised linear models (GLM) respectively, '+' indicates a positive association and '-', a negative association. GLMM distributions are indicated (P = poisson, NB = negative binomial). All GLM models use a negative binomial distribution. Post hoc Tukey tests were used to examine the effect of each factor level and significant differences (p<0.05) are reported.

<table>
<tr><td rowspan="2">Terrestrial Species</td><td colspan="4">Landscape Scale
Full Model: GLMM
Grazing*Vegetation+(1|Year)+(1|Season)</td><td colspan="2">Microhabitat Scale
Full Model: GLM
Grass + Grass height + FWD + CWD + Carissa ovata + LL<5mm+LL>5mm + TM + BG+ CanopyCover</td></tr>
<tr><td>Terms in optimal model</td><td>Dist</td><td>P value</td><td>Post Hoc</td><td>Terms in optimal model</td><td>P value</td></tr>
<tr><td rowspan="2"><i>Carlia munda</i></td><td rowspan="2">Grazing</td><td rowspan="2">NB</td><td rowspan="2">0.03</td><td rowspan="2">M>H
V>H</td><td>Carissa ovata (-)</td><td>0.02</td></tr>
<tr><td>BG (-)</td><td><0.01</td></tr>
<tr><td rowspan="2"><i>Heternotia binoei</i></td><td rowspan="2">Grazing* Vegetation</td><td rowspan="2">P</td><td rowspan="2"><0.01</td><td rowspan="2">MB>HI
MB>MI
RB>HI
VI>HI
VI>MI</td><td>FWD (+)</td><td><0.01</td></tr>
<tr><td>Carissa ovata (+)</td><td><0.01</td></tr>
<tr><td rowspan="3"><i>Morethia taeniopleura</i></td><td>Grazing</td><td rowspan="3">NB</td><td>0.02</td><td>M>H</td><td>Carissa ovata (+)</td><td><0.01</td></tr>
<tr><td rowspan="2">Vegetation</td><td rowspan="2"><0.01</td><td rowspan="2">B>I</td><td>BG (-)</td><td>0.02</td></tr>
<tr><td>Grass (+)</td><td><0.01</td></tr>
<tr><td><i>Ctenotus robustus</i></td><td>Grazing * Vegetation</td><td>P</td><td>0.01</td><td>VB>HB</td><td>Grass (+)</td><td><0.01</td></tr>
<tr><td><i>Menetia greyii</i></td><td>Vegetation</td><td>P</td><td>0.08</td><td>Not significant</td><td>TM (+)</td><td>0.11</td></tr>
<tr><td rowspan="2">Litter skinks</td><td rowspan="2">Grazing</td><td rowspan="2">NB</td><td rowspan="2"><0.01</td><td rowspan="2">M>H
V>H</td><td>BG (-)</td><td><0.01</td></tr>
<tr><td>Grass (+)</td><td><0.01</td></tr>
<tr><td rowspan="2">Terrestrial Geckos</td><td rowspan="2">Grazing*Vegetation</td><td rowspan="2">NB</td><td rowspan="2"><0.01</td><td rowspan="2">MB>HI
RB>HI
VI>HI</td><td>FWD (+)</td><td><0.01</td></tr>
<tr><td>Carissa ovata (+)</td><td><0.01</td></tr>
<tr><td>Arboreal Species</td><td colspan="4">Landscape Scale
Full Model: GLMM
Grazing*Vegetation+(1|Year)+(1|Season)</td><td colspan="2">Microhabitat Scale
Full Model: GLM
MeanDist.NearTree+Mean Bark Index+Hollows +Canopy Connectivity + Trees dead+Trees <5cm DBH+ Trees 5-10 cm DBH+ Trees 10-20cm DBH+ Trees 20-30cm DBH+Trees >30cm DBH +Canopy Cover</td></tr>
<tr><td rowspan="2"><i>Gehyra dubia</i></td><td>Grazing</td><td rowspan="2">NB</td><td><0.01</td><td>H>M
V>M</td><td rowspan="2">Trees 5-10cm DBH (-)</td><td rowspan="2">0.01</td></tr>
<tr><td>Vegetation</td><td><0.01</td><td>I>B</td></tr>
<tr><td rowspan="2"><i>Cryptoblepharus australis</i></td><td rowspan="2">Vegetation</td><td rowspan="2">NB</td><td rowspan="2"><0.01</td><td rowspan="2">I>B</td><td>Trees 10-20cm DBH (-)</td><td><0.01</td></tr>
<tr><td>Mean bark index (+)</td><td>0.05</td></tr>
<tr><td rowspan="2">Arboreal geckos</td><td>Grazing</td><td rowspan="2">NB</td><td><0.01</td><td>H>M
V>M</td><td>Trees 5-10cm DBH (-)</td><td>0.02</td></tr>
<tr><td>Vegetation</td><td><0.01</td><td>I>B</td><td>Hollows (+)</td><td>0.06</td></tr>
</table>



Carlia munda
a)
Abundance
0
1
2
3
4
5
Heavy
Moderate
Rotational
Variable
Grazing treatment
Heteronotia binoei
b)
● Box
■ Ironbark
Abundance
0
1
2
3
4
5
Heavy
Moderate
Rotational
Variable
Grazing treatment
Morethia taeniopleura
c)
● Box
■ Ironbark
Abundance
0
1
2
3
4
5
6
7
8
9
10
Heavy
Moderate
Rotational
Variable
Grazing treatment
Ctenotus robustus
d)
● Box
■ Ironbark
Abundance
0
1
2
3
4
5
Heavy
Moderate
Rotational
Variable
Grazing treatment
Menetia greyii
e)
Abundance
0
1
2
Box
Ironbark
Vegetation Type

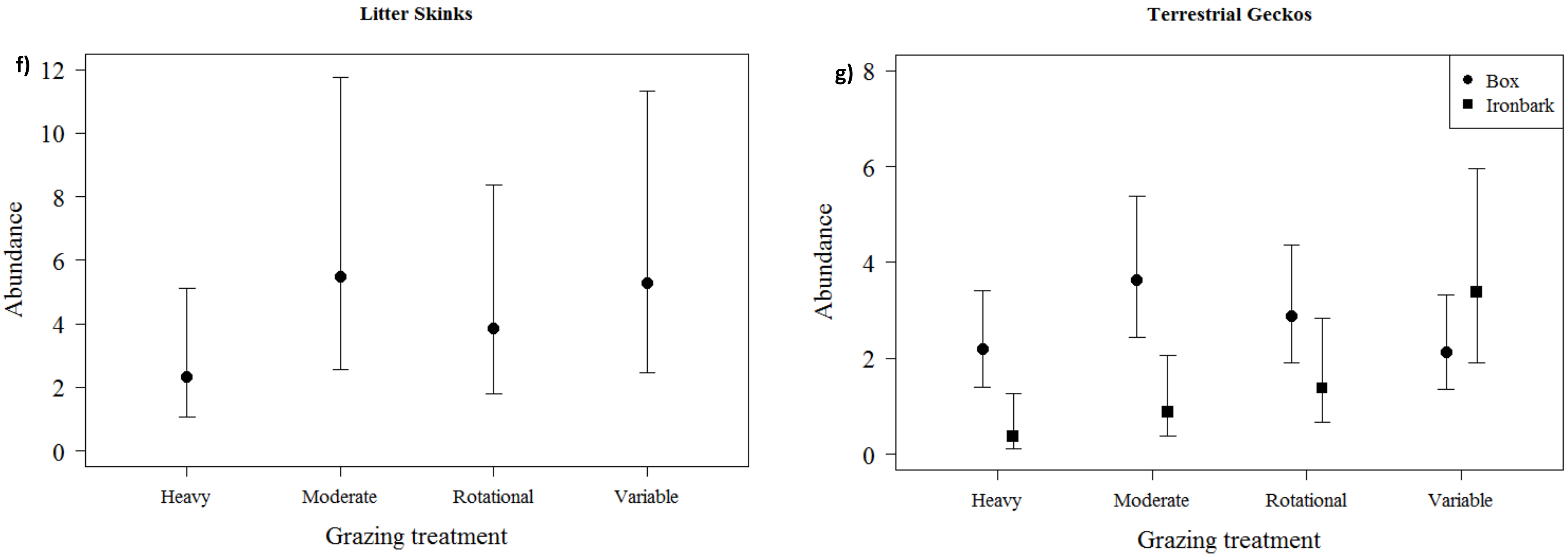


Figure 6.5 Fitted values with 95% confidence intervals for the optimal individual terrestrial reptile species and functional group models.

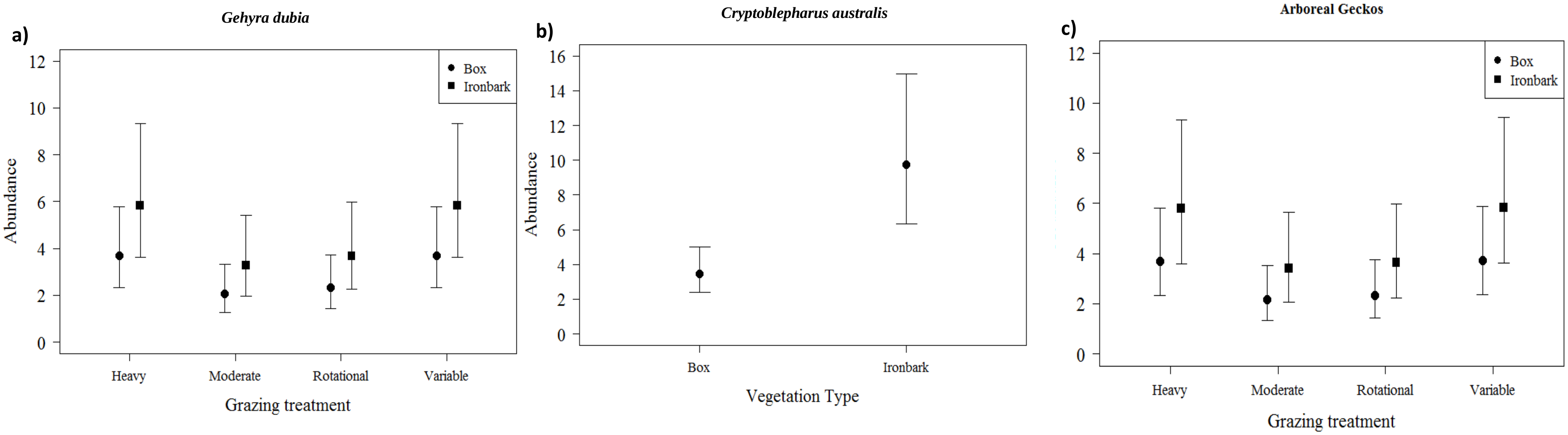


Figure 6.6 Fitted values with 95% confidence intervals for the optimal individual arboreal reptile species and functional group models

Only two arboreal species could be analysed separately (Table 6.4, Figure 6.6a-c). *Gehyra dubia* responded to grazing and vegetation (Figure 6.6a), and were least abundant in M and R and most abundant in H and V. There was no significant effect of grazing on *C. australis*. Both species were more abundant in Ironbark. *Gehyra dubia* was negatively associated with small trees (trees 5 – 10 cm DBH) whereas *C. australis* was negatively associated with trees 10 – 20 cm DBH and positively associated with the Bark Index (they were more common on trees with more complex bark). Arboreal geckos responded negatively to small trees (5 – 10 cm DBH) and positively to the number of trees with hollows and cavities.

Discussion

While habitat features at ground level were significantly modified by grazing treatment, the arboreal habitat was not affected. In H, ground-level microhabitat was significantly altered, and vegetation structural complexity was reduced. Diverse structural habitat is of great importance to ground-dwelling reptile communities as they create a mosaic of thermal and other conditions (Dorrough et al. 2012). The simplified ground habitat found in H had major implications for the ground-dwelling herpetofauna in this study.

Conversely, the only differences I found in arboreal habitat features among the grazing treatments were in terms of canopy connectivity and number of Trees > 30 cm DBH. R had significantly lower canopy connectivity than H, and V had more large, overstory trees. In both cases, if grazing were the driving mechanism, then I would have expected to see the largest differences among the highest contrast treatments (i.e., H vs. M). Further, younger size classes of trees were not different among the grazing treatments, suggesting no difference in recruitment. It is possible that changes to arboreal habitat will be identified in the future, as a result of long-term soil compaction, decreased water infiltration, and increased soil temperature (Yates et al. 2000; Castellano and Valone 2007). Trees may take a long time to respond to grazing disturbance, but after 17 years of the Wambiana Grazing Trial, the impact on overstory trees and arboreal habitat features is minimal.

Arboreal reptile response to grazing

Arboreal reptiles were not only resistant to the impacts of heavy livestock grazing, but had an apparent preference for H and V. However, while there was a diverse assemblage of arboreal reptiles at my sites, overall abundance patterns were driven by *G. dubia*. Most arboreal reptile species were much less abundant than *G. dubia*, so my community analysis was limited to four species. While community composition was not strongly affected by grazing treatment, the abundance of individual species (namely *G. dubia*) was affected (positively) by grazing.

The most abundant arboreal reptiles, *G. dubia* and *C. australis*, flourished in all of the grazing treatments, including the heavily stocked paddocks, where many ground-dwelling reptiles suffered. *Cryptoblepharus australis* did not respond to grazing, and was, therefore resistant to the effects of heavy grazing, whereas *G. dubia* showed an increaser pattern, increasing in abundance with increasing stocking rate. Both species were apparently buffered from the direct negative impacts of grazing, such as microhabitat loss. This supports a similar study, where several arboreal lizard species were more abundant in communal rangelands (high disturbance area) compared to adjacent protected rangeland (low disturbance) (Smart et al. 2003).

Here, the arboreal community was not negatively impacted by heavy grazing, but this may not be the case elsewhere, depending on the extent of tree clearing, fire, and other indirect impacts on arboreal habitats. Tree clearing, often associated with grazing, is a major threat to arboreal fauna (Gibbons and Lindenmayer 2002; Parsons et al. 2017). Indirectly, long-term soil compaction, may suppress new tree growth (Fischer et al. 2004) and grazing can interact with browsing by large native herbivores, resulting in changes to arboreal structure (Ogada et al. 2008; Pringle 2008). Fischer et al. (2009) suggest that current grazing management styles are leading to major tree declines. As keystone structures, loss of trees will have major impacts on the distribution and biodiversity across vast regions of the world (Manning et al. 2006). Both dead and living trees, and the accumulation of course woody debris, are prime habitat for diverse animal communities (Whiles and Grubaugh 1996). Even damaged trees increase structural complexity, and can increase occupancy of arboreal lizards (Pringle 2008). Unlike other areas used for livestock grazing, the Wambiana Grazing Trial has not been cleared within the last 100 years and therefore has many old, overstory trees. Additionally, fire is not regularly used to suppress woody growth at this location. While open-canopy woodlands such as the Wambiana Grazing Trial have naturally sparse tree cover, the trees that are present support a wide variety of wildlife, especially old trees with hollows and flaking bark (Gibbons and Lindenmayer 2002; Bryant et al. 2012).

I could only model *G. dubia* and *C. australis* individually, but made observations of other arboreal reptiles on the Wambiana Grazing Trial. For example, *O. castelnaui* and *H. bitorquatus* were found in every grazing treatment and were not linked to vegetation type. Both *O. castelnaui* and *H. bitorquatus* use loose bark and hollows as diurnal refugia and forage on branches and the trunks of trees at night (Gibbons and Lindenmayer,2002; Fitzgerald et al. 2010). Both species appear resistant to the effects of grazing. *Strophurus* *williamsi* were generally found in the lower strata (on small trees and shrubs) and were not present in either H or V. By using the lower strata, *S. williamsi* may be less tolerant to the impacts of grazing than other arboreal reptiles. In my analyses, I have applied a binary notion of arboreality (either arboreal or terrestrial), but in reality, arboreal species use vertical habitat strata to different extents. In a more diverse arboreal community, it may be beneficial to classify species along an ‘arboreality gradient’ and use this as a predictor of resistance to disturbance. This has been used effectively to predict bird response to livestock grazing (Martin and Possingham 2005) and the resilience of frogs and lizards to extreme climatic events (Scheffers et al. 2014).

Terrestrial reptile response to grazing

Unlike arboreal reptiles, terrestrial reptiles generally had a negative association with increasing grazing pressure. This relationship was clearly seen in overall abundance, most individual species responses, and at a functional group level. The community compositional differences were complex and subtle, making interpretation of these results difficult on their own. The community analysis is greatly complemented by the assessment of individual species using GLMMs, where I had the benefit of treating year and season as random effects.

As a group, litter skinks performed as typical decreaser species, supporting the results from other Australian grazing studies with similar terrestrial reptile assemblages (Woinarski and Ash 2002; James 2003; Kutt and Woinarski 2007). The litter skinks that were analysed separately mostly showed the same negative response to increased grazing. *Carlia munda* and *M. taeniopleura* were both least abundant in the heavily stocked sites. *Ctenotus robustus* also responded negatively to heavy grazing, in accordance with the response of *Ctenotus sp.* in other grazed locations, and likely due to a reduction of thermal refuges at ground level in heavily grazed areas (Hacking et al. 2014; Abom and Schwarzkopf 2016).

The response of terrestrial geckos is clearly influenced by the most abundant terrestrial gecko *H. binoei.* While seemingly unaffected by grazing in the Box vegetation type, *H. binoei* was significantly less abundant in H Ironbark. In other vegetation types, *H. binoei* is more abundant in areas of heavy grazing (Woinarski and Ash 2002), further suggesting this species' response to grazing is greatly influenced by the surrounding vegetation community. Ground-dwelling reptiles often respond to habitat characteristics such as woody debris, leaf litter and fallen logs, which are actually a function of arboreal habitat structure (Fischer et al. 2004). The importance of tree-provided structure to ground features further supports the importance of retaining trees in grazed environments, for both the arboreal and terrestrial fauna.

The terrestrial reptile assemblage at this location was dominated by abundant diurnal skinks susceptible to grazing. At other locations, particularly more arid areas, the terrestrial reptile assemblage often has a higher proportion of increaser species, that prefer more open, less complex ground environments (Read 2002; Read and Cunningham 2010; Germano et al. 2012). One agamid species found during the study, *D. nobbi*, would likely prefer open habitats and higher ground temperatures, however, due to low capture numbers I could not detect differences in its abundance among grazing treatments.

My interpretation of reptile responses to grazing is limited by the knowledge of species' habitat requirements, for thermoregulation, predator avoidance and food. Here, I suggest the negative response of many species to grazing is driven by a loss of microhabitat complexity, but I have not determined the mechanism allowing arboreal groups or species to be resistant. It is likely there are complex indirect mechanisms driving arboreal reptile abundance and it would be beneficial to test these. Reptiles can be affected by changed predator-prey dynamics in grazed environments (e.g. Curry and Hacker 1990; Knox et al. 2012; Pafilis et al. 2013; Pettigrew and Bull 2014). Most grazing response mechanisms are suggested or assumed, and very few have been experimentally tested or examined in detail (but see Rosi et al. 2009; Villar et al. 2013). A better understanding of the mechanisms behind individual species' responses may make it possible to predict species responses to grazing.

My results illustrate the importance of examining arboreal and terrestrial community composition separately, and individual species in more detail, rather than focusing on just overall biodiversity measures such as abundance and richness. Species and functional groups often respond to disturbances in different (even opposite) ways (Chapter 1), thus I highlight the importance of analysing community response data appropriately.

Management implications

Measures of plant and animal resistance and resilience have been successfully used to build risk-based frameworks to guide rangeland management (Chambers et al. 2017). An understanding of the attributes that influence resistance, such as arboreality, can help when devising grazing management strategies. In this case, the recommended grazing strategy for conserving arboreal geckos would be different compared to a grazing strategy aimed at conserving diurnal litter skinks. The varied response of vertebrates to different grazing strategies calls for a nuanced approach to management recommendations (Chapter 1).

Across the globe, a diversity of biomes support livestock grazing systems and these systems vary in their extent of vertical strata (Asner et al. 2004). Therefore, my findings will be more relevant to rangelands from similar biomes. Diverse arboreal reptile communities may be unique to Australian rangelands, however arboreal reptiles, mammals and birds, are found in rangelands globally (Chapter 1). Furthermore, trees not only harbor extensive microhabitats for arboreal species, but indirectly provide habitat for terrestrial species (Fischer et al. 2004). It is widely accepted that the retention of trees increases biodiversity and landscape scale species richness (Benton et al. 2003; Manning et al. 2006). Therefore, one universal management practice to increase or retain arboreal and terrestrial fauna may be to retain standing trees and woody debris. Unlike more intense agricultural land-uses (e.g. cropping), rangelands where trees are retained and stocking rates are moderate, are potentially areas where animal production and biodiversity conservation can co-exist.

Summary

Domestic livestock grazing directly alters ground-level habitat but its effects on arboreal habitat are poorly known. Similarly, the response to grazing of ground-dwelling fauna has been examined, but there are few studies of arboreal fauna. Globally, grazing has been implicated in the decline of vertebrate fauna species, but some species appear resistant to the effects of grazing, either benefiting from the structural changes at ground level or avoiding them, as may be the case with arboreal species. Here I examine arboreal and terrestrial habitat responses and reptile community responses to grazing, to determine whether arboreal reptile species are more

resistant than terrestrial reptile species. I conducted arboreal and terrestrial reptile surveys on four different grazing treatments, at a long-term experimental grazing trial in northern Australia. To compare the grazing response of arboreal and terrestrial reptile assemblages, I used community, functional group and individual species-level analyses. Species responses were modelled in relation to landscape-scale and microhabitat variables. Arboreal reptile species were resistant to the impact of grazing, whereas terrestrial reptiles were negatively affected by heavy grazing. Terrestrial reptiles were positively associated with complex ground structures, which were greatly reduced in heavily grazed areas. Arboreal lizards responded positively to microhabitat features such as tree hollows. Arboreal and terrestrial reptiles have different responses to the impact of livestock grazing. This has implications for rangeland management, particularly if management objectives include goals relating to conserving certain species or functional groups. Arboreal reptiles showed resistance in a landscape that is grazed, but where trees have not been cleared. I highlight the importance of retaining trees in rangelands for both terrestrial and arboreal microhabitats.

Chapter Seven

Adapted from: Neilly, H., O'Reagain, P., Vanderwal, J. & Schwarzkopf, L. (2018) Profitable and sustainable cattle grazing strategies support reptiles in a tropical savanna rangeland. *Rangeland Ecology & Management* 71(2), 205-212.

Profitable and sustainable cattle grazing strategies support reptiles in a tropical savanna rangeland

Introduction

Livestock grazing is the most widespread land-use in the world, covering 25% of the global land surface (Asner et al. 2004). Most livestock grazing takes place on rangelands, generally defined as open landscapes with naturally occurring forage plants suitable for livestock, and millions of people in both the developed and developing world are dependent upon them economically and socially. In northern Australia, livestock grazing is the dominant land use across the one and a half million square kilometers of tropical savannas, and many people depend upon this industry for their livelihood (Crowley 2015). To ensure a sustainable grazing industry, we need to identify grazing strategies that minimize negative impacts on land condition and biodiversity.

Globally, the impact of livestock grazing on biodiversity is mixed. It can be either positive or negative, and depends upon the evolutionary history of the system, its productivity, and the intensity of grazing disturbance (Cingolani et al. 2005; Milchunas et al. 1988). In Australia, grazing by domestic livestock is generally viewed as being negative for biodiversity (Eldridge et al. 2016) and is, in some cases, extremely detrimental (James et al. 1999). Under inappropriate management, and particularly when coupled with drought, livestock grazing can lead to the loss of deeper rooted perennial grasses, reduce ground cover and soil health leading to increased runoff and reduced ecosystem services (Facelli and Springbett 2009; Eldridge et al. 2011; McKeon et al. 2009). Subsequently, these changes to vegetation structure can affect the fauna using them as habitat. However, when managed appropriately, rangelands can be maintained in good condition (O'Reagain and Bushell 2011). Ecological processes on rangelands are often relatively 'intact' compared to those in more intensive agricultural areas, particularly when trees are not cleared and exotic pasture species are not introduced (McIntyre and Hobbs 1999). Indeed, the extensive rangelands of northern Australia are largely dominated by native grasses, despite the ingress of exotic grasses like Buffel grass (*Cenchrus ciliaris*) and Indian Couch (*Bothriochloa pertusa*) in some areas. The relatively intact nature of these rangelands suggests that if managed appropriately, they can not only be used for food production but also make a valuable contribution towards achieving landscape-scale conservation objectives (Chapter 1).

While nature reserves undoubtedly serve a critical role in conservation, they are inadequate on their own to conserve biodiversity into the future (Margules and Pressey 2000). This is, in part, due to the social and economic limitations on their total area, and subsequent management. Therefore, the importance of well-managed rangelands as complementary 'off-reserve' conservation areas cannot be overlooked. Furthermore, due to the vast areas covered by rangelands, small management changes could have significant implications for conservation (Niamir-Fuller et al. 2012).

For ‘off-reserve’ conservation to be a success, rangelands need to serve a dual purpose: economically viable animal production for the grazier, and simultaneously, the maintenance of the ecological processes that support biodiversity. We need to understand the response of biodiversity to grazing, and integrate this knowledge with an understanding of economic and social outcomes. Essentially, we must determine the relative trade-off between conservation and production objectives. In an industry that is facing severe financial challenges, with many operations struggling to remain viable (McLean et al. 2014), integrated information on biodiversity and profitability outcomes is needed to convince land managers to adopt wildlife-friendly practices, and inform relevant incentive schemes. Unfortunately, there has been a limited capacity to accurately link measures of economic performance with measures of biodiversity, as a multidisciplinary approach to data collection is rare.

The basic principles of sustainable grazing management are relatively well known, i.e., stock around the long-term carrying capacity of the landscape, adjust stocking rates according to pasture (forage) availability, and regularly spell, or rest, paddocks to allow recovery from grazing (O’Reagain et al. 2014). In northern Australia, these kinds of conservative and flexible grazing strategies achieve the best land condition by maintaining healthy soil and vegetation communities, and are also most profitable in the long term (O’Reagain and Scanlan 2012). Therefore, it is reasonable to hypothesise that grazing strategies that maintain land in better condition and are most economically sustainable, are also likely to have better biodiversity outcomes for both flora and fauna (Curry and Hacker 1990).

We are, however, unable to directly compare animal production and biodiversity data unless we have studies designed to do so (Chapter 1). Rangeland scientists typically utilize grazing trials to assess animal production and land condition under different grazing treatments, and usually focus data collection on important pasture species or soil characteristics (Orr and O'Reagain 2011; O'Reagain et al. 2011). Conversely, ecologists often conduct biodiversity surveys in existing grazed environments, where floral or faunal communities in areas of different grazing intensity are compared (e.g. Landsberg et al. 2003; Dorrough et al. 2012). While biodiversity has sometimes been studied within experimental grazing trials (Kutt et al. 2012; Villar et al. 2014; Bylo et al. 2014) the opportunity to combine this data with simultaneously collected economic or land condition data has not been realized. Furthermore, few large-scale grazing trials are conducted over time periods long enough to adequately measure long-term profitability or to capture changes in land condition or biodiversity, particularly in areas with marked climatic variability.

In this study, I examined the effect of four cattle grazing regimes on profitability, land condition and reptile abundance and species richness over three years, on an existing long-term grazing trial in an Australian tropical savanna rangeland. The specific aim of the trial is to assess the performance of different grazing strategies in relation to animal production, economic performance and resource condition (O'Reagain et al. 2011). I selected reptiles as a biodiversity measure to assess grazing impacts due to their diversity in this location, the fact that their scale of movements are conducive to this grazing trial, and the responsiveness of reptiles to land-use type, compared to more vagile groups, such as mammals or birds (Woinarski and Ash 2002). I predicted that overall reptile abundance and richness would be higher where profitability was higher and land condition was better. That is, I predicted there would not be a trade-off between biodiversity and profitability among the four grazing treatments, but instead that low profitability and poor biodiversity outcomes would coincide.

Additionally, I predicted that season and vegetation type would strongly influence patterns of reptile abundance and richness.

Materials and methods

This study was conducted at the Wambiana Grazing Trial, see Chapter Two for a detailed site description.

Cattle management

Experimental animals were Brahman-cross steers between 18-30 months old, managed according to standard industry practice (O'Reagain et al. 2009). Profitability was calculated as the annual gross margin, i.e., the total mass of beef produced per annum multiplied by its market value less the costs of production, such as interest costs on livestock capital, plus husbandry and supplementation costs (O'Reagain et al. 2011). As in previous drought years, in 2013/14 and 2014/15 animals in the heavy stocking rate treatment also had to be drought-fed due to the extreme shortage of forage in these paddocks.

Pasture measurements and land condition

Land condition was indexed by total ground cover and the percentage of perennial, productive and palatable grass species (3P grasses) by dry weight of end-of-wet-season pasture mass. A high proportion of 3P grasses indicates a productive and sustainable landscape (McIvor et al. 1995). Pasture total standing dry matter (TSDM), species contribution to yield and ground cover were assessed annually at the end of the wet-season (May) and in the late dry-season (October) using the dry-weight-rank procedure (t'Mannetje and Haydock 1963) in the program BOTANAL (Tothill et al. 1992). One hundred quadrat ($0.25\ m^2$) placements were made at regular intervals along each of two permanent transects running the length of each paddock. To ensure representative sampling, the length of transects across each soil type was roughly proportional to the percentage area of that soil in a particular paddock. Major herbaceous plant species were identified to species, while less common species were identified to genus.

Reptile Survey

A total of six reptile surveys were conducted over three years (2013, 2014 and 2015) in April (end of the wet season) and October (end of the dry season). Twenty-four 1-ha sampling sites were established across the four selected grazing treatments (Kutt et al. 2012). Due to the relative size of each vegetation community, 16 sites were located within the Box and 8 within the Ironbark community. A trap array was situated in the bottom right-hand corner of each site consisting of: 4 x 30 cm diameter pitfall buckets spaced 10m apart arranged in a 'T' configuration; 10 m and 20 m lengths of drift fence, intersecting the pitfall buckets; and 6 funnel traps, situated at the ends of the drift fence. Pitfall and funnel traps were checked twice daily over each 10-night trapping session. Captured animals were removed from traps, weighed, measured, marked and then released.

Statistical Analysis

Reptile abundance and species richness was correlated with profitability and land condition indices across the four grazing treatments using Pearson's correlation coefficients. Analysis was confined to two years; July 2013 – June 2014 and July 2014 – June 2015, in which there were available paired samples of profitability, land condition and mean reptile abundance and richness from each treatment paddock (n=16).

To examine the response of reptiles in more detail, reptile abundance and reptile species richness from each sampling site was collated for a trapping session (n=144). Generalized linear mixed models with a negative binomial distribution were used to examine reptile abundance and species richness in relation to grazing treatments, vegetation type, season, year, and the interactions between these factors as fixed effects, with site as a random effect. Variables were explored for collinearity before including them in the model and model distribution was selected to avoid over-dispersion. The optimal models were chosen by comparing models based on corrected Akaike's Information Criteria (AICc). Pairwise comparisons were made using Tukey's tests. The final models were validated by examining the deviance residuals and fitted values with 95% confidence intervals were plotted. All analyses were performed in R (R Core Team 2014).

Results

Rainfall varied markedly over the three years of the study from 601 mm in 2012/2013 to as little as 246 mm in 2014/2015, the 4th driest year in the 105-year rainfall record for the area (Table 7.1). As a result, pasture yields in 2014/2015 were extremely low in the H treatment (<200 kg · ha-1) and it was necessary to reduce the stocking rate in this treatment to 6 ha · AE-1.

Table 7.1 Rainfall and stocking rates applied in different treatments over the three years of the study

	2012/13	**2013/14**	**2014/15**
Rainfall (mm)	601	517	246
Stocking rate (ha·Adult equivalent-1)			
Heavy	3.84	3.88	5.98
Moderate	7.54	7.36	8.05
Variable	6.63	7.18	9.40
Rotational	7.71	7.17	7.62

In total over the six reptile surveys, 1386 reptiles were captured in pitfall and funnel traps with 30 different species recorded. Mean reptile abundance and richness from 2013-2015 was highest in the moderate grazing treatment (M) followed by the variable (V), rotational wet-season spelling (R) and lowest in the heavy grazing treatment (H) (Figure 7.1a), although the effect of grazing treatment alone was not significant. In the optimal reptile abundance generalized linear mixed model, grazing interacted with year. Tukey's tests revealed many significant differences between the grazing-year interaction terms, including that reptile abundance in the H treatment in 2015 was significantly lower than all other grazing-year interaction terms (Table 7.2).

In terms of profitability, mean gross margin over the three years of the study was also lowest in H (-$15 ha-1), due largely to the high cost of supplemental feeding. In contrast, gross margins were far higher and positive in the M, V and R treatments (Figure 7.1b). This pattern was similar to that found for the 18-year mean gross margin, in which values for M, V and R were the same, and H was lower (Figure 7.1b). For land condition indices, the treatment

Table 7.2 The relationship between reptile abundance and reptile species richness and grazing treatment, vegetation type, season and year as described by a generalized linear mixed model with a negative binomial distribution. Site is used as a random effect. The top three models are reported based on AICc values. When the terms in the model where significant (P<0.05), post hoc Tukey tests where used to examine the effect of each factor level.

Response Variable	Model	df	Log Likelihood	AICc	ΔAICc	AICc weight	Post hoc test
Reptile Abundance	Grazing*Year +Season*Year +Vegetation*Year	20	-383.145	813.1	0.00	0.621	Grazing * Year: Heavy 2013> Heavy 2014, Heavy 2015, Rotational 2015, Variable 2015 Moderate 2013 > Heavy 2015, Moderate 2015, Rotational 2015, Variable 2015 Rotational 2013> Heavy 2015, Rotational 2015, Variable 2015 Variable 2013 > Heavy 2015, Rotational 2015, Variable 2015 Heavy 2014, Moderate 2014, Moderate 2015> Heavy 2015 Rotational 2014>Heavy 2015, Rotational 2015 Variable 2014> Heavy 2015, Rotational 2015, Variable 2015 Season*Year: Dry 2013 > Wet 2013, Dry 2014, Wet 2014, Wet 2014, Wet 2015 Wet 2013, Dry 2014, Wet 2014, Wet 2015 > Dry 2015 Vegetation*Year Box 2013 > Box 2015, Ironbark2015 Ironbark 2013 > Ironbark 2014, Box 2015, Ironbark 2015 Box 2014 > Box 2015, Ironbark 2015 Ironbark 2014, Box 2015 > Ironbark 2015 Grazing: n.s Grazing*Vegetation: Moderate Box > Heavy Ironbark Variable Ironbark > Heavy, Ironbark
	Grazing +Season*Year +Vegetation*Year	11	-395.659	815.3	2.20	0.207	
	Grazing*Year +Grazing*Vegetation +Season*Year +Vegetation*Year	23	-380.663	816.5	3.41	0.113	
Richness	Season*Year	8	-261.845	540.8	0.00	0.418	Season*Year Dry 2013>Dry 2015, Wet 2014 Wet 2013, Dry 2014, Wet 2015, >Dry 2015 Vegetation*Year Box 2013>Ironbark 2015 Ironbark 2013>Ironbark 2015 Vegetation n.s
	Season*Year +Vegetation*Year	11	-258.518	541.0	0.28	0.364	
	Season*Year +Vegetation	9	-261.780	542.9	2.15	0.143	

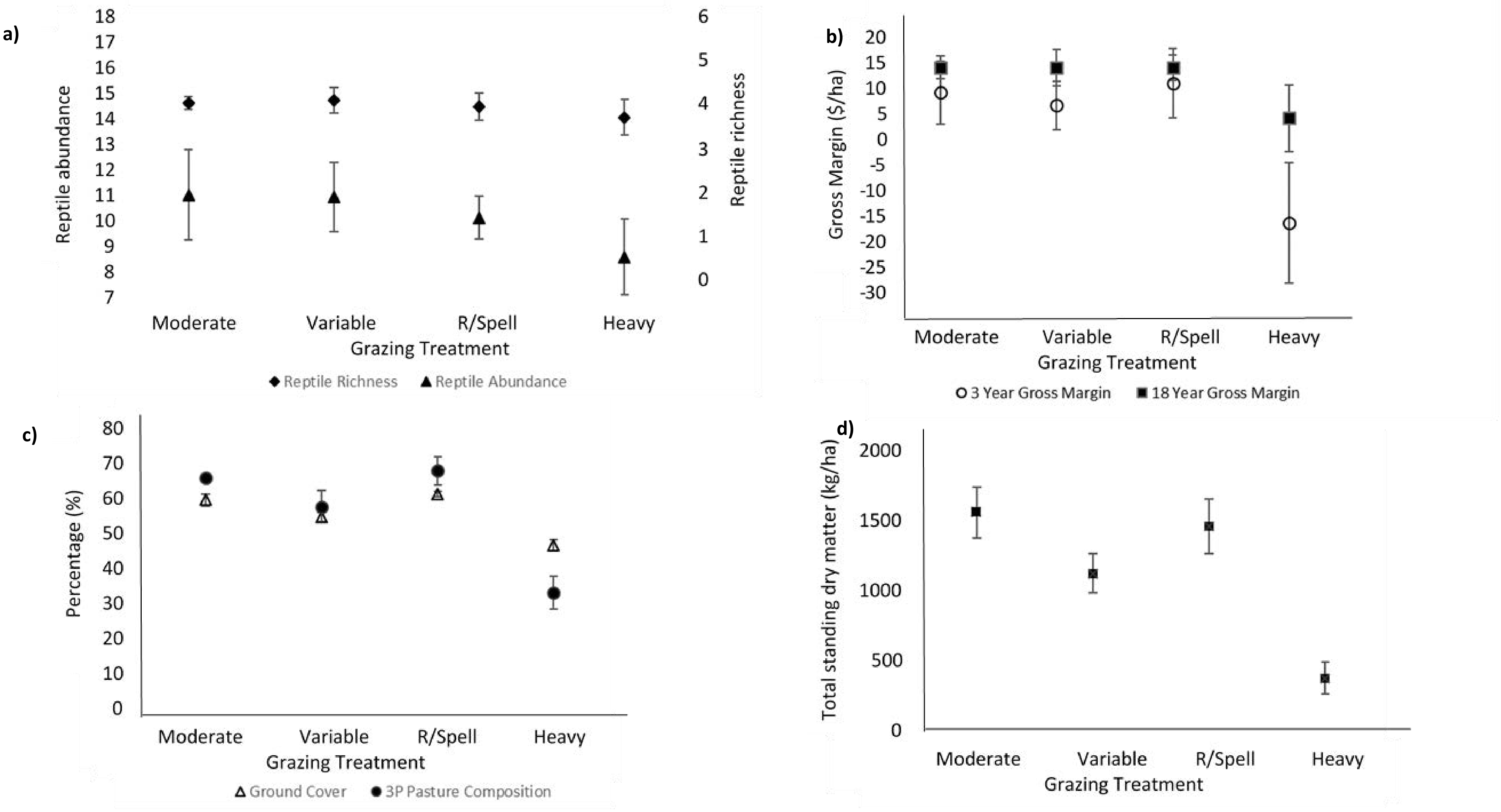


Figure 7.1 The observed trends among the four grazing treatments: Moderate, Variable, Rotational wet-season spelling and Heavy, for measures of: (a) mean reptile abundance and richness over the six reptile surveys conducted from 2013 – 2015; (b) profitability as measured by 3-year gross margin ($ · ha-1) from 2013-2015 and the long-term 18-year gross margin ($ · ha-1) from 1997 – 2015; (c) 3P pasture species composition (%) and ground cover (%); and (d) Total Standing Dry Matter (kg · ha-1). All values are means +/- standard error.

responses of percentage of 3P pasture composition, total standing dry matter, and ground cover, all closely followed the trends shown by the 3-year gross margin (Figure 7.1c and d). In each case, land condition indices were highest in the M and R treatments, slightly lower in V and lowest in the H treatment.

Reptile abundance and richness were more highly correlated with profitability and land condition measures in 2014/2015 than in the 2013/2014 (Figure 7.2 and 7.3). Overall, reptile abundance in 2013/2014 was more highly correlated with profitability and landscape condition indices than reptile richness, although these correlations were not significant ($P>0.05$). In 2014/2015 reptile abundance and richness were most highly correlated with gross margin (abundance: $r = 0.87$, $p<0.01$; richness: $r = 0.89$, $p<0.01$). The correlation coefficients in 2014/2015 of both reptile abundance and reptile richness with the three land condition measures were similar, ranging from $r = 0.67$ – $r = 0.78$.

Although not the focus of my study, I also examined the effects of vegetation type, season, and year on reptile abundance and richness. The optimal reptile abundance model contained a significant grazing-year interaction term (Figure 7.4a), but also season-year and vegetation-year interaction terms (Table 7.2, Figure 7.4b and c). In 2013, there was a higher abundance of reptiles in the ironbark than in the box landtype but the reverse was true in 2015 (Figure 7.4b). In 2013 there was higher reptile abundance in the wet season, whereas there was a higher abundance of reptiles in the dry season in 2015 (Figure 7.4c). The response of reptile species richness to season varied among years.

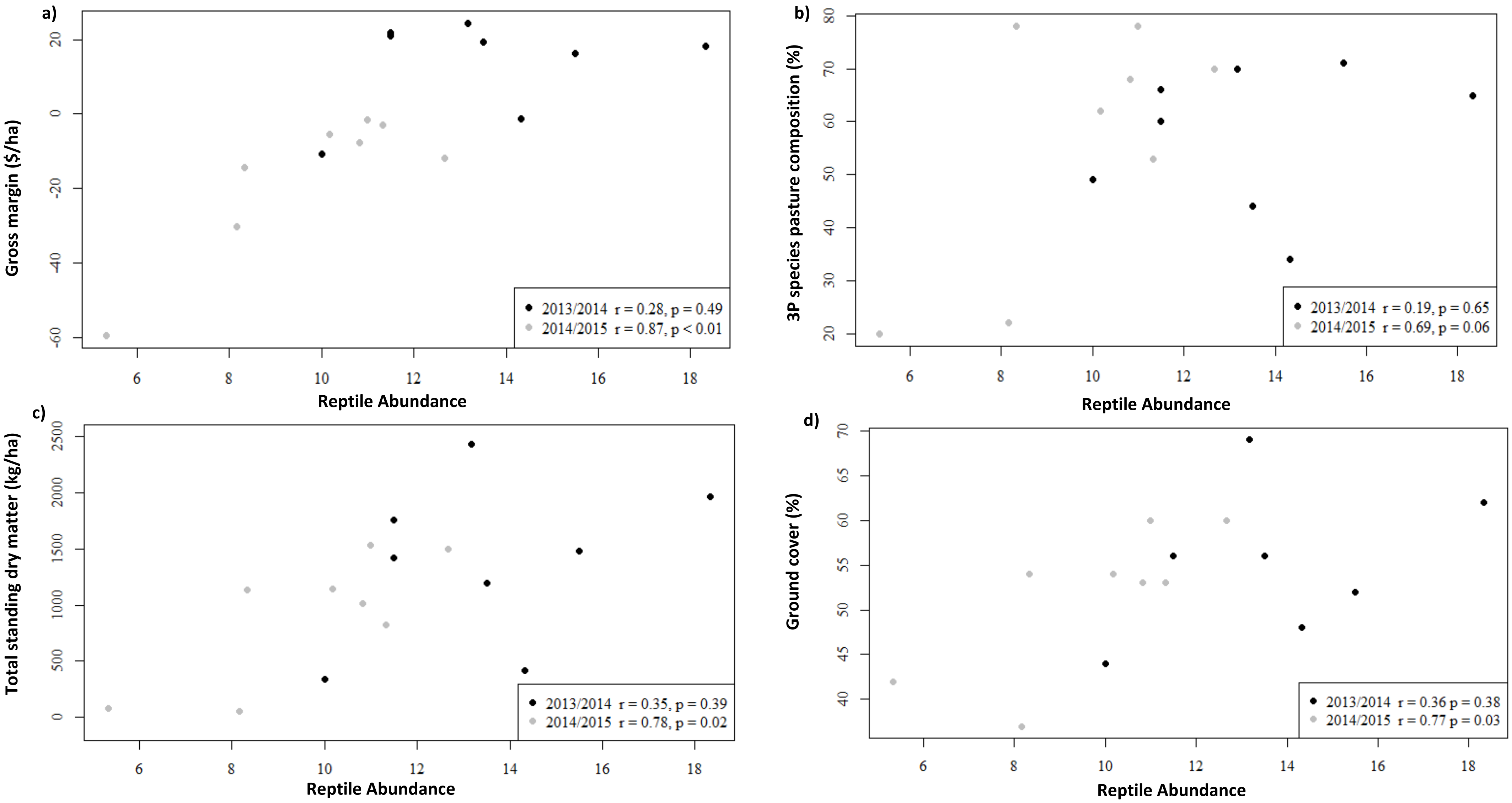


Figure 7.2 Pearson's correlation co-efficients and significance tests of paired samples in the years July 2013 – June 2014 and July 2014 – June 2015, to measure the association between reptile abundance and: a) profitability; b) 3P species pasture composition; c) total standing dry matter and; d) groundcover. The *r* values range from -1 to 1 with 0 indicating no association.

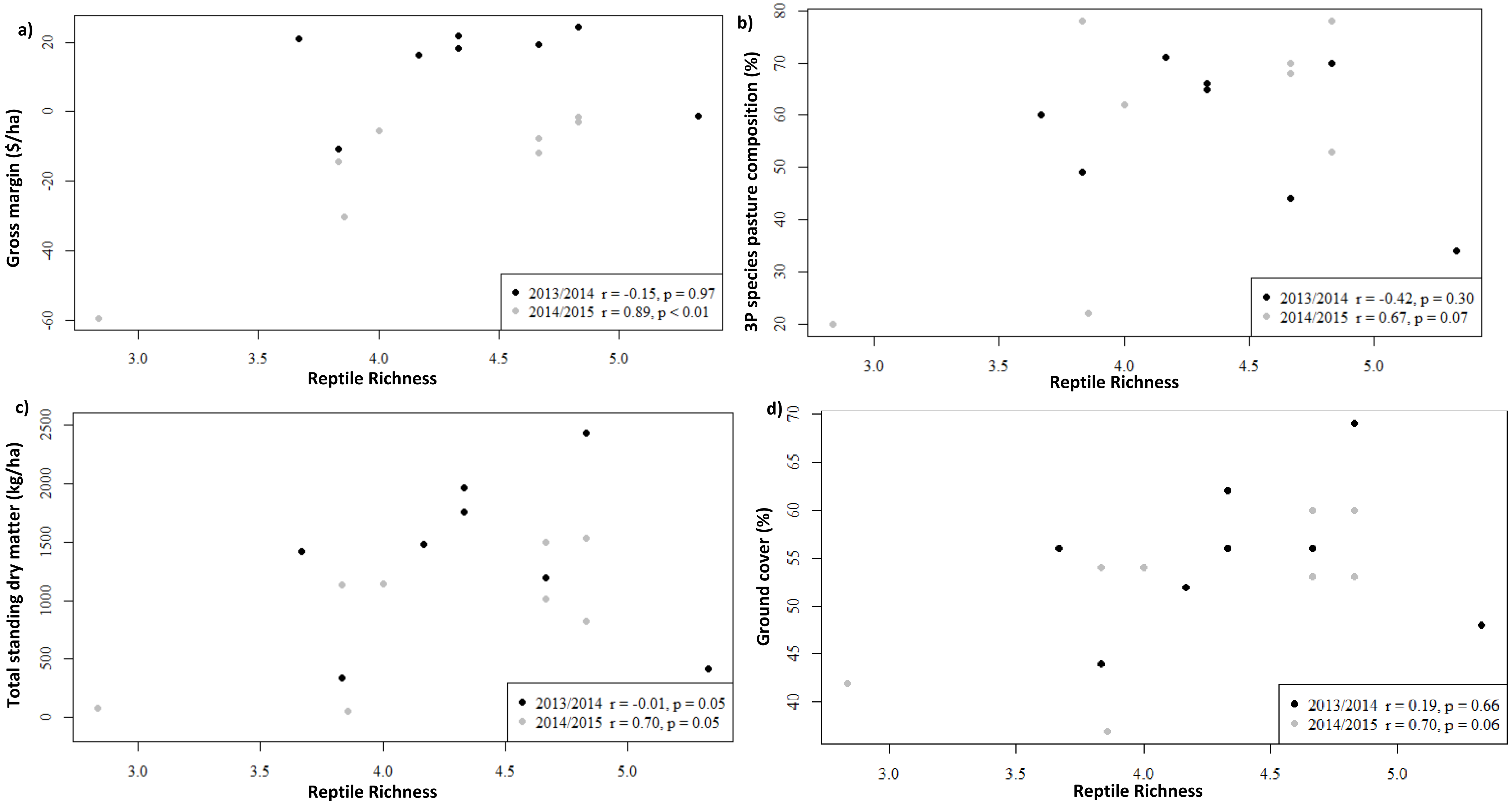


Figure 7.3 Pearson's correlation co-efficients and significance tests of paired samples in the years July 2013 – June 2014 and July 2014 – June 2015, to measure the association between reptile richness and: a) profitability; b) 3P species pasture composition; c) total standing dry matter and; d) groundcover. The *r* values range from -1 to 1 with 0 indicating no association.

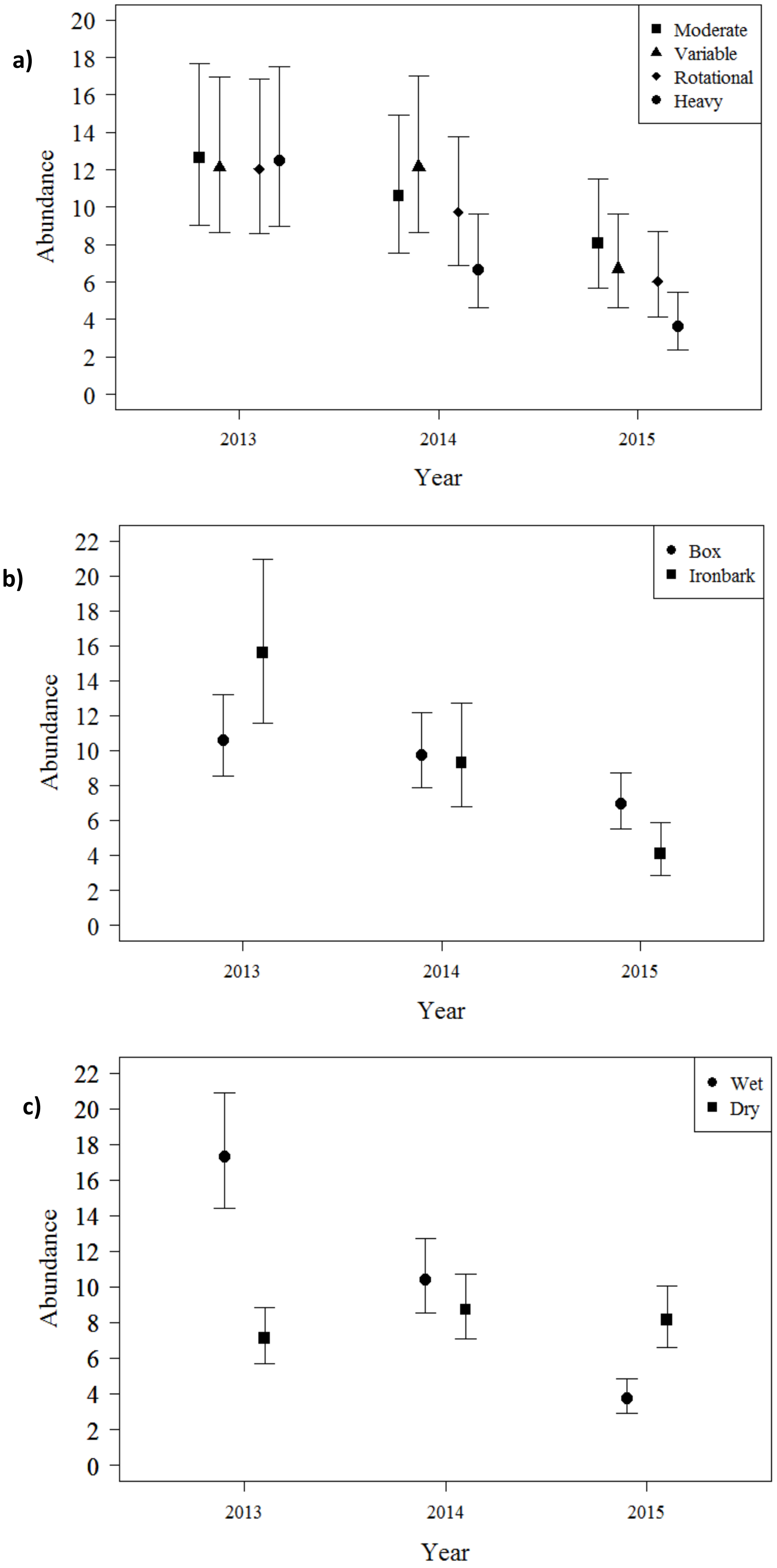


Figure 7.4: The fitted values with 95% confidence intervals for the fixed terms in the optimal negative binomial GLMM, reptile abundance ~ Grazing*Year + Vegetation*Year + Season*Year + (1|Site): a) Grazing * Year; b) Vegetation*Year and; c) Season * Year.

Discussion

My results suggest that there is no trade-off between long-term profitability of cattle grazing and reptile abundance and richness in this relatively unaltered, tropical savanna rangeland. The H treatment performed the worst economically compared to the M, V and R treatments. Not only were profits and land condition better in the relatively well-managed M, V and R treatments, but reptile abundance and richness avoided the negative impacts of the H treatment seen in the drier years. Compared to other grazing trials, the mixture of soil types and use of paddocks 2-10 times larger than is typical, mean that I have confidence that the results from this study are more likely to be realistic and representative of actual cattle grazing properties in the region.

The key to this outcome is that the better-managed strategies (M, V and R) largely maintained land condition which is the essential foundation for long-term profitability. In contrast to the H strategy these treatments promoted a high proportion of deep-rooted productive, perennial grasses. These are far more drought tolerant and ensured there was adequate forage for the cattle through a whole range of seasons, maximizing individual animal performance (O'Reagain et al. 2009). Although total animal production (kg · ha-1) was higher in the H strategy, profitability was severely eroded by lower prices caused by poorer animal condition, the expense of drought feeding in poor years and the higher interest costs associated with greater investment in livestock capital (O'Reagain et al. 2011). Although these findings are derived from steers grazing paddocks that are relatively small (100 ha) by most commercial standards (1000-6000 ha), detailed bio-economic modelling confirms that moderate stocking rates also optimize profitability and land condition with breeders (cows and calves) at the whole of enterprise level (Scanlan et al. 2013).

Reptile abundance and richness in 2015 was lower in the H relative to the other strategies, presumably because the poorer land condition was detrimental to a reptile assemblage dominated by ground-dwelling leaf litter skinks. Terrestrial reptiles, particularly those associated with leaf litter and ground cover are widespread and typical of savanna fauna, and are negatively impacted by the effects of heavy grazing (Kutt and Woinarski 2007; Kutt and Fisher 2011; Frank et al. 2013). However, other reptile groups, such as agamids, may benefit from the more open ground layer that heavy grazing tends to promote (Read and Cunningham 2010; Germano et al. 2012). Likewise, arboreal reptile species can often thrive in heavily grazed environments (Knox et al. 2012; Chapter 6). At my study site, the reptile community was dominated by terrestrial litter skinks with very few agamids, and my ground-based trapping methodology is likely to have been biased against arboreal herpetofauna that use the ground infrequently (Nordberg and Schwarzkopf 2015). Other work at the site however, has shown that the terrestrial reptile abundance is driven by habitat structure changes at ground level (Chapter 6). Although it has not been tested for this system, changes in habitat structure may indirectly influence the ability of reptile species to avoid predation, find suitable prey and effectively thermoregulate (Valentine et al. 2006; Hacking et al. 2014; Abom et al. 2015).

In addition to the effects of grazing management, reptiles responded to climatic, seasonal and vegetation differences. In the latter case, the less-productive ironbark vegetation community may be relatively more sensitive to the negative impacts of drought and overgrazing, possibly due to its inherent lower fertility (O'Reagain pers. obs.; unpublished data). Management strategies, particularly stocking rates, thus should be adapted to land types and regions (Smith et al. 2012). Grazing pressure in larger, spatially variable paddocks with different land types is also seldom uniform. Accordingly, it is also important to manage for the vulnerable land types within the paddock, and not just for the paddock as a whole.

Over the three years of this study, the grazing trial experienced a year with average rainfall, followed by two drought years. The strong correlation between reptile abundance and richness with profitability and land condition in 2014/2015 was likely caused by the dry conditions at the time. Although reptile abundance and richness declined in all treatments in 2015, this decline was greatly exacerbated by the heavy grazing pressure in the H treatment and its impacts on habitat availability (Chapter 6). In contrast, the M, V and R strategies buffered the effects of the drought to various degrees, likely due to the greater proportion of 3P grasses. A similar effect has been noted with cattle production (O'Reagain et al. 2016) with drought effects emerging far sooner in heavily stocked treatments. The amplification of drought impacts under less sustainable grazing management is likely to become even important as climate variability becomes increasingly pronounced with predicted climate change (Lohmann et al. 2012).

The relatively subtle differences between M, V and R treatments for all of the variables considered are expected. On most rangelands, stocking rate is a more important determinant of management outcomes than either grazing system or the application of pasture resting or spelling (O'Reagain et al. 2014). In the present study, the two conservatively stocked, fixed stocking strategies (M and R) performed slightly better, in terms of reptile abundance and land condition, than did the variable stocking strategy. Although relatively light stocking rates were applied in the V treatment in more recent years, the tendency for slightly reduced reptile abundance in the V stocking paddocks likely reflects the very high stocking rates applied 12 years earlier, immediately preceding the 2002 – 2007 drought (O'Reagain and Bushell 2011). It is surprising that the R treatment did not perform better in terms of land condition and biodiversity relative to the M strategy, as wet season spelling has a marked beneficial effect on land condition (Ash et al. 2011; Scanlan et al. 2014). However, relatively muted responses to spelling on these landtypes has also been reported by Jones (2016), and it is possible that the benefits of spelling were partially negated by the higher stocking rates applied to the non-spelled parts of the system during the wet season (O'Reagain and Bushell 2011).

The applicability of the present results to other rangeland systems will likely depend on the rainfall, edaphic properties and evolutionary history of ungulate herbivores at other locations. Australia lacks large native grazing ungulates, so Australian rangelands are likely to be more vulnerable to the impacts of livestock grazing, compared to rangelands on other continents. Given the documented episodes of historical over-grazing in Australia (Mckeon et al. 2009), the modern-day reptile community may be impoverished and dominated by species with some level of grazing tolerance, while grazing-sensitive species have already decreased in abundance or become locally extinct (James et al. 1999; Fensham and Fairfax 2008; Dorrough et al. 2012; Kay et al. 2016). Aside from the impacts of grazing *per se,* other management practices often associated with grazing enterprises can also have major landscape impacts (Price et al. 2010). My data comes from a tropical savanna rangeland that is relatively 'intact', i.e., with little weed encroachment, with no tree clearance, little or no pasture improvement, and no fertilization. Furthermore, while fire is commonly used as a management tool in conjunction with grazing, and has an important impact on vertebrate communities (e.g. Fuhlendorf et al. 2006; Kutt and Gordon 2012), the interaction between fire and grazing was not explicitly addressed in this study. Where grazing regimes include other disturbances such as these, the cumulative impact on the landscape or indeed the impact of these other elements on their own, may be more important than the differences among stocking rates (Brennan and Kuvlesky 2005). While this study was conducted in a controlled experimental setting, other rangeland systems may be subject to a more complex set of confounding management practices, which would need to be considered holistically.

The extent of an agriculture-biodiversity trade-off in any rangeland system will depend on what is meant by 'biodiversity' in a particular case. As I have shown here, if the conservation goals at this site included maximizing reptile abundance and richness, I could recommend that heavy grazing be avoided and a conservative or flexible approach to grazing be applied. However, reptiles are unlikely to be representative of all vertebrate fauna, indeed birds and mammals have shown varied responses to different grazing strategies (Chapter 1). Therefore, rangeland management for the purpose of off-reserve conservation, should be tailored to the specific conservation goals at that location. An accurate understanding of the 'opportunity cost' to landowners of adopting a specific conservation-friendly practice, would be particularly useful when devising rangeland management incentive schemes and guiding government policy.

Management implications

Rangeland scientists have long asserted that the key to sustainable pastoralism and animal production is to maintain the soil, vegetation and perennial forage which are also essential elements for supporting native wildlife (Curry and Hacker 1990). My findings, that there was no trade-off between reptile abundance or richness and profitability or land condition, support this assertion. These results go further, providing possibly the first direct empirical data demonstrating that there is a considerable economic benefit to be gained by managers by adopting grazing strategies that maintain land condition and by implication, maintain biodiversity. This kind of multidisciplinary research is the key to challenging the belief that rangeland management and conservation are intrinsically opposing goals, allowing us to explore the potential for ‘off-reserve’ conservation on rangelands.

Summary

Rangelands are areas used primarily for grazing by domestic livestock, however, because they support native vegetation and fauna, their potential role in conservation should not be overlooked. Typically, ‘off-reserve’ conservation in agricultural landscapes assumes a trade-off between maintaining the ecological processes that support biodiversity, and successful food production and profitability. To evaluate this potential biodiversity trade-off in rangelands, we need to understand the effect of different livestock grazing strategies on biodiversity, in relation to their performance in terms of profitability and land condition. I monitored reptile community responses to four cattle-grazing strategies (Heavy, Moderate and Variable stocking rates and a Rotational wet-season spelling treatment) in a replicated, long-term grazing trial in north Queensland, Australia. Simultaneously, measures of profitability and land condition were collected for the different grazing strategies. Overall, reptile abundance was not negatively impacted by the more sustainably managed treatments (Moderate, Variable and Rotational) compared to Heavy stocking, although the effect of grazing treatment alone was not significant. Profitability and land condition were also higher in these treatments compared to the heavy stocking rate treatment. As drought conditions worsened over the three years, the negative impact of the Heavy stocking treatment on both profitability and biodiversity became more pronounced. Not only did heavy stocking negatively impact reptiles, it was also the least profitable grazing strategy over the long term, and resulted in the worst land condition. This suggests that in this tropical savanna rangeland there was no trade-off between economic performance and reptile abundance and diversity. Grazing regimes with a moderate stocking rate or flexible management strategies were better able to buffer the effects of climate variability resulting in a more resilient reptile community and better economic outcomes in dry years.

Chapter Eight: General Discussion

Rangelands, used for domestic livestock grazing, have potential to be used for ‘off-reserve’ conservation. To achieve off-reserve conservation, rangelands need to be managed to maintain positive economic outcomes for producers, and the ecological processes that support biodiversity (Norris 2008). We need to understand how domestic livestock grazing impacts biodiversity, and combine this ecological knowledge with production data (Eyre et al. 2011). Our ability to link economic and ecological knowledge on grazing lands has been lacking, however, because there are few studies of both economic income from grazing and biodiversity effects of grazing in the same locations. Long-term, multidisciplinary, landscape-scale grazing trials help remedy this, by providing an opportunity to measure both these factors in the same experiment. The Wambiana grazing trial is, thus, a unique and valuable experimental field site that has facilitated a successful collaboration of agricultural scientists, graziers and ecologists. Here, I have examined the overall effect of grazing treatments on vertebrate fauna, examined individual species’ responses and response mechanisms, and linked these ecological variables to profitability and land condition.

In chapter three, I examined the bird community responses to grazing treatment, vegetation type and rainfall. I found that ground-foraging guilds were more responsive to grazing treatments compared to foliage- and aerial-foraging guilds, but that individual species dynamics within a foraging guild could be contradictory, so while one species may decrease, another may increase, but strong responses were more likely close to the ground. Red-backed fairywrens were identified as a decreaser species, positively associated with grass cover and *Carissa ovata* cover. Foraging guilds and individual species also responded to vegetation type and rainfall. This study provided insight into bird community responses at a paddock scale. I concluded that a greater understanding of bird community responses to grazing can lead to more meaningful management recommendations on rangelands, as increaser and decreaser species could be identified and used to indicate subtle effects of grazing, or species-specific management could be undertaken.

In chapter four, I measured the response of an arboreal marsupial, the common brushtail possum (*Trichosurus vulpecula vulpecula*) to different cattle grazing strategies and vegetation types, and examined whether microhabitat selection was driving this response. I found that brushtail possums were resistant to the impact of heavy grazing in both vegetation types, but preferred the heavy grazing treatment in the Box vegetation. Complex arboreal habitat and low ground cover was preferred, and high grass cover and low tree species richness were avoided. Most individuals exclusively used one vegetation type, with few using both, suggesting a 'matrix' vegetation between the Box and Ironbark may have been creating a movement barrier. I concluded that vegetation type should provide a context for determining the benefits to arboreal wildlife of adopting a particular grazing management strategy.

In chapter five, I investigated the response of a marsupial ecosystem engineer, the rufous bettong (*Aepyprymnus rufescens*) to the grazing treatments and vegetation types, and tested whether microhabitat selection is driving this response. I found that rufous bettongs preferred ironbark and avoided heavy grazing. As such, they avoided the areas of highest cattle utilisation. On average, individuals preferred high grass and other terrestrial microhabitat variables of moderate complexity. My results indicate that habitat selection is contributing to the response of a marsupial ecosystem engineer to different grazing strategies. I concluded that mammalian digging and burrowing ecosystem engineers should be a conservation focus on rangelands due to their influence on a suite of species, and their ability to potentially mitigate the negative impacts of cattle grazing on soil health.

In chapter six, I examined both arboreal and terrestrial habitat responses, in conjunction with reptile community responses to the grazing treatments. I found that arboreal reptile species were resistant to the impact of domestic livestock grazing whereas terrestrial reptiles were negatively affected by heavy grazing. Terrestrial reptiles were positively associated with structural complexity measures such as ground cover (e.g., % cover of grass, leaf litter, woody debris), which were greatly reduced in heavily grazed areas. Arboreal lizards responded positively to microhabitat features such as tree hollows. My results indicated that arboreal and terrestrial reptiles had different responses to the impact of livestock grazing. Arboreal reptiles showed resistance in a landscape that is grazed, but where trees have not been cleared. I highlighted the importance of retaining trees in rangelands for both terrestrial and arboreal microhabitats.

Finally, in chapter seven, I compared reptile community responses to cattle grazing strategies with measures of long-term profitability and land condition. I found that reptile abundance was not negatively impacted by the more sustainably managed treatments compared to the heavy grazing treatment. Profitability and land condition were also higher in these treatments compared to the heavy grazing treatment. As drought conditions worsened over the three years, the negative impact of the heavy grazing treatment on both profitability and biodiversity became more pronounced. I concluded that in this tropical savanna rangeland there was no trade-off between economic performance and reptile abundance and diversity. Grazing regimes with a moderate stocking rate or flexible management strategies were better able to buffer the effects of climate variability resulting in a more resilient reptile community and better economic outcomes in dry years.

My research shows that the effect of different grazing strategies on vertebrates is complex and is strongly influenced by vegetation type and season. Overall, biodiversity measures such as abundance and species richness indicated the response of some faunal groups to grazing (e.g., reptile abundance), however in birds and mammals, community composition and individual species responses to grazing provided a much more detailed insight into the dynamics of these taxa. In birds, reptiles and mammals, I identified species that appeared to benefit from heavy grazing ('increasers'), those that were negatively influenced by heavy grazing, or preferred the more conservatively grazed strategies ('decreasers'), and species that showed no response to the grazing treatments. Terrestrial reptiles, particularly litter skinks, had the highest number of 'decreaser' species, suggesting that this group is strongly impacted by heavy grazing. This is likely due to their exclusive use of the ground, and lower vegetation strata, the areas most impacted by cattle grazing. Arboreal reptiles, mammals and most birds can avoid the direct impacts of cattle. My testing of response mechanisms of individual species was restricted to microhabitat use in this thesis, however it is important to study response mechanisms more fully.

Strictly speaking, the terms 'increaser' and 'decreaser' relate to species responses to a grazing gradient (Landsberg et al. 2003), whereas I have examined discreet grazing strategies. It would be possible to analyse these results with grazing as a continuous variable (as was done by Kutt et al. 2012), using mean stocking rates. However, there is a benefit in considering discreet strategies as they can involve more than just the stocking rate, e.g. the rotational movement of stock and responding to seasonal conditions. These elements of a grazing strategy may be just as important as stocking rate in determining their performance.

Limitations of this research

The major benefits of working at the Wambiana experimental grazing trial have been the ability to isolate the effects of different grazing strategies without the confounding influence of other land management practices, and the ability to integrate multidisciplinary datasets. However, the former benefit also presents limitations in terms of the representativeness of my results in the 'real world'. Fire, in particular, has not been experimentally applied at Wambiana. Fire is often linked with cattle grazing in tropical savannas, and the interaction between these two disturbances can have an important effect on vertebrate communities (e.g. Fuhlendorf et al. 2006; Kutt and Gordon 2012).

Additionally, the spatial scale of the trial was more appropriate for some taxa than others. The scale was most suitable for studying reptile and small mammal responses to the grazing treatments. Unfortunately, due to very low captures of small mammals I was unable to analyse their abundances or richness in a meaningful way. Individual brushtail possums and rufous bettongs were marked, so although they could move freely among sites and treatments, I was able to track individual movements and treatment use. My interpretation of bird responses to the treatments was limited to the paddock scale, as highly vagile fauna will respond to drivers at a larger scale than this grazing trial.

A potential bias in this study, and possibly in all modern-day Australian grazing studies, is the impact of historical grazing on current faunal assemblages. Historical grazing effects may influence vertebrate communities, and we are often unable to take these into account (Kay et al. 2016). The perceived resilience of certain groups may be an artefact of the grazing history at that location. In Australia, native fauna did not co-evolve with ungulate herbivores. When domestic livestock grazing was introduced around 200 years ago, stocking rates were often very high and caused severe damage to soil and vegetation, particularly in riparian zones (James et al. 1999; Fensham and Fairfax 2008). It is possible that under this pressure, those species sensitive to grazing would have already decreased in abundance or become locally extinct. Therefore, we may be sampling an impoverished assemblage, comprised of species with some level of tolerance to disturbance (Dorrough et al. 2012). Without historical knowledge, our ability to truly interpret species response to grazing is limited, as the major effects may have already taken place many years ago. Furthermore, in northern Australian rangelands there is very little land that is actually free from grazing that could be used as a baseline for comparison.

Management implications

Livestock grazing in Australia is considered a marginal economic activity (Holmes 2015). In northern Australia, the pastoral industry has survived as a low input, low output system. But, as conditions change, it is predicted that the industry will need to balance targeted intensification with the growing environmental awareness of society and the consumer (Ash and Stafford-Smith 2003). There is a greater understanding by graziers that financial sustainability can only be achieved if the 'natural-resource base' is preserved, and the negative impacts of over-grazing are avoided (Holmes 2015).

In each chapter of this thesis, specific management implications have been addressed. Overall, considering measures of profitability, land condition and faunal diversity, the heavy grazing treatment (2 x long term carrying capacity) could be considered the least ideal grazing strategy. Within the conservative or flexible treatments (moderate, variable and rotational wet season spelling) it is difficult to declare one fauna community ‘better’ than the other. Instead, I suggest that the red meat industry work together with ecologists to define specific conservation goals, such as protecting a certain species or encouraging particular assemblages, or maintaining mosaics of different assemblages. A targeted approach to conservation on rangelands allows for prioritisation, as opposed to simply aiming to maximise abundance and/or diversity. Our ability to make targeted management decisions will be supported by further research.

Red meat producers could consider the presence of ‘sensitive’ species as an indicator of sustainable grazing management, and conversely, increases in ‘resistant’ species may be early indicators of overgrazing. The presence of certain native wildlife could indicate that a producer is managing their property in a sustainable way, however producers need the capacity to demonstrate the presence of sensitive species. Technological advances in motion-sensor cameras and the development of standardised camera-trapping methodology and image recognition software, may make this achievable. For corporate graziers with branded beef, a claim of being ‘sustainable’ or ‘protecting sensitive fauna species’ could be highly valued by consumers. A sustainability star-rating system, may be a valuable marketing tool.

Future research

Overall, the Wambiana grazing trial is good example of a relatively intact rangeland system, mainly because trees are not cleared, and pasture has not been improved by fertilisation or the introduction of exotic grass species. In addition, the trial is surrounded by well managed country. As such, my results may represent a 'best case scenario'. It would be beneficial, therefore, to test my findings at a larger scale and in areas where other disturbances (fire, tree clearing, fertiliser, exotic pasture species) could impact native wildlife in addition to grazing itself.

It would be beneficial to focus future research on more detailed investigations of compositional changes and species response mechanisms. Compared to measures of overall abundance and richness, the grazing responses of individual species and the mechanisms driving those responses may be more useful for informing off-reserve conservation (Derner *et al.* 2009). Understanding more about individual species, especially in relation to their ecosystem services, is relevant to red meat producers. For example, at Wambiana, many vertebrates and invertebrates facilitate soil nutrient cycling, pollination, seed dispersal, germination and the spread of mutualistic mycorrhizal fungi that affect plant growth, and potentially net primary productivity. Further research into the influence of different grazing regimes on these functions is recommended. It may be possible to manipulate grazing strategies to promote certain species that provide desirable ecosystem services. In the case of digging mammals, their presence improves soil structure and chemistry (Fleming et al. 2014). If we could quantify these soil benefits and communicate this information to producers, we could provide them with grazing strategies to encourage digging mammals on their properties. This would benefit landholders and would be an important step towards conservation of these species. Novel ideas are needed to achieve conservation outcomes in production landscapes. Considering the scale of rangelands, working out the best ways to achieve off-reserve conservation should be a priority area for applied conservation research in Australia.

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Appendix 1: Terrestrial and arboreal reptile functional groups.

Taxonomy follows Wilson (2015)

Litter Skinks

Carlia munda

Morethia taeniopleura

Ctenotus robustus

Ctenotus strauchii

Menetia greyii

Carlia rubigo

Pygmaeascincus timlowi

Proablepharus tenuis

Terrestrial Geckos

Lucasium steindachneri

Diplodactylus conspicillatus

Heteronotia binoei

Arboreal Geckos

Gehyra dubia

Strophurus williamsi

Oedura castlenaui

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Appendix 2: Ch 5: Habitat Characteristics

Table 1: Two-way ANOVA results exploring the effect of grazing treatment: Heavy (H), Moderate (M), Variable (V) and Rotational wet season spelling (R), and vegetation type: Box (B) and Ironbark (I), on terrestrial and arboreal habitat characteristics. Post-hoc Tukey's test are used to explore significant results (p=0.05).

Terrestrial Habitat Feature	Mean ± SE	Explanatory Variables	F Statistic	P Value	Post Hoc
Bare ground (% cover)	20.52 ± 2.49	Veg*Graze	5.906	**0.001**	HI>HB HI>MB HI>MI HI>VB HI>RB HI>VI HI>RI
Leaf litter <0.5mm (% cover)	45.32 ± 2.17	Veg*Graze	7.419	**<0.001**	HB>HI HB>MB HB>RB VB>HI VI>HI
Leaf litter>5mm (% cover)	0.82 ± 0.28	Veg*Graze	4.041	**0.009**	MI>HB MI>MB MI>RB MI>RI MI>VB
Grass (% cover)	18.85 ± 1.79	Veg	1.437	0.234	-
		Graze	10.993	**<0.001**	M>H R>H V>H
Grass height (cm)	40.27 ± 2.28	Veg	1.245	0.268	-
		Graze	49.672	**<0.001**	M>H R>H V>H
Carrissa ovata (% cover)	11.80 ± 0.91	Veg	206.840	**<0.001**	B>I
		Graze	10.010	**<0.001**	H>V M>R M>V
Coarse woody debris (% cover)	0.76 ± 0.09	Veg*Graze	9.521	**<0.001**	VI>HB VI>HI VI>MB VI>MI VI>RB VI>RI VI>VB
Fine woody debris (% cover)	0.69 ± 0.09	Veg	0.005	0.942	-
		Graze	0.531	0.662	-
Termite mounds (% cover)	0.69 ± 0.07	Veg*Graze	8.970	**<0.001**	RI>HI VB>HI RI>MB VB>MB RI>VI
Canopy cover (%)	34.70 ± 3.23	Veg	2.958	0.102	-
		Graze	2.244	0.116	-

Arboreal Habitat Feature	**Mean ± SE**	**Explanatory Variables**	**F Statistic**	**P Value**	**Post Hoc**
Mean distance to.nearest tree (m)	4.11 ± 0.05	Veg	0.537	0.472	-
		Graze	0.984	0.421	-
Hollows (%)	11.34 ± 1.46	Veg	0.151	0.702	-
		Graze	0.057	0.981	-
Canopy connectivity (%)	34.70 ± 3.23	Veg	0.338	0.568	-
		Graze	5.757	**0.005**	H>R
Trees dead	1.16 ± 0.16	Veg	6.962	**0.016**	B>I
		Graze	0.998	0.415	-
Trees <5cm Diametre at breast height (DBH)	3.04 ± 0.86	Veg	3.509	0.076	-
		Graze	2.139	0.129	-
Trees 5-10cm DBH	1.45 ± 0.20	Veg	0.713	0.409	-
		Graze	0.431	0.733	-
Trees 10-20 DBH	1.80 ± 0.23	Veg	6.156	**0.022**	B>I
		Graze	1.000	0.414	-
Trees 20-30 DBH	1.01 ± 0.16	Veg	0.003	0.955	-
		Graze	0.422	0.739	-
Trees >30 DBH	0.50 ± 0.10	Veg	1.125	0.302	-
		Graze	3.908	**0.024**	V>H V>R
Mean Bark Index (1-3)	2.0 ± 0.03	Veg	2.028	0.171	-
		Graze	0.497	0.689	-

Appendix 3: Ch 5: Model co-efficients

Table 1: The estimated regression parameters, standard errors, *t*-values and *P*-values for the fixed effects in the negative binomial GLMM: Terrestrial reptile abundance ~ grazing treatment + vegetation type + (1|year) + (1|season)

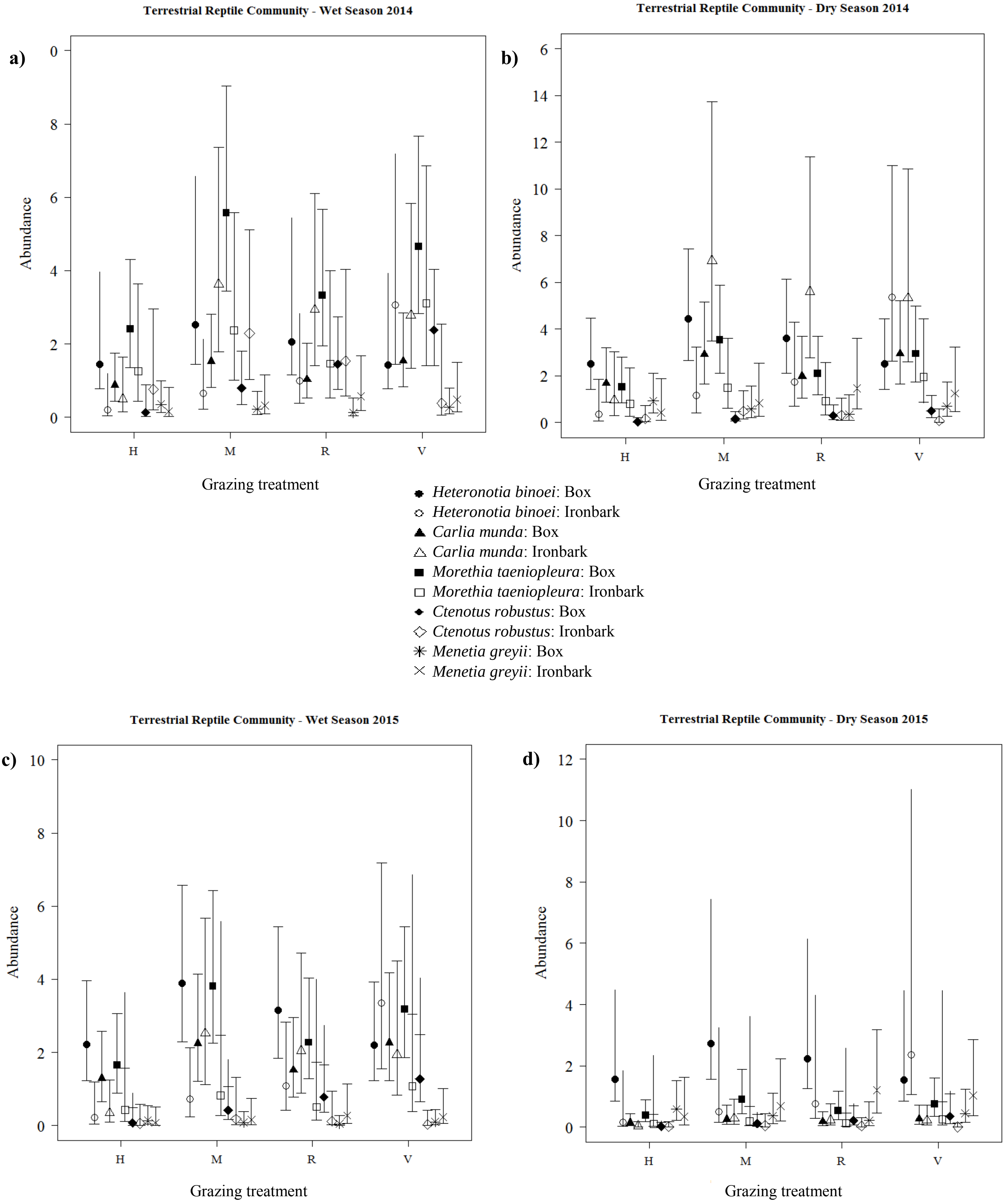
	Estimate	Std. error	*t*-value	*P*-value
Intercept	1.490	0.259	5.755	<0.01
GrazeModerate	0.750	0.179	4.201	<0.01
GrazeRotational	0.502	0.183	2.751	0.01
GrazeVariable	0.704	0.180	3.918	<0.01
VegIronbark	-0.305	0.132	-2.313	0.021

Table 2: The estimated regression parameters, standard errors, *t*-values and *P*-values for the fixed effects in the negative binomial GLMM: Arboreal reptile abundance ~ grazing treatment + vegetation type + (1|year) + (1|season)

	Estimate	Std. error	*t*-value	*P*-value
Intercept	1.304	0.229	5.700	<0.01
GrazeModerate	-0.512	0.207	-2.480	0.01
GrazeRotational	-0.461	0.204	-2.258	0.024
GrazeVariable	0.021	0.190	0.108	0.914
VegIronbark	0.455	0.147	3.094	<0.01

Appendix 4: Ch 5: ManyGLM Community Analysis

Figure 1: The fitted values with 95% confidence intervals of the negative binomial multivariate GLM for: the terrestrial reptile community at (a) the end of the wet season 2014; (b) the end of the dry season 2014; (c) the end of the wet season 2015; and the end of the dry season 2015, for each of the grazing treatments Heavy (H), Moderate (M), Variable (V) and Rotational wet season spelling (R).


Terrestrial Reptile Community - Wet Season 2014
a)
0
8
6
4
2
0
Abundance
H
M
R
V
Grazing treatment
Terrestrial Reptile Community - Dry Season 2014
b)
6
14
12
10
8
6
4
2
0
Abundance
H
M
R
V
Grazing treatment
● *Heteronotia binoei*: Box
○ *Heteronotia binoei*: Ironbark
▲ *Carlia munda*: Box
△ *Carlia munda*: Ironbark
■ *Morethia taeniopleura*: Box
□ *Morethia taeniopleura*: Ironbark
◆ *Ctenotus robustus*: Box
◇ *Ctenotus robustus*: Ironbark
✳ *Menetia greyii*: Box
× *Menetia greyii*: Ironbark
Terrestrial Reptile Community - Wet Season 2015
c)
10
8
6
4
2
0
Abundance
H
M
R
V
Grazing treatment
Terrestrial Reptile Community - Dry Season 2015
d)
12
10
8
6
4
2
0
Abundance
H
M
R
V
Grazing treatment