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The impact of weeds and prescribed fire on faunal diversity

PhD thesis submitted by

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Statement of contribution and declaration on ethics

The data chapter 2 in this thesis include published work in collaboration with Wayne Vogler and Lin Schwarzkopf. However, I have been in charge with project design, obtain research funding, collecting of field data. As well as statistical analyses, synthesis and preparation of manuscripts for submission to peer reviewed journals.

All data collected were in line with ethics guidelines for treatment of animals of James Cook University (Animal Ethics Approval Number A1354), and legal requirements of Australia (Scientific Purposes Permit Number WITK05527908).

Signature Date

Preface

Publications arising from this thesis

***Chapter 2* –** Abom, R., Vogler, W., Schwarzkopf, L., 2015. Mechanisms of the impact of a weed (grader grass, *Themeda quadrivalvis*) on reptile assemblage structure in a tropical savannah. *Biological Conservation* 191:75–82.

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***Chapter 4* –** Abom, R., Schwarzkopf, L., (*In Review*) Mammal responses to fire in a native tropical savannah invaded by a weed (grader grass, *Themeda quadrivalvis*). *Biological Invasions*.

***Chapter 5* –** Abom, R., Schwarzkopf, L., (*Submitted*) Native mammals perceive a more accurate landscape of fear than introduced species. *Animal Behavior*.

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Abstract

Human mediated transport has allowed some species to extend their range beyond their natural ability to disperse. Many exotic annual grasses are highly adaptable and can establish population in their introduced ranges because they can tolerate high variability in local climatic conditions, annual rainfall, and nutrient availability. The most successful invader grasses transform the ecosystems they invade. Invasive grasses can alter the natural fire frequency by increasing local fuel load, and then they flourish under the new conditions they create. This thesis examines the impacts of the introduced weed grader grass (*Themeda quadrivalvis*) and fire on vertebrate assemblages in tropical savannahs in northern Queensland, Australia.

To determine the effects of weeds and fire, and their interaction, on savannah vertebrates, I conducted a two-year vertebrate fauna survey in tropical savannah woodland at Undara Lava Tubes National Park. My survey sites were carefully chosen to provide me with plots that were not spatially auto correlated, and that included either native grasses, or native grasslands invaded by grader grass. After one year examining the influence of the presence of the weed on vertebrate fauna (reptiles), my sites were burned. I expanded my survey to include more recently burned sites, and continued to survey these through their recovery for 15 months. This allowed me to monitor the recovery of reptile and mammal assemblages after fire. Finally, I conducted an experiment to determine the influence of predation on foraging in mice, using giving-up density experiments. To conduct these experiments, I offered native and introduced mice food items in known quantities in trays, in open and closed environments, and

determined the amount of time they were willing to forage in these trays, using the amount of food remaining in the trays as a measure of willingness to forage.

Invasive grasses are among the worst threats to native biodiversity, but the mechanisms causing negative effects are poorly understood. To investigate the impact of an invasive grass on reptiles, I compared the reptile assemblages that used native kangaroo grass (*Themeda triandra*), and black spear grass (*Heteropogon contortus*), to those using habitats invaded by grader grass (*Themeda quadrivalvis*). There were significantly more reptile species, in greater abundances, in native kangaroo and black spear grass than in invasive grader grass. To understand the sources of negative responses of reptile assemblages to the weed, I compared habitat characteristics, temperatures within grass clumps, food availability and predator abundance among these three grass habitats. Environmental temperatures in grass, invertebrate food availability, and avian predator abundances did not differ among the habitats, and there were fewer reptiles that fed on other reptiles in the invaded than in the native grass sites. Thus, native grass sites did not provide better available thermal environments within the grass, food, or lower predator abundance. Instead I suggest that habitat structure was the critical factor driving weed avoidance by reptiles in this system, and recommend that the maintenance of heterogeneous habitat structure, including clumping native grasses, with interspersed bare ground, and leaf litter are critical to reptile biodiversity.

Land managers often use fire as a management tool, to reduce accumulation of fuel, and by extension, the impact of wildfires on flora, fauna and the built environment. Many grassy weeds are tall, and grow in dense stands with high biomass. Grassy weeds often burn at a higher intensity than native grasses, which may alter the influence of fires on

fauna. Thus, the response of fauna to fire in weedy environments may be complex. Here I examined reptile and mammal responses to fire in savannah open woodland habitats in native kangaroo and black spear grass habitats, and in habitats invaded by grader grass.

I compared reptile richness, abundance and assemblage composition in a group of replicated habitats that had not been burnt for 2 years, directly after they were burned, and up to 15 months after burning, when grasses had regrown. Reptiles are excellent model systems to examine the influence of fire on fauna, because they respond strongly to habitat structural features, and are only moderately vagile. I found that reptile abundance and richness were highest in unburnt habitats (2 years after burning), and greatly reduced in all habitats immediately after burning, most strongly in grader grass. Abundance and richness recovered in all three habitats one year after burning, but assemblage composition had changed. Three skinks and one monitor lizard were present only in the longest unburnt kangaroo grass sites, and their populations did not recover 15 months after burning. In weedy habitats, reptile abundance was more strongly reduced immediately after fire than in other habitats. Even in fire-prone, often-burnt habitats such as these, in which richness and abundance were not strongly influenced by fire, assemblage composition was.

As above, I also examined mammal richness and abundance in replicated unburnt, burnt, and revegetated native and weedy sites. Mammal abundances were higher in unburnt native grasses than in unburnt weedy sites. The lowest mammal abundances occurred in sites revegetated after fire. All mammals, except rufous bettongs (*Aepyprymnus rufescens*) and tropical short-tailed mice (*Leggadina lakedownensis*) were reduced in abundance following fire. Eastern chestnut mice (*Pseudomys gracilicaudatus*) and common planigales (*Planigale maculata*) returned with returning grass cover. Over the course of my study, I detected a gradual decline in northern brown bandicoots (*Isoodon macrourus*). Mammal responses to fire in weeds were idiosyncratic, some species were more abundant in weedy habitats following fire, some less, and some returned to their prior abundance. My study indicated that in, tropical savannahs, a naturally fire-prone habitat, overall mammal abundance, but not richness, decreased with frequent fires (≤ 2 years), in both weeds and native grass, whereas individual species responses varied greatly.

Differential predation risk among habitats, or ‘the landscape of fear’ can have profound impacts on foraging strategies of prey. Few studies, however, have described the landscape of fear in the wild, in relation to actual predator densities. Using giving up density experiments, and vertebrate surveys, I described the landscape of fear of two rodent species in relation to predator abundances in open savannah woodland. I offered native eastern chestnut (*Pseudomys gracilicaudatus*) and introduced house mice (*Mus musculus*) food in the open, and under the cover of grass. When eastern brown snakes (*Pseudonaja textilis*) were absent, both eastern chestnut and house mice consumed more food items under cover. When snakes were present, eastern chestnut mice consumed more food items in the open than under cover. House mice, on the other hand reduced their foraging activity undercover, but did not increase foraging in the open in the presence of snakes. The abundance of other predators did not correlate with food intake in different habitats. Native mice apparently can adjust their antipredator behaviour to remain successful in the presence of native predators.

In conclusion, my study provides the first insights into the responses of reptile and mammal assemblages to native savannah invaded by grader grass, and the interaction between fire and the presence of grader grass. I describe how fauna respond to habitat

modifications after fire, and after vegetation cover had returned to levels similar to pre-fire. My study found that reptiles and mammal community composition in these naturally fire-prone savannah systems were sensitive to the presence of the weed, and to frequent fires (≤ 2 years), especially in the weedy parts of the habitat. I suggest managers leave longer intervals between prescribed fire in tropical savannahs, which burn frequently anyway, and suggest that fewer fires might help to maintain faunal biodiversity in fire-prone habitats. I also suggest that decisions to burn weeds should include an awareness of the likelihood of enhancing certain species while discouraging others, and conservation decisions should be based on fire sensitive species given a multi-species response.

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CHAPTER 1. GENERAL INTRODUCTION

Human mediated transport has allowed some species to extend their range beyond their natural ability to disperse (Vitousek *et al*., 1996). Highly successful invader species have the ability to transform the ecosystem they invade and cause large-scale habitat degradation (D’Antonio and Vitousek 1992; Vitousek *et al*., 1996; DiTomaso 2000; Pimentel *et al*., 2005; Kier and Vogler 2006; Arim *et al*., 2012; Setterfield *et al*., 2014). There are many different types of invasive weeds with different growth structures, such as woody weeds, shrubs, legumes, cactus, annual and perennial grasses (Brown and Carter 1998; Clarke *et al*., 2005; Keir and Vogler 2006; Rahlao *et al*., 2009; Bateman and Ostoja 2012; Kuebbing *et al*., 2014; Novoa *et al*., 2014), and therefore it is difficult to generalise the effects of invasive vegetation in native systems (Arim *et al*., 2012). Hence, I will focus on invasive grasses, in particular grader grass (*Themeda quadrivalvis*), and how invasive grasses shape native grassland systems by changing fuel conditions; flourishing under the new conditions they create. I will also address how fauna may respond to invasive grasses and novel fire regimes caused by weeds.

Invasive grasses

Invasive grasses are among the worst threats to natural ecosystems, because they can rapidly change the ecosystem they invade (D’Antonio and Vitousek 1992). Exotic grasses can often tolerate high variability in resources such as water and nutrients (Keeley *et al*., 2003; Keir and Vogler 2006; Alba *et al*., 2015). Traits that make invasive grasses successful invader species are their ability to rapidly germinate, high seedling vigour and growth rate, prolific seed production, and significantly taller growth form compared to native perennial grasses (McIvor and Howden 2000; DeFalco *et al*., 2003; Setterfield *et al*., 2005; Keir and Vogler 2006; Han *et al.,* 2008; Vogler and Owen 2008; Chapter 2 this thesis). Invasive grasses often outcompete native grasses by overgrowing them, reducing solar radiation reaching the ground, and altering soil water and nutrient availability (Vogler and Owen 2008; Wilsey *et al*., 2009). Once invasive grasses are established, they often alter and simplify the native habitat structure by growing closer together, reducing floral diversity (Hughes *et al*., 1991; Tews *et al*., 2004; Kutt and Kemp 2012; Lindsay and Cunningham 2012). Annual invasive grass species also produce higher biomass than native perennial grasses, which reduces habitat heterogeneity in invaded communities (Wilsey *et al*., 2009; Price *et al*., 2010; Lindsay and Cunningham 2012; Alba *et al*., 2015).

Disturbance caused by the introduction of exotic grasses has increased in all major grassland communities worldwide. The invasive grass (*Melinis minutiflora*) in the Brazilian Cerrado savannah reduced tree seedling survival in invaded plots (Hoffman and Haridasan 2008), and invasive Johnson grass (*Sorghum halepense*) reduced native grass dominance in a tall grass prairie in North America (Rout *et al*., 2013). There may be reduced establishment of invasive grasses in African savannah, because of grazing from large herbivores (Musil *et al*., 2005; Foxcroft *et al*., 2010). Even in Africa, however, invasive purple fountain grass (*Pennisetum setaceum)* promotes fire in otherwise fire-free arid shrub zones, increasing the spread of this grass in South Africa (Rahlao *et al*., 2009).

Invasive grasses have the ability to alter ecosystem processes by growing in monocultures, simplifying habitat structure, and suppressing native grass germination by forming dense stands and weed mats (D’Antonio and Vitousek 1992; Mack *et al*., 2000; Ridenour and Callaway 2001; Ogle *et al*., 2003; Bower *et al*., 2014). In spite of these profound effects, the simple removal of invasive grasses is not always a good route to restoration of native habitats, because removal of invasive grasses creates bare ground, which depletes soil moisture, and dramatically increases light levels, causing a hostile environment for native grass recruitment (D'Antonio *et al*., 1998). A study by D'Antonio *et al*., (1998) demonstrated that the removal of exotic weeds did not increase new species recruitment in low diversity and slow growing perennial grassland in Hawaii. Corbin and D'Antonio (2004), however, found that within two years of establishment, the presence of native perennial bunchgrass reduced exotic grass growth, suggesting that increases in cover of native vegetation can sometimes increase resilience, and reduce invasive grass establishment. Where possible, land managers should support decisions that promote re-establishment of native grasses (Corbin and D'Antonio 2004; Fridley *et al*., 2007; Cook and Grice 2013).

Invasive grader grass (*Themeda quadrivalvis*) in Australia

Grader grass (*Themeda quadrivalvis*) is typical of an annual invasive grassy weed in many ways. It is common in disturbed systems worldwide, occurring in the United States, New Caledonia, Southeast Asia, Papua New Guinea, the Middle East and tropical America, often as a noxious weed (Keir and Vogler, 2006). After its accidental introduction to Australia in the 1930s from India (Bishop 1981), grader grass spread quickly across large regions of central and northern Queensland, Northern Territory, and northern Western Australia, and the climatic conditions in Australia are favourable for grader grass to spread more (Fig. 1; Keir and Vogler 2006).

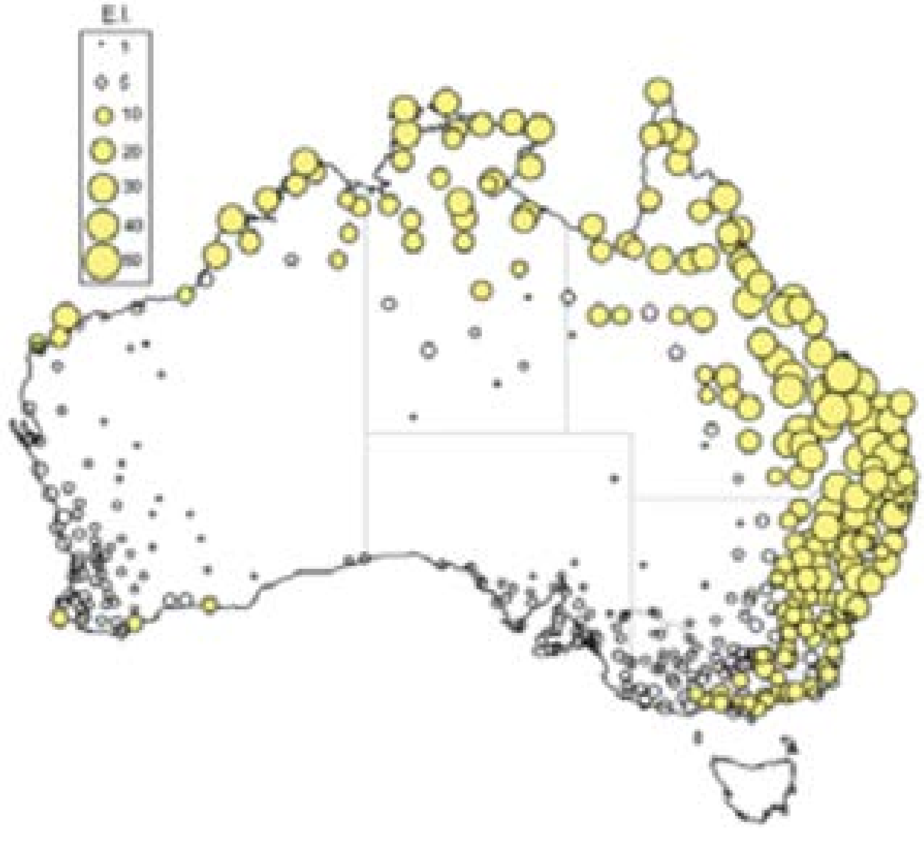
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Figure 1. Distribution map of grader grass (left) from database records, source: Queensland, New South Wales, and Northern Territory Herbariums, and Australian Virtual Herbarium: http://www.chah.gov.au/avh). The potential distribution of grader grass (right) in Australia based on modelling with CLIMEX software. The size of each yellow dot corresponds to the Ecoclimatic Index (EI) value for that location, representing the suitability of the climate for the persistence of grader grass areas with EI values of less than 10 (shown as unfilled circles) are considered only marginally suitable, while those over 30 represent a very favourable climate (with permission to use distribution maps Keir and Vogler 2006).

Grader grass is a tall (> 2m) fast-growing, annual grass, which seeds prolifically and germinates rapidly. Mature grader grass is reddish to golden in colour and is rigid, fibrous, and unpalatable to native and domestic herbivores (Fig. 2; McIvor and Howden 2000; Keir and Vogler 2006). At Undara National Park, the study area, grader grass grows in areas where the native grasses are dominated by the congener native Kangaroo grass (*Themeda triandra*), and black spear grass (*Heteropogon contortus*).

Although native perennial kangaroo grass is similar in appearance to grader grass, both mature kangaroo and black spear grass are much shorter (< 1.5m) than mature grader grass (Fig. 2; McIvor and Howden 2000; Keir and Vogler 2006). Kangaroo and black spear grass grow in clumps, or hummocks, spaced at regular intervals in open woodland, whereas grader grass emerges as a single stolon, and grows in a sward rather than hummocks (Fig. 2).

Figure 2. Pictures show grader (left), kangaroo (middle), and black spear (right) grass, pictures at the top show seed heads and bottom pictures illustrate the growth form of the different grasses.

Black spear grass develops a characteristic black seed-head with a long awn at one end and a sharp spike at the other, whereas kangaroo grass is similar in morphology to its congener grader grass, kangaroo grass has longer spikelets than grader grass (Fig. 3). However, grader grass produce three times more biomass than native kangaroo and black spear grass, and to reduce the accumulation of grader grass, land managers most frequently use fire (Keir and Vogler 2006; Vogler and Owen 2008).

Figure 3. Grader grass seed head (left) – spikelets are 4-7mm long, and kangaroo grass seed head (right) – spikelets are 8-14mm long. (Photo credit: Wayne Vogler).

Invasive weeds in fire-prone grasslands

Weeds and fire are major, non-independent forces shaping vegetation composition and structure in naturally fire-prone tropical savannahs (D’Antonio and Vitusek 1992; Foxcroft *et al*., 2010; Lindsay and Cunningham 2012; Alba *et al*., 2015). In general, grass-dominated systems are relatively flammable, with the ability to recover rapidly following the fire (Foxcroft *et al*., 2010; Setterfield *et al*., 2014; Alba *et al*., 2015). Land managers often use fire as a management tool to both reduce weed encroachment, and decrease fuel loads caused by weeds (Emery and Gross 2005; Price *et al*., 2012). However, fires fuelled by invasive grasses burn hotter and more intensely than native grass fires, potentially creating severe fires at times and places where natural fires do not occur, or are not so intense, causing a positive feedback cycle in which more homogenous grass cover promotes fire, which in turn promotes a more rapid spread of weeds (D’Antonio and Vitousek 1992; Corbett *et al*., 2003; D’Antonio and Hobbie 2005; Setterfield *et al*., 2010).

The conditions that favour fire occur frequently in grasslands, and invasive annual grasses recover more rapidly than native species, which increases grassland susceptibility to fire (D'Antonio and Vitousek 1992). Invasive grasses change vegetation flammability, and cause an increase in fire severity (Keeley *et al*., 2003; Setterfield *et al*., 2010; Russel-Smith *et al*., 2012; Alba *et al*., 2015). For example, invasion by beard grass (*Andropogon guyanus)* in an Australian tropical savannah increased fuel load, causing hotter fires (Rossiter *et al*., 2003; Setterfield *et al*., 2010). Fuels are one ecosystem component linked with fire by feedback loops, and shifts outside the natural range of fuel conditions can result in directional shifts in fire regimes (Rossiter *et al*., 2003; Brooks *et al*., 2004). New fire regimes are coupled with localized losses of native plant species, especially reducing fire-sensitive flora, which creates opportunities for non-native grasses to expand (D'Antonio *et al*., 1999; Keeley *et al*., 2003; Brooks *et al*., 2004; Foxcroft *et al*., 2010; Alba *et al*., 2015). A review by Keeley (2006) showed that invasive grass cover increased with frequent fires. More frequent grass fires increase burn area, and hotter burns reduce the availability of bushes, logs, hollows and tree trunks in these habitats (Hughes *et al*., 1991; Hoffman *et al*., 2004; Setterfield *et al*., 2010; Haslem *et al*., 2011; Russel-Smith *et al*., 2012; Tng *et al*., 2014). Reducing burning of invasive grasses to prevent such effects can be problematic, however, because it may cause more severe fires when fires do occur (Murphy and Russell-Smith 2010). In general, invasive grasses cause altered fire regimes by changing fuel conditions, and then they flourish under the new conditions they create (Brooks *et al*., 2004).

Fire frequency increases with invasive grass establishment, and many weedy grasses in Northern Australia support frequent, high intensity fires (< 1 year between fires, Rossiter *et al*., 2003). Yates *et al*., (2008) showed that Australian savannahs are vulnerable to large-scale and frequent fires. The increase in fuel load and rapid germination following fire by beard grass has substantially amplified the fire season in Northern Australia, increasing fire management costs (Setterfield *et al*., 2014). Similarly, the increase in fuel load by invasive grasses in Hawaii increased the fire frequency more than threefold, and cheat grass (*Bromus tectorum*) invasion caused a tenfold increase in fire frequency in North America (Hughes *et al*., 1991; Milton 2004; Bradley *et al*., 2006). Although reversing fire frequency is costly and labour intense, one way would be to remove annual exotic grasses and re-seed with native vegetation combined with the exclusion of fire (Keeley 2001; Milton 2004; Vogler and Owen 2008; Setterfield *et al*., 2014; Yelenik *et al*., 2015). Restoring native habitats invaded by exotic grasses by revegetation of native plants may reduce the fuel load, which over time may reduce the fire return frequency (Cione *et al*., 2002).

Faunal diversity, invasive weeds, and fire in tropical savannahs

The diversity of reptiles and small mammals is often reduced in habitats invaded by weeds (Martin and Murray 2011; Litt and Steidl 2011; Chapter 2). The negative influence of weeds on reptiles may be driven by a variety of factors. Food availability may be reduced in weeds (Valentine 2006; Martin and Murray, 2011), predators may be more abundant or more successful in weeds (e.g., Thompson 1987), habitat structure of weeds may alter behaviour, affecting movement and social interactions (Newbold, 2005; Downes and Hoefer, 2007; Rieder *et al*., 2010; Steidl *et al*., 2013; Hacking *et al*., 2014), or reducing opportunities for thermoregulation (Valentine 2006; Downes and Hoefer, 2007; Carter *et al*., 2014; Hacking 2014). For mammals, areas with high seed output such as weeds and crop fields can often harbour higher densities of rodents

(Ylönen *et al*., 2002; Litt and Steidl 2011), whereas medium-sized mammals' mobility in dense weeds may be much reduced (McGregor *et al*., 2013).

An increase in fire intensity by invasive grasses, at times when natural fires seldom occur, may delay flowering events and reduce insect availability, which may negatively impact small vertebrates (Corbett *et al*., 2003; Radford and Andersen 2012; Kwok & Eldridge 2015). Hotter fires can consume more vegetation, promoting grass dominance, which may change faunal resource dynamics, effecting food availability, shelter opportunities, and predator susceptibility in native fauna (Barnard 1987; D'Antonio and Vitousek 1992; Valentine *et al*., 2007; Parker-Allie *et al*., 2009; Pastro *et al*., 2011; Penman *et al*., 2011; McGregor *et al*., 2014). In addition, hotter fires from more intense burns may increase mortality rates in small vertebrates (Griffiths and Christian 1996; Barlow and Peres 2004; Smith *et al*., 2012; Cross *et al*., 2015). Repeated fires may reduce a species' geographic range, and fire-sensitive species may become locally extinct (Parr and Andersen 2006; Driscoll and Henderson 2008; Penman *et al*., 2011; Russel-Smith *et al*., 2012). On the other hand, tropical savannah ecosystems are shaped by natural fires and are highly diverse, suggesting that the fauna of tropical savannahs are resilient to naturally occurring fires (Woinarski *et al*., 2004; Andersen *et al*., 2005; Pianka *et al*., 2012). Even in communities highly resilient to fire, however, increased fire frequency and intensity altered by invasive weeds can open the understory vegetation structure in savannahs and open woodlands, negatively impacting fauna that shelter in dense grasses (Barlow and Peres 2004; Yates *et al*., 2008; Robinson *et al*., 2013; Smith *et al*., 2013; Burgess *et al*., 2014; Alba *et al*., 2015).

High intensity fire in weeds may also negatively affect reptiles more than grass fires in native habitats, because reptiles in native savannah may prefer the habitat structure and composition created by the low intensity fires characteristic of native savannah

(Braithwaite 1987; Friend 1993; Trainor and Woinarski 1994; Singh *et al*., 2002a; Corbett *et al*., 2003; Pastro *et al*., 2011; Pianka *et al*., 2012). Small to medium-sized mammal species are also sensitive to frequent fires and gradually decline, or suddenly collapse in abundance, in habitats with repeated burning with slow recovery rates after fire (Pardon *et al*., 2003; Andersen *et al*., 2005; Converse *et al*., 2006; Horn *et al*., 2012; Francl and Small 2013; Griffiths and Brook 2014; Kelly *et al*., 2014; Griffiths *et al*., 2015; Mendonça *et al*., 2015; Radford *et al*., 2015). Some mammals avoid burnt habitats and occur in lower abundances after fire, returning with emerging vegetation cover (Clarke and Kaufman 1990; Vieira 1999; Breed and Ford 2007; Bock *et al*., 2011; Kirchner *et al*., 2011). Changing fire regimes, in association with changing land use and weed encroachment, are suspected of causing declines in small and medium weight-range mammals in Australia (Johnson 2006; Griffiths and Brook 2014; Radford *et al*., 2015). Many birds can easily move away from burnt grass habitats, but frequent fires in habitats invaded by weeds promote a shift in the bird assemblage, causing an increase in abundances of granivorous and omnivorous birds following fire (Woinarski 1990; Valentine *et al*., 2012). A more heterogeneous habitat with a more structurally complex vegetation gradient may moderate the effects of fire on bird communities (Barton *et al*., 2014; Hovick *et al*., 2014; Burgess and Maron 2015). The response of reptiles and mammals to weeds and fire may be complex and potentially influenced by their ability to disperse, in contrast to bird assemblages.

There are gaps in the literature on the impacts of invasive weeds on fauna, and few studies have investigated the underlying mechanisms causing negative effects of weeds on vertebrate communities (Valentine 2006; Hacking *et al*., 2014). Land managers use fire to reduce weeds, but studies of the effects of fire in weedy habitats often focus on the response of native flora following fire (Alba *et al*., 2015). Few studies investigate faunal responses directly and shortly (≤ 2 years) after fire, and even fewer studies have investigated individual species response before, directly after, and shortly after fire after vegetation cover has returned. Hence, to make informed management decisions in fire-prone, weed infested systems, it is important to understand the response of these ecosystems (including fauna) to intense and frequent fires. It is equally important to understand how native fauna use weedy habitats by investigating key changes that may be caused by weeds that could influence fauna, including influences of weeds on structural complexity, food availability, thermal regimes, and predator densities. In this study I will investigate the influence of these factors on vertebrate (reptile) community composition and individual species responses. I provide the first study investigating faunal responses to native savannah invaded by grader grass. I describe the influence of grader grass on reptile species assemblage composition in native and weedy grass habitats, and I examined factors that might influence reptile habitat use. I quantified habitat characteristics likely to be used by reptiles (such as grass spacing, and amounts of various habitat features such as logs and leaf litter) (e.g., Jellinek *et al*., 2004). I measured environmental temperatures within grass clumps, because reptiles are ectotherms, and temperature is a critical feature determining habitat use (e.g., Taylor and Fox 2001). I also quantified food availability, by assessing the overall biomass of invertebrates in the different grasses types (e.g., Diaz and Carrascal 1991; Christie *et al*., 2013). Finally, because predation may influence the use of habitat by reptiles (e.g., Diaz and Carrascal 1991), I determined the abundance of avian and reptilian predators of reptiles in the native and grader-grass-infested savannah.

I describe reptile and mammal responses to fire, because these two groups are highly abundant, and typically respond strongly to habitat disturbances (Braithwaite 1987, Litt and Steidl 2011; Pianka *et al*., 2012, Smith *et al*., 2013, Hacking *et al*., 2014). I compared reptile and mammal assemblage composition in native and weedy habitats before, immediately after, and up to fifteen months after prescribed burning, to determine if there were detectable changes in assemblage composition and habitat complexity. This research provided insight into the resilience of tropical Australian reptile and mammal populations to fire in the short-term, in different habitats. Determining the short-term effects of fire is highly relevant in environments that burn very frequently (often more than once per year, Price *et al*., 2012).

Finally, predation risk can have profound impacts on foraging strategies of prey organisms, and it is of great importance to an individual to identify and respond specifically to particular predators to avoid predation. Here I investigated rodents' perceived risk of predation by offering a depletable food source under grass cover and in the open (away from grass) in habitats with a known predator structure and measures of actual predator abundance.

Organisation of data chapters

To investigate the effects of invasive weeds and fire on native faunal community assemblage structure in native tropical savannah, and I addressed specific questions. My thesis chapters are structured as a series of stand-alone publications that are connected by theory and is organised as follows. First, I determined the use of native and invasive grader grass (*Themeda quadrivalvis*) by reptiles, and identified the key mechanisms that influenced reptile diversity in these habitats (Chapter 2). Then I determined the impact of fire on faunal assemblages, comparing reptile (Chapter 3) and mammal (Chapter 4) assemblages in habitats that were unburnt (not burnt for 2 years), directly after burning, and when grasses had returned pre-fire levels 15 months after fire, in native and in native savannah invaded by grader grass. In Chapter 5, I described the landscape of fear of rodents in relation to actual predator abundances in a tropical savannah. Finally, I discuss my findings including management recommendations and future research directions (Chapter 6). I include a paper authored with an honours student (Hacking *et al*., 2014) as an appendix. I helped this student conduct this study, and it formed an important part of my PhD study.

CHAPTER 2. MECHANISMS OF THE IMPACT OF A WEED (GRADER GRASS, *Themeda quadrivalvis*) ON REPTILE ASSEMBLAGE STRUCTURE IN A TROPICAL SAVANNAH

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Introduction

Invasions by non-native grasses are among the worst threats to natural habitats; because they can rapidly change the ecosystem they invade (D'Antonio and Vitousek 1992). Non-native annual grasses can often tolerate high variability in resources such as water and nutrients, and can have rapid germination rates, higher seedling vigour and growth rate, and they may grow significantly taller than native perennial grasses (McIvor and Howden 2000; Setterfield *et al*., 2005; Keir and Vogler 2006; Vogler and Owen 2008). These and other mechanisms make annual exotic grasses successful invaders that can outcompete native perennial grasses (Vogler and Owen 2008; Wilsey *et al*., 2009). Once they have established, invasive grasses often alter and simplify habitat structure, because they may have different growth forms and high biomass, growing closer together, and change leaf litter composition, reducing native leaf litter load (Hughes *et al*., 1991; Tews *et al*., 2004; Kutt and Kemp 2012; Lindsay and Cunningham 2012).

Tropical savannah reptiles provide an excellent study system with which to examine the influence of grassy weeds on vertebrate assemblages, because reptiles have high species richness, and can occur in high abundances (Braithwaite 1987). They often respond quickly to habitat structural alterations such as weed establishment, and have small home ranges and low vagility compared to birds and large mammals, which may make their responses more immediate and easier to measure (Pianka 1967; Valentine *et al*., 2007; Price *et al*., 2010; Gainsbury and Colli 2014). Weeds often have negative influences on reptile assemblage composition (reviewed by Martin and Murray 2011), but not always (e.g., Fischer *et al*., 2003; Garden *et al*., 2007). The influence of weeds on reptile assemblage composition and abundance may be driven by a variety of factors. Food availability may be altered in weeds (Valentine 2006; Martin and Murray 2011), predators may be more abundant or more successful in weeds (e.g., Thompson 1987), habitat structure of weeds may alter behaviour, such as movement and social interactions (Newbold 2005; Downes and Hoefer 2007; Rieder *et al*., 2010; Steidl *et al*., 2013), or influence thermoregulation (Valentine 2006; Downes and Hoefer 2007). Studies examining the likely sources of the impacts of weeds are required to predict the effects of weeds in different habitats and on other faunal assemblages (Martin and Murray 2011).

I examine the effects of an invasive grass on reptile assemblage composition and diversity, using a natural system invaded by grader grass (*Themeda quadrivalvis*). Grader grass is typical of invasive grassy weeds in many ways. It is common in disturbed systems worldwide, occurring in the United States, New Caledonia, Southeast Asia, Papua New Guinea, the Middle East and tropical America, often as a noxious weed (Keir and Vogler 2006). After its accidental introduction to Australia in the 1930s from India, grader grass spread quickly across large regions of central and northern

Queensland, the Northern Territory, and northern Western Australia (Keir and Vogler 2006). Grader grass is a fast-growing, annual grass, which seeds prolifically and germinates rapidly. Mature grader grass is rigid, fibrous, and unpalatable to native and domestic herbivores (McIvor and Howden 2000; Keir and Vogler 2006).

To determine the responses of reptiles to weeds, I quantified the reptile assemblages in native grass habitats that had been invaded by grader grass (*Themeda quadrivalvis*), and compared them to those found in adjacent native kangaroo grass (*Themeda triandra*) and black spear grass (*Heteropogon contortus*) habitats. To describe possible mechanisms influencing reptile composition in the three habitats, I also compared various characteristics that might influence reptile use of habitat. I quantified habitat characteristics likely to be use of the habitat by reptiles (such as grass morphology, and amounts of various habitat features) (e.g., Jellinek *et al*., 2004). Because reptiles are ectotherms, temperature is a critical feature determining habitat use (e.g., Taylor and Fox 2001) so I measured environmental temperatures within grass clumps because food availability is a major factor determining habitat use of many animals, I quantified food availability, by assessing the overall biomass of invertebrates in the different grasses (e.g., Diaz and Carrascal 1991; Christie *et al*., 2013). Finally, because predation may influence the use of habitat by reptiles (e.g., Diaz and Carrascal 1991) I determined the abundance of avian and reptilian predators of reptiles in the native and weed-infested habitats.

Methods

Study system

Undara Volcanic National Park (18°19`29.92``S, 144°36`28.31``E) covers an area of 66 000 ha, and is a part of the McBride Volcanic System, 850 m above sea level, approximately 420 kilometres northwest of Townsville, Queensland. Study sites were located in open savannah woodland at Undara. Tree species in the woodland included bloodwood (*Corymbia pocillum*), rough-leaved cabbage gum (*Corymbia confertiflora*), narrow-leaved ironbark (*Eucalyptus crebra*), Darwin woollybutt (*Eucalyptus miniata*), silver oak (*Grevillea parallela*), and bat's wing coral trees (*Erythrina vespertilio*), with a grassy understory. I selected 24 sites with 8 sites in each of the three different dominant grass habitats (Fig. 1), either grader grass (*Themeda quadrivalvis*), native kangaroo grass (*Themeda triandra*), or black spear grass (*Heteropogon contortus*). Sites were spatially separated so that site clusters included at least two, and typically all three dominant grass types, and sampling sites within each cluster were separated by at least 100 m (usually more, Fig. 1).

Native kangaroo and black spear grass are both perennial, grow to about 1.5 m, and provide good fodder for grazing (McIvor and Howden 2000). Black spear grass develops a characteristic black seed-head with a long awn at one end and a sharp spike at the other, whereas kangaroo grass is similar in morphology to its congener grader grass, with longer spikelets. Kangaroo and black spear grass grow in clumps, or hummocks, spaced at regular intervals in open woodland, whereas grader grass emerges as a single stolon, and grows in a sward rather than hummocks.

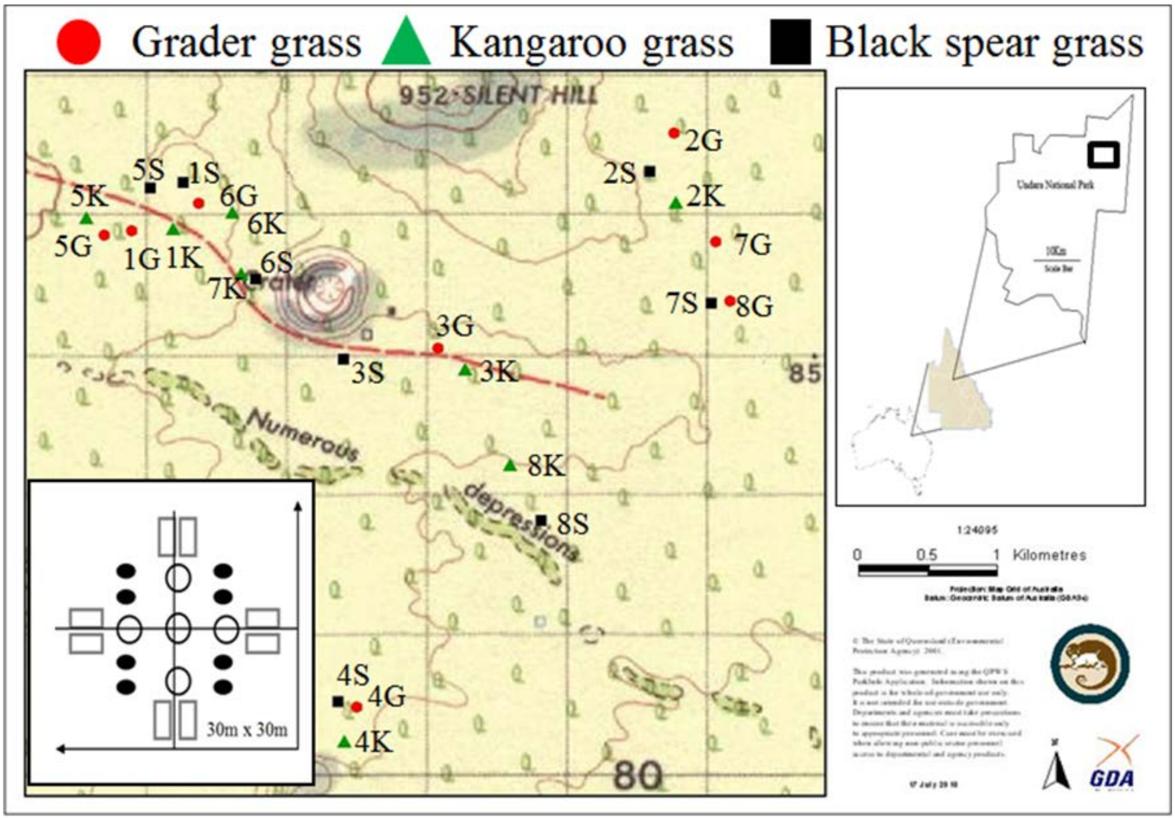

Figure 1. Location of sampling sites (50 x 50m) at Undara volcanic national park (top right corner, box indicate sampling area) and reptile and insect trap array (30 x 30m, bottom left corner) for each site, pitfall traps (open circles), funnel traps (boxes), and insect traps (filled circles).

History of sampling sites

Sampling sites were located on the basalt plains of Undara (Gunn 1974; Fig. 1). At Undara, collapsed lava tubes meander throughout the park, and are characterised by evergreen vegetation similar to that found along the east coast of Australia (Atkinson and Atkinson 1995). Prior to becoming a national park in 1992, Undara was a grazing property, but it had not been grazed by cattle for 16 years when I started my study. Undara is also subject to prescribed fire as a management tool, but savannah grasslands are naturally fire-prone systems (Foxcroft *et al.*, 2010), and Undara Volcanic National Park is burnt, at least partially, by wildfires every 3 to 5 years. In addition to this, park rangers use prescribed burning to reduce weeds and the build-up of fine fuels, rotationally burning in the early dry season (April – May) (Queensland’s Fire and Rescue Authority Act 1990). Sampling sites in the current study had been burnt on rotation every 2 years since 2002, and there were also wildfires in October 2003 and November 2008 that burned the entire park, including some sampling sites (Chapter 3). The grasses on the study site consisted of mixed stands of kangaroo and black spear grass, which were sometimes dominated by one or the other grass, with introgressions of grader grass. Areas dominated by spear grass sites had a higher proportion of other grasses on them than areas dominated by kangaroo grass. Grader grass was more common on roadsides and in previously cultivated areas, but had also invaded areas of native grass that appeared undisturbed.

Sampling periods, trap Array, and measurements

I trapped reptiles over two years (eight trapping periods) in four distinct trapping periods per year: pre-wet (21 Oct – 14 Nov 2008 and 2009), mid-wet (3 – 26 March 2009 and 2010), early-dry (14 April – 6 May 2009 and 2010), and mid-dry seasons (14 July – 12 Aug 2009 and 2010) with 19 to 21 trap days in each season. Trapping sites were selected so at least two, and often all three grass species occurred >100 m of one another. I selected sites to ensure that there was no spatial clumping of particular grass types. This was possible because of the highly heterogeneous nature of the grasses growing in that area, and because all three grasses were widely represented in the area. Climatic data were obtained from the weather station at Undara Volcanic National Park, deployed by the Queensland Department of Agriculture, Fisheries and Forestry. Annual average air temperature 21.6 ± 0.1, range 3.2 – 46.3ºC and relative humidity 67 ± 0.53, range 5.5 – 100% with highest precipitation between November and March (maximum daily range 14.2 – 50.6 mm). Grass temperatures were acquired using one iButton™ (Thermodata Pty Ltd, South Yarra) temperature data logger placed inside a clump of grass in each grass habitat at each site for the duration of each census period.

I monitored seasonal changes in vegetation cover and in structural complexity. I conducted habitat surveys for each sampling site in each trapping period, using four 50–metre transects at each site, spaced 16.6 m apart, and habitat variables were recorded in linear centimetres on this transect. At each sampling occasion, I recorded the cover of, dominant grass (total number of cm of grader, kangaroo, or black spear grass intercepting the 50 m tape on all 4 transects, converted to % cover), of mixed grasses (calculated by summing the % cover of all other grass species), broad-leaf vegetation (% cover of herbaceous plants and legumes), leaf litter, logs, rocks, exposed soil, and canopy cover above the transect.

I used a 30 x 30 m trapping grid at each of the 24 survey sites (Fig. 1). Five pitfall traps (20l, straight-sided buckets) were placed in the ground with the lip level with the ground’s surface, with one centre bucket and four ‘arms’ (Fig. 1). Traps were spaced 10-m apart and connected *via* a drift fence (50-cm high UV resistant fibreglass drift fence, Cyclone™), which crossed every pitfall trap, and extended a further 5 m beyond the last pitfall trap on each ‘arm’ of the cross. To reduce desiccation risk and exposure of captured animals, a moistened sponge and a piece of cloth were placed inside each pitfall trap, and the bottom of each trap was lined with a 5-cm layer of leaf litter. Eight funnel traps (dimensions, 180W x 730L x 170H mm) were arranged at each site. Funnel traps were placed on both sides of the drift fence on each arm of the cross, against the 5 m of drift fence projecting past the last pitfall trap on each arm, approximately 2 m from the end, with a shade cloth covering the funnel trap (Fig. 1). To prevent small vertebrates in traps being attacked by ants, I used ant sand (Antex, 2g/kg Bifenthrin) as a deterrent, sprinkled around the mouth of the pitfall trap and underneath funnel traps. All traps were checked and cleared twice daily, in the early morning (5:30 – 8:30) and in the late afternoon (16:00 – 18:00), and captured reptiles were identified to species using Wilson (2005).

Invertebrates were caught in two different types of trap, and I deployed a total of 8 traps per sampling site (Fig. 1). Pit traps, which consisted of plastic cups (diameter and height, 75 x 140 mm), with the lip level with the ground, and flight-intercept traps, which were transparent plastic squares (50 x 50 mm) with a pit-trap beneath them to catch invertebrates that encountered them. Pit traps contained a solution consisting of one part concentrated ethylene-glycol (Repco^{TM}), mixed with three parts of water and a few drops of detergent (Ecostore^{TM}) to break the surface tension of the solution (Schmidt *et al.*, 2006). Flight-intercept traps were elevated to maximum grass height to intercept flying insects. All invertebrates caught were decanted from the pit trap solution and preserved in 70% ethanol solution.

I always used the same observer (RA) to reduce observer bias when conducting bird surveys. Each sampling site (50 by 50 m) was surveyed for birds a minimum of five and a maximum of ten times over each trapping period, to investigate the abundance of avian predators of reptiles. Birds were identified to species using binoculars and a field guide (Simpson and Day 2004).

Statistical analysis

Habitat variables

Prior to analysis, I calculated the mean cover of habitat variables over the eight trapping periods and relativised them (dividing the abundance of each variable by the maximum abundance of that habitat variables detected at any sampling site). I examined habitat composition by comparing the habitat variables among the three dominant grass habitats (grader, kangaroo, and black spear grass). I used MANOVAs with Wilk’s Lambda (λ) as the test statistic to compare the sites, followed by ANOVAs and Tukey’s HSD post-hoc tests when significant differences were detected among habitat variables (SPSS V.20).

I tested for collinearity among the ten habitat variables, and evaluated variables using pairwise correlations. Of the 45 pairwise correlations, only three correlations were above r = 0.7, and none was above the more stringent, but commonly used, threshold of r = 0.85, so I included all variables in the GLMMs described below.

Patterns in reptile abundance and richness

Reptile capture data were all standardised to 100 trap nights, and I reduced the influence of rare species by removing all species that occurred at less than three sampling sites. I investigated reptile abundance and richness in the three different grasses using generalised linear models (GZLM, SPSS V.20). I constructed separate models using a Gaussian-error distribution with identity link function with reptile abundance and richness as dependent variables, and grass type as the predictor, and examined Wald chi-square statistics and confidence intervals to compare among grasses. To investigate significant differences in reptile abundance and richness among dominant grass sites I followed the modelling with pairwise comparisons (least significant difference or LSD tests) of estimated means.

Reptile assemblage structure in different grasses

To compare standardised (to 100 trap night) reptile assemblages among grader, kangaroo, and black spear grass, I reduced the influence of highly abundant species on pattern interpretation, by using a relativising transformation, dividing the abundance of each reptile species by the maximum abundance of that species caught at any sampling site. The data were analysed using one-way PerMANOVA, a distance-based nonparametric multivariate analysis that provides a pseudo *F*-statistic value and derives a *P*-value from permutation tests, followed by post-hoc pair-wise comparisons to detect differences among treatments (Anderson 2001). I used the Sorensen (Bray-Curtis) distance measure, 9999 randomisations and a random number seed for the PerMANOVA test in PC-Ord (McCune and Mefford 1999). I explored the relationships in reptile assemblage composition among sampling sites using non-metric multidimensional scaling (NMDS; Kruskal 1964). Reptile assemblage structure (relativised as above) was used as the primary data matrix, while dominant grass sites (categorical variables) and quantitative habitat variables were relativised (as above) and used as the second data matrix. I employed the autopilot “slow and thorough”, using Sorensen (Bray-Curtis) distance measures, and dimensionality was determined by a Monte Carlo test and significance test of stress in relation to dimensionality (number of axes in final analysis) in PC-Ord (McCune and Mefford 1999). I extracted axis and cumulative scores by using Bray-Curtis (Sorensen) dissimilarity index with original end point selection, city-block projection geometry and calculation of residuals. To illustrate reptile assemblage trends among treatments, I constructed bi-plots from NMDS sites and species scores.

Relationships between reptile abundance, richness and habitat variables

I investigated reptile richness and abundance by using generalised mixed-effect models (GLMMs) with Gaussian error distributions and the identity link function. Grass type had strong influence on reptile abundance and richness and therefore used grass type as random factor to explore which habitat variables influenced reptile abundance and richness. I used standardised reptile richness and abundance (to 100 trap nights), and relativised transformed habitat variables (as above for grader, kangaroo, and black spear grass, mixed grass, broad leaf vegetation, leaf litter, rocks, logs, exposed soil, and canopy cover). I used the lmer function in the lme4 package (Bates *et al*., 2013), dredge (automated model selection) and model average function in the MuMIn package (Barton 2013) in the statistical program R v2.15.2 (R Development Core Team 2012). I constructed two global models, one for reptile abundance, and one for reptile richness including all above habitat variables and grass type. I compared all possible models (10 predictors and grass type as random variable) using the “dredge” function to tease out which habitat variables were most important to reptile richness and abundance. Models were ranked according to model fit using the corrected Akaike information criterion (AICc), and models within ≤ 2 ΔAICc were considered highly supported (Burnham and Anderson 2002).

Grass temperatures, insects, and predator abundance

I compared mean untransformed grass temperatures (°C) and mean overall volume of insects in ml (Table 3), as well as the number of reptile predators of reptiles (Table 2) detected per 100 trap nights, and the number of avian predators of reptiles (Table 4) sampled over a standardised 5 sampling days, as response variables, and compared among the three grass habitats using generalised linear mixed-effect models (GLMMs) with a Gaussian-error distribution and identity link to investigate the effects of grass type on these variables. For grass temperature, I modelled season as a random effect, while for insect and predator abundance analyses I modelled sampling site as the random effect, and for both I used robust estimation and the Satterthwaite approximation. I used pairwise comparisons (least significant difference, LSD) to investigate significant differences among grass treatments (SPSS V.20).

Results

Habitat description

I detected significant differences in habitat variables among the different grass sites (MANOVA $\lambda = 0.158$, $P = 0.003$). All grass habitats, although dominated by one species, contained a mixture of different grasses, but habitats dominated by grader grass were more nearly monocultures than were kangaroo grass habitats or black spear grass (Table 1). Also, mixed grasses were most common (i.e., they covered significantly greater areas) in black spear grass habitats than in grader grass habitats (Tukey's HSD, $P < 0.05$, Table 1 and 2). Leaf litter and logs were more common (i.e., they covered significantly larger areas) in kangaroo and black spear grass habitats than in grader grass habitats, and there was significantly more exposed soil available in kangaroo grass habitats than in grader grass habitats, spear grass habitats were intermediate (Tukey's HSD, $P < 0.05$, Table 1 and 2).

Table 1. Mean % cover (SE) of habitat variables among grass habitats, significant tests are based on tests of relativised transformed data (Tukeys HSD post hoc test $P < 0.05$*).

	Grader$^{(a)}$	Kangaroo$^{(b)}$	Black spear$^{(c)}$
Dominant grass	71.0 (6.1)	59.1 (4.1)	48.4 (3.3)$^{*(a)}$
Mixed grass	19.4 (4.8)$^{*(c)}$	21.5 (3.5)	35.2 (3.2)
Broad leave	3.7 (1.1)	1.6 (0.3)	1.6 (0.8)
Log	0.2 (0.1)$^{*(b,c)}$	1.3 (0.2)	0.8 (0.1)
Leaf litter	1.6 (0.9)$^{*(b,c)}$	8.8 (1.7)	8.3 (1.7)
Rock	0.8 (0.4)	0.3 (0.3)	1.6 (0.9)
Exposed soil	3.2 (0.9)	7.4 (1.6)	4.1 (1.1)
Canopy cover	21.6 (5.4)	14.9 (4.2)	21.0 (5.0)

Table 2. Results from an Analyses of Variance comparing mean % cover of habitat variables (relativised transformed) among sampling sites at significant levels (ANOVA, $P < 0.05$* < 0.001**).

Variables	MS	*df*	*F*
Dominant grass cover	0.121	2	5.906*
Mixed grass	0.196	2	4.807*
Broad leaf	0.177	2	2.373
Log	0.461	2	13.594**
Leaf litter	0.475	2	7.626*
Rock	0.053	2	1.115
Exposed soil	0.133	2	3.174
Canopy cover	0.063	2	0.570
Error		21	

Reptile captures, abundance and richness in different grasses

I conducted eight trapping periods, comprising of 18,863 trap nights, and captured a total of 721 individuals from 48 species and 9 families (number of species in each family was: Agamidae *n* = 1, Colubridae *n* = 2, Elapidae *n* = 10, Gekkonidae *n* = 5, Pygopodidae *n* = 2, Pythonidae *n* = 3, Scincidae *n* = 18, Typhlopidae *n* = 4, and Varanidae *n* = 2, Table 3).

Table 3. Complete list of reptile species, and number of individuals captured in grader grass (G), kangaroo grass (K), and in black spear grass (S) habitats. Species used as predators of reptiles as indicated *.

Family	Species	G	K	S
Agamidae	*Diporiphora australis*	3	20	6
Colubridae	*Boiga irregularis**		2	1
	*Dendrelaphis punctulata**			1
Elapidae	*Acanthopis antarticus**		1	
	*Cryptophis boschmai**			1
	*Demansia psammophis**	5	9	9
	*Demansia torquata**		1	
	*Furina barnardi**			1
	*Furina diadema**	1		2
	*Furina ornata**		1	
	*Pseudoechis australis**		1	
	*Pseudonaja nuchalis**		1	1
	*Pseudonaja textilis**	11	6	11
	*Suta suta**	1		
Gekkonidae	*Amalosia rhombifer*		5	3
	Gehyra dubia	4	3	3
	Heteronotia binoei	1	8	6
	Strophurus williamsi	2	3	2
Pygopodidae	*Delma tincta*	5	4	7

Table continue on next page…

	*Lialis burtonis**		3	
Pythonidae	*Antharesa stimsoni**	1	1	
	*Morelia spilota mcdowelli**			1
Scincidae	*Anomalopus gowi*	1		
	Carlia jarnoldae		4	2
	Carlia munda	4	1	3
	Carlia pectoralis	1	4	2
	Carlia schmeltzii	21	55	43
	Carlia vivax	27	22	18
	Cryptoblepharus adamsi		21	4
	Ctenotus brevipes			1
	Ctenotus spaldingi	1	1	4
	Ctenotus taeniolatus	5	15	23
	Glaphyromorphus cracens	10	18	15
	Lerista ameles	1		
	Lygisaurus foliorium	9	54	27
	Menetia greyii	13	16	16
	Menetia timlowi		1	2
	Morethia taeniopleura	5	24	16
	Proablepharus tenuis	4	17	9
	Viburnsiscincus mundivensis			1
Typhlopidae	*Ramphotyphlops broomi*	1	1	1
	Ramphotyphlops ligatus			1
	Ramphotyphlops proximus	1		1
	Ramphotyphlops ungvirostris		1	
Varanidae	*Varanus scalaris**		10	3
	*Varanus tristis**			1

Skinks comprised 75% of all captured reptiles. Skinks in the genus *Carlia* were the most commonly captured species across all sampling sites, comprising 29% of all reptiles trapped. *Carlia schmeltzii* was the most numerous species (22% of skinks), followed by *Lygisaurus foliorium* (17%), and *C. vivax* (12%). *Carlia munda* and *C. vivax* were the only species captured more frequently in grader grass than in the other grass habitats. Eastern brown snakes (*Pseudonaja textilis)* were the most frequently encountered snakes, comprising 39% of all snake captures (Table 3). Overall reptile recapture rates were very low (2.7%, number of individuals recaptured divided by total reptile captures from each dominant grass), although highest in grader (3.7%, *n* = 5/138), intermediate in kangaroo (2.7%, *n* = 9/333), and lowest in black spear (2%, *n* = 5/248) grass sites. One marked *C. vivax* moved between sampling sites 250 m apart, both were grader-grass dominated sites, and one *Ctenotus taeniolatus* moved from a kangaroo to a black spear grass site, spaced 600 m apart.

The generalized linear models describing reptile abundance (GZLM Wald x^2 = 27.99, *df* = 2, 21 *P* < 0.001, Fig. 2A), and reptile richness (GZLM Wald x^2 = 6.10, *df* = 2, 21 *P* = 0.047, Fig. 2B) differed significantly among dominant grass types. Pairwise comparisons showed that reptile abundance was significantly higher in grass habitats dominated by the two native grasses (LSD, kangaroo *P* = 0.001, and black spear grass *P* = 0.013), and similarly, reptile richness was significantly higher in kangaroo (LSD, *P* = 0.025), and black spear grass (LSD, *P* = 0.044) than in grader grass sites (Fig. 2A and B).

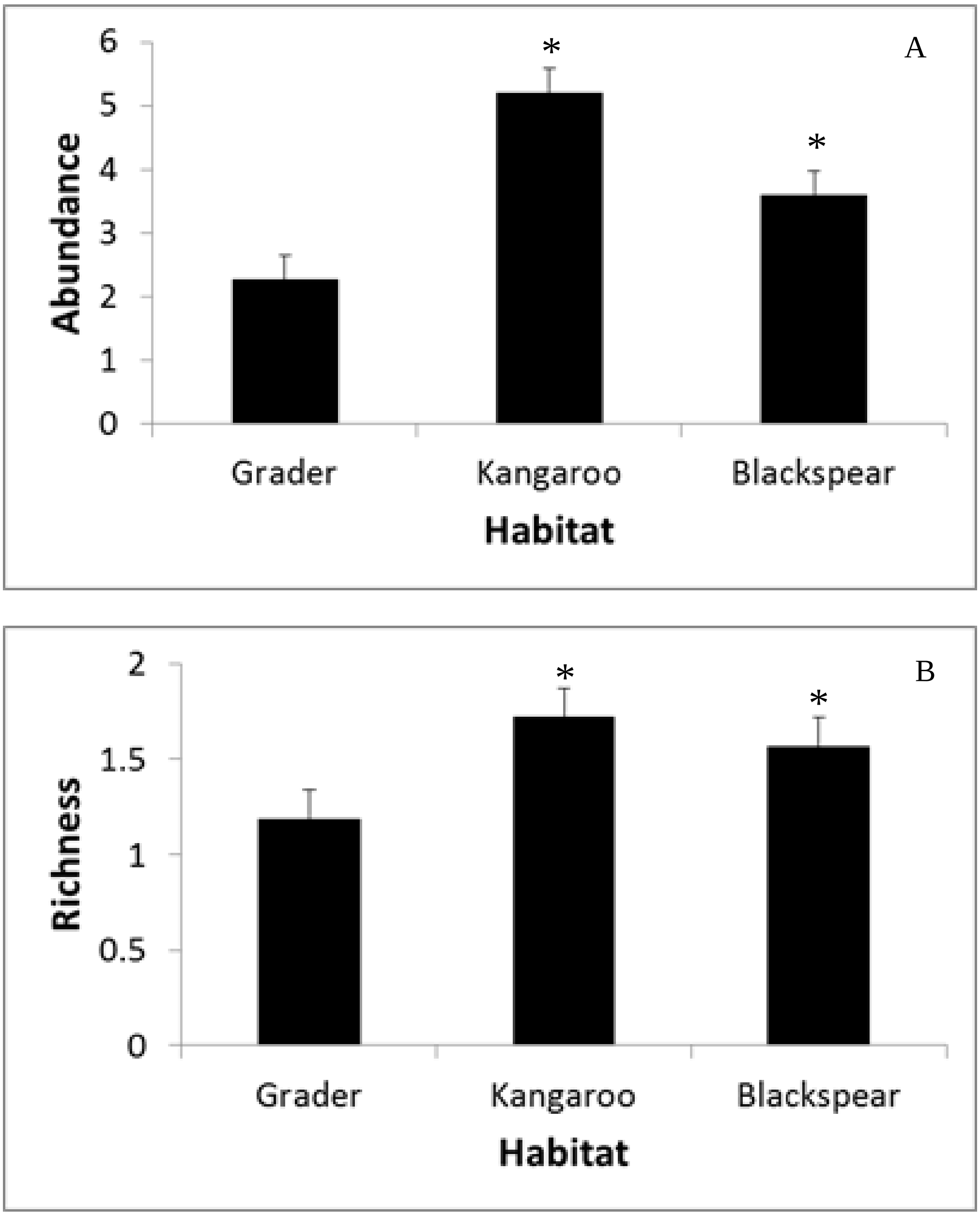

Figure 2. Standardised (to 100 trap nights) average reptile abundance (A), and richness (B) in grader, kangaroo, and black spear grass habitats ± SE (LSD* = $P < 0.05$).

Reptile assemblage structure in different grasses

The reptile assemblage varied significantly among habitat types (PerMANOVA $F_{2,21}$ = 1.6538, P = 0.035), and was significantly different in grader and kangaroo grass sites (t = 1.6887, P = 0.003). There was no significant difference in reptile composition between kangaroo and black spear grass sites ($P > 0.05$). In the NMDS analyses, I detected a stable 2-dimensional solution (stress = 0.218) explaining 68.96% of the variance (Fig. 3A and B). Most reptile species were positively associated with native kangaroo and black spear grass habitats (circled), although species such as *C. munda* and *P. textilis* were more closely associated with grader grass sites (Fig. 3A and B).

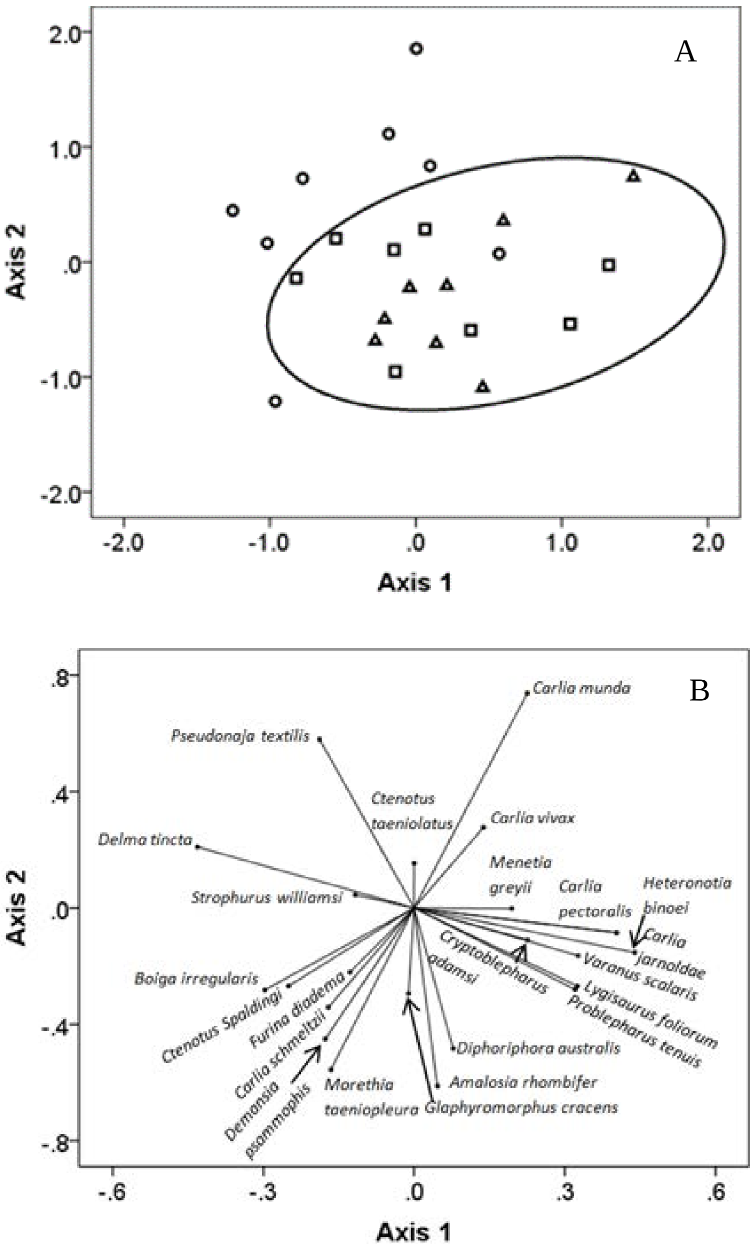

Figure 3. (A) Assemblage structure for 23 species of reptile (relativised by species maximum), shown as a two-dimensional NMDS ordination (stress = 0.218). The first axis represents 43.77% of the variation, and the second axis 25.19%. Symbols: circles = grader grass, triangles = kangaroo grass, and squares =, black spear grass sites. The oval encompasses all native grass sites. (B) The species driving the NMDS results (r2 > 0.20). *Carlia munda* and *Pseudonaja textilis* are associated with grader grass sites, while most other species cluster towards native grass sites.

Associations between reptile abundance and richness and habitat variables

I found that models with two or more habitat variables had very little support, and therefore I used the automated model selection with one habitat variable and treatment (dominant grass type) to examine reptile abundance and richness in relation to habitat characteristics. Sites with higher broad-leaf vegetation cover had lower abundance (w_i = 32%) and richness (w_i = 38%) of reptiles (Table 4, Fig. 4A and B). Sites with increased cover of kangaroo grass and leaf litter supported higher reptile abundance and richness ($\Delta_i \leq 2$, Table 4).

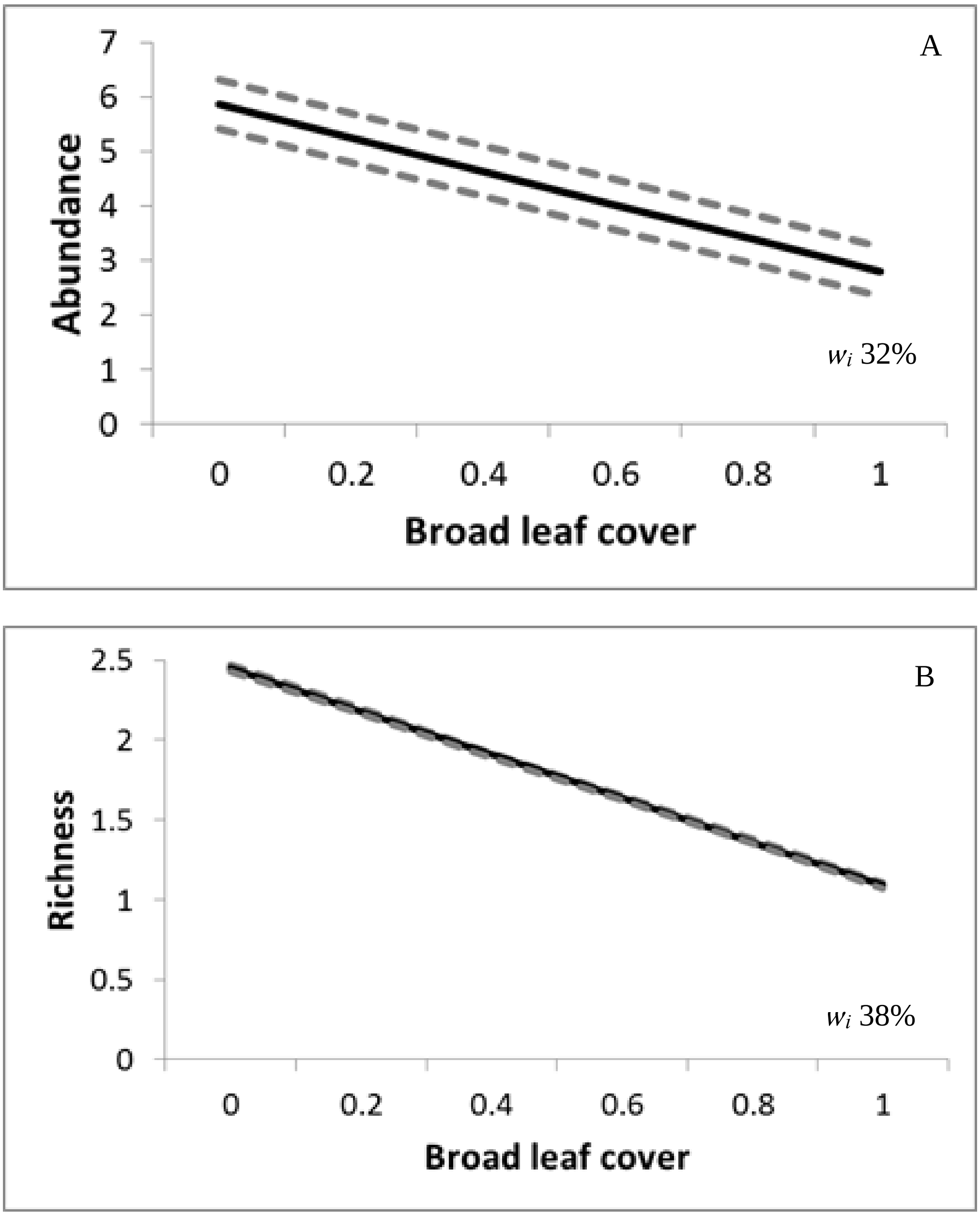

Figure 4. Predictions (mean = solid line) of the negative influence of broad leaf vegetation cover (which had the strongest influence on both reptile abundance (A) and richness (B) with 95% confidence intervals (grey dotted lines) and model weight (*wi*).

Table 4. The influence on reptile abundance and richness of habitat variables and grass types: grader, kangaroo, and black spear grass (random variable). Only models with a ΔAICi ≤ 2 are displayed, number of parameters (K), log likelihood (logLik), corrected AIC (AICc), rank according to best model (ΔAIC_C), model weight (*wi*), and model deviance explained (R^2).

Models (Abundance)	K	logLik	AIC_C	ΔAIC_C	w_i	R^2
Broad leaf + (grass type)	4	-35.3040	80.7132	0	0.3197	0.4949
Kangaroo + (grass type)	4	-35.7961	81.6974	0.9842	0.1955	0.5108
Leaf litter + (grass type)	4	-35.8594	81.8240	1.1108	0.1835	0.4921
Models (Richness)						
Broad leaf + (grass type)	4	-12.3108	34.7268	0	0.3793	0.3274
Leaf litter + (grass type)	4	-12.7437	35.5927	0.8659	0.2460	0.3467

Model averaging suggested that kangaroo grass, and leaf litter had strong positive effects on reptile abundance, whereas broad-leaved vegetation had a negative influence; and kangaroo grass, leaf litter and logs had high positive importance on reptile richness, while broad leaved vegetation, and grader grass had strong negative influences on reptile richness (i.e., these models had 95% confidence levels not overlapping zero, Table 5). The remaining habitat variables had overall lower relative importance, and only minor effects on reptile abundance and richness (Table 5).

Table 5. Model-averaged single variable results using habitat characteristics to explain reptile abundance and richness.

Variables (Abundance)	β	SE	95%CI Lower	95%CI Upper	Relative importance
Broad leaf	**-3.07**	**1.20**	**-5.56**	**-0.57**	**0.32**
Kangaroo grass	**2.57**	**0.87**	**0.76**	**4.38**	**0.20**
Leaf litter	**2.35**	**0.94**	**0.39**	**4.31**	**0.18**
Black spear grass	3.77	3.91	-4.39	11.94	0.08
Log	1.75	1.00	-0.33	3.83	0.05
Bare ground	1.99	2.23	-2.67	6.64	0.04
Mixed grass	-1.56	2.08	-5.90	2.78	0.04
Grader grass	-1.53	1.13	-3.89	0.83	0.03
Rock	-0.89	0.68	-2.30	0.52	0.02
Canopy cover	-0.53	0.62	-1.82	0.75	0.01
(Richness)					
Broad leaf	**-1.36**	**0.44**	**-2.27**	**-0.45**	**0.38**
Leaf litter	**0.88**	**0.26**	**0.34**	**1.41**	**0.25**
Grader grass	**-0.93**	**0.30**	**-1.57**	**-0.30**	**0.13**
Log	**0.80**	**0.26**	**0.25**	**1.35**	**0.10**
Black spear grass	1.35	1.18	-1.11	3.80	0.04
Kangaroo grass	**0.64**	**0.27**	**0.08**	**1.21**	**0.03**
Bare ground	0.99	0.82	-0.72	2.71	0.02
Mixed grass	-0.58	0.77	-2.19	1.03	0.02
Canopy cover	-0.18	0.24	-0.69	0.32	0.01
Rock	-0.01	0.27	-0.57	0.57	0.01

Habitat variables model average with 95% confidence levels not overlapping zero in **bold**. β = model average coefficient estimate.

Grass temperatures, insects, and predator abundance

Mean temperatures in grass were significantly higher in the second sampling year (GLMM, $F_{1,260} = 7.168$, $P = 0.008$, mean ± SE, 1st year 25.92 ± 1.47 and 2nd year 27.34 ± 1.55 °C). However, I did not detect any significant differences among mean temperatures in grader (26.76 ± 1.54 °C), kangaroo (26.63 ± 1.54 °C), and black spear grass (26.47 ± 1.53 °C) (GLMM, $F_{2,260} = 0.105$, $P = 0.901$).

I captured a smaller volume of insects in kangaroo (9.98 ± 4.23 ml), compared to grader (13.45 ± 2.70 ml), and black spear (17.12 ± 6.20 ml) grass, although these differences were not significant (GLMM, $F_{2,21} = 1.875$, $P = 0.178$, Table 6).

Table 6. Untransformed mean volume (ml) insects captured as a measure of food availability, sorted in order except for Gastropoda which is class ± SE.

Insects	Grader	Kangaroo	Black spear
Araneae, Orthoptera, Blattaria, Isopoda	3.94 ± 1.06	1.88 ± 0.27	3.74 ± 1.15
Diptera, Coleoptera, Hymenoptera, Lepidoptera, Gastropda	10.02 ± 1.89	5.67 ± 1.66	7.70 ± 1.40

Number of birds that consume reptiles (Table 7) did not differ significantly (GLMM, $F_{2,21} = 0.280$, $P = 0.758$) among grader (6.52 ± 1.66), kangaroo (6.53 ± 1.66), and black spear grasses sites (8.04 ± 1.66). There was, however, a significant difference in the abundance of reptiles that consume other reptiles among grass types (GLMM, $F_{2,15} = 4.823$, $P = 0.042$, Table 3). There were significantly more reptile predators of other reptiles in kangaroo (1.41 ± 0.37) than in grader grass (0.64 ± 0.18, LSD, $P = 0.015$), and the difference in reptile predator abundance between grader and black spear grass (1.54 ± 0.58) approached significance (LSD, $P = 0.084$, Table 3).

Table 7. Bird species detected in grader grass (G), kangaroo grass (K), and in black spear grass (S), and that consume reptiles.

	Species	G	K	S
Bustard	*Ardeotis australis*	5		
Butcherbirds	*Cracticus nigrogularis*	7	15	12
	Cracticus torquatus		1	
Coucal	*Centropus phasianinus*	2		2
Currawong	*Strepera graculina*	6	11	11
Kingfishers	*Dacelo leachii*		1	
	Dacelo novaeguineae		1	1
	Todiramphus macleayii		1	
Raptors	*Circus assimilis*	1		
	Falco berigora		1	
	Milvus migrans	1		

Discussion

Both the abundance and richness of reptiles was strongly and positively associated with native grasses. There was significantly lower reptile abundance and richness in the invasive grader-grass-dominated habitats than in native grass habitats. Thus, in my study, weeds reduced reptile richness and abundance in these habitats. It is likely that my measures of abundance and richness reflected actual habitat use by these species, rather than reduced detectability in weeds, for two reasons. First, I recaptured small, but significant numbers of animals, and the percentage of recaptures was highest in the grader grass (where the captures were lowest), strongly suggesting we were not detecting fewer of the resident animals in that grass type. Second, in another study (Hacking *et al*., 2014) found reptiles actively avoided grader grass structure, both in the wild and in experimental situations. Here, I argue that the structure of each grass plays an important role in determining the reptile assemblage, and that the structure of the weed reduces use by most reptiles in the assemblage.

Differences in habitat structure between invasive and native grass habitats

Grader grass grows in a dense sward, and in a monoculture (pers. obs.; Vogler and Owen 2008). In my study, sites dominated by grader grass had less leaf litter, bare ground and logs compared to sites dominated by native kangaroo and black spear grass (Table 2). Exotic annual grasses typically grow more closely spaced than native grasses, reducing spatial heterogeneity and lowering overall plant diversity (Lindsay and Cunningham 2012), whereas native grasses, such as kangaroo and black spear grass, grow in clumps or hummocks (pers. obs.; McIvor and Howden 2000), and this promotes a greater diversity in microhabitat conditions, because there are areas of grass surrounded by leaf litter and bare ground (Lindsay and Cunningham 2012; Hacking *et al*., 2014). I may have detected fewer logs in the invasive grass because grader grows in disturbed areas. Although I did not detect significantly less canopy cover above my sites, there may have been logs in the areas invaded by grader grass, because historical disturbances such as grading, plowing and higher fire intensity may have reduced the number of logs in the grader grass. I note, however, that the past disturbance particular to the grader grass *per se* was unlikely to be the only factor driving richness and abundance of reptiles in this grass type, because it was colonized, in high abundances, by some species, and not others (see below).

As with canopy cover, the grass types did not differ in terms of their distribution of rocks, again suggesting that differences in reptile abundance and richness between my weed-invaded and native grass sites were not driven by the absence of habitat features critical to certain species (such as arboreal or scansorial groups). Instead, I argue that the grass structure itself, i.e., hummocks versus swards, and reduced habitat heterogeneity, especially the lack of leaf litter and bare ground, in the grader grass dominated sites reduced richness and abundance of reptile species in these locations.

Differences in reptile abundance and richness in invasive and native grass habitats

Reptile abundance and richness were significantly lower in sites dominated by invasive grader grass, compared with sites dominated by native kangaroo and black spear grasses. Both reptile richness and abundance increased with increasing habitat cover of kangaroo grass, and leaf litter, whereas increases in broad-leaved vegetation and grader grass cover reduced reptile abundance and richness. Habitat heterogeneity in vegetation cover is typically very important for reptile diversity and its presence often supports higher reptile abundance (Meik *et al*., 2002; Singh *et al*., 2002; Garden *et al*., 2007; Price *et al*., 2010; Pike *et al*., 2011; Bateman and Ostoja 2012; Danielsen *et al*., 2014; Bruton *et al*., 2015). Non-native grasses reduce the extent of native grass (Hacking *et al*., 2014), and sites that are dominated by grass swards (or bare ground), tended to have lower reptile species richness and lower abundances than habitats with hummock grasses, which create a more diverse vegetation structure (Garden *et al*., 2007; Foxcroft *et al*., 2010; Price *et al*., 2010; Kutt and Fisher 2011; Kutt and Kemp 2012). Dense, uniform grass cover may affect the mobility of reptiles, reducing their ability to forage, escape predators, and engage in social interactions (Steidl *et al*., 2013).

Reptiles clearly had preferences for specific grass types. For example, in the current study, arboreal geckos (*Amalosia rhombifer*), skinks (*Cryptoblepharus adamsi*), dragons (*Diphoriphora australis*) and goannas (*Varanus scalaris*), and cryptic leaf litter skinks (*Glaphyromorphus cracens*, *Lygisaurus foliorum*, and *Problepharus tenuis*) were captured in much greater numbers in kangaroo grass sites than at other sites. On the other hand, striped skinks (the genus *Ctenotus*) were encountered in higher abundances in black spear grass sites. These species, however, all preferred native grass. Two species of rainbow skink (*Carlia munda* and *C. vivax*) were detected in slightly higher abundances in grader grass, consistent with their habitat preferences for dense grasses (Singh *et al*., 2002; Fisher *et al*., 2003). Snakes were rarer than lizards, making it difficult to detect habitat preferences, but the colubrids (*Boiga irregularis* and *Dendrelaphis punctulata*), and small elapids (*Acanthopis antarcticus*, *Cryptophis boschmai*, *Demansia psammophis*, *D. torquata*, and *Pseudonaja nuchalis*), occurred more frequently in native grasses than in grader grass sites. In contrast, eastern brown snakes (*Pseudonaja textilis*) were more common in grader and black spear grass than in kangaroo grass sites.

Rather than simply passively “not occurring” weedy vegetation, reptiles may actively avoid using it, because of its physical characteristics (Valentine *et al*., 2007; Hacking *et al*., 2014). Desert horned lizards (*Phrynosoma platyrhinos*) in sagebrush habitats in North America become less abundant with as ground cover of invasive cheat grass (*Bromus tectorum*) increases, and had significantly reduced mobility when moving through weeds compared to native habitat (Newbold 2005; Rieder *et al*., 2010). In Namibia, an increase in bush encroachment into savannah significantly reduced the abundance of two arboreal lizards (*Pedioplanis undata* and *Lygodactylus bradfieldi*), and displaced the assemblage of savanna lizards (Meik *et al*., 2002). Endemic Brazilian savanna lizards declined close to abandoned non-native *Eucalyptus* plantations (Gainsbury and Colli 2014), suggesting they were strongly associated with native vegetation structure, and preferred not to use invasive vegetation (Gainsbury and Colli 2014). In my study, large bodied lizards such as goannas (*Varanus scalaris*) were not detected in grader grass. Absence of these lizards may occur because they experience reduced mobility in grader grass, or because grader grass lacked preferred structures such as logs, open ground, or leaf litter (Christian and Bedford 1996). Similarly, semi-arboreal fence skinks (*Cryptoblepharus adamsi*) were not detected in grader grass, possibly due to lack of structural features. In general, complex habitat structure may be preferred by arboreal reptiles, and others requiring more diverse habitat features for foraging, perching, basking, and refuge (Garden *et al*., 2007; Mott *et al*., 2010; Pike *et al*., 2011; Steidl *et al*., 2013).

The presence of broad-leaved vegetation significantly reduced abundance and richness of reptiles in my study, but was not related to particular grass habitats. Because my sampling was focused on the different grasses and their characteristics, I did not measure the characteristics of broad-leaved vegetation that reduced abundance and richness of reptiles. I suspect that under broad-leaved vegetation it is much cooler and shadier than in habitats without broad-leaved cover, deterring ground dwelling reptiles (Valentine 2006). Available food may also be reduced in broad-leaved vegetation (Valentine 2006). Given the importance of this variable to reptile abundance and richness, it would be interesting to determine the mechanism of its effects.

Mechanisms influencing the abundance and richness of reptiles

In my study, temperatures within grass clumps were very similar among habitats, which contrasts with the findings of some other studies reporting cooler temperatures in weeds (Valentine 2006) or less opportunities for thermoregulation in weeds (Downes and Hoefer 2007; Hacking *et al.*, 2014). I recorded temperatures only within grass clumps, and not in a range of habitat types at each site. Although temperatures were the same inside clumps of different grass species, grader grass sites had less open ground than native grass sites, greatly reducing thermal heterogeneity at the level of the site. Hacking *et al.*, (2014) measured temperatures in different habitats within sites, and found that grader grass sites were cooler, on average. Thus, differences among sites in habitat thermal heterogeneity may have important implications for thermoregulatory behavior, although I did not detect thermal differences within grass clumps. The similarity in temperatures among grasses suggests that shelter temperatures for reptiles actually using grass clumps were similar, and therefore, the weeds were apparently not thermally inappropriate shelter sites for reptiles in my study, even though areas surrounding the grass may have been less thermally attractive.

Invertebrate (food) abundance was also very similar among all three habitats in my study, presumably providing similar advantages to the reptile assemblages using these grasses. Other studies have found differences in invertebrate assemblages using weeds (Valentine 2006), suggesting that reptiles may avoid weeds because, although invertebrates were available in the weeds, they are not preferred foods of the reptiles examined. A more detailed examination of the invertebrate assemblage in my study area in terms of food availability for one species of skink found little difference in the taxonomic groups and sizes of invertebrates inhabiting the grader grass (Hacking *et al*., 2014). It is possible that because grader grass is a congener of one of the native grasses, kangaroo grass, I did not detect much difference in the invertebrate assemblages using native and introduced grass in this study.

There were also no significant differences in the number of avian predators using the different habitats in my study, suggesting that increased avian predation was not the source of differences between reptile assemblages among the different habitats in my study. Overall, the lack of difference in within-grass thermal environments, invertebrate food availability, and avian predation among grass habitats suggests that these were unlikely to be the factors driving the differences I observed in reptile richness and abundance among grass habitats.

I detected *more* reptile predators in native grasses than in grader grass sites, which suggests that there was higher predation pressure on reptiles in native grasses than in the weedy areas. Structurally depauperate habitats tend to have lower reptile diversity in general, including reptile predators (Price *et al*., 2010; Garda *et al*., 2013). For example, snakes were much less common in cheat grass-invaded sagebrush habitats than in uninvaded habitats (Hall *et al*., 2009). The relatively high numbers of reptile predators in native environments suggests that the lower number of reptiles using grader grass was not driven by increased predation in the weedy environments, because predation in the weed was unlikely to be increased. There is, however, one possible exception to this. Eastern brown snakes consume other snakes as part of their diet (Shine 1989), and were equally common in grader and black spear grass. A high density of reptilian predators of snakes in these grasses could have reduced snake use of grader grass. This argument does not hold, however, for black spear grass, which had moderate reptile density, and high abundance of eastern brown snakes. I suggest that increased predation from reptiles was unlikely to be driving avoidance of grader grass in my study.

Given that food abundance, shelter temperatures, and avian predation pressure appeared to be similar among habitats, and reptile predation was actually likely to be lower in weedy habitats, it seems unlikely that any of these were important factors driving differences among habitats in terms of reptile assemblage composition. I suggest that reduced habitat heterogeneity itself, and reduction in abundance, or complete absence of specific habitat features such as logs and leaf litter were the factors reducing abundance and richness of reptiles in grader grass. Hacking *et al*., (2014) reached a similar conclusion for this habitat for a single skink species. The dense growth form of grader grass may increase the costs of locomotion (Newbold 2005), make social interactions more difficult (Steidl *et al*., 2013), and reduce reproductive success (Martin and Murray 2011). Opportunities for thermoregulation are also likely to be reduced in grader grass (Valentine *et al*., 2007; Hacking *et al*., 2014). Thus, with a couple of notable exceptions, the homogenous structure of grader grass likely to reduce the fitness of most reptile species.

Conclusion

I found reduced richness and abundance of reptiles in weedy sites. The similarity of in-grass temperatures, food availability, and avian predators among grass sites suggest that these factors did not drive lower reptile richness and abundance in grader grass. Instead, I propose that reduced habitat heterogeneity and structural habitat complexity reduced reptile richness and abundance in native habitats invaded by grader grass. Law and Dickman (1998) noted that many species require a variety of different habitats to persist, and called for managers to preserve habitat heterogeneity, rather than specific habitat types. I make a similar point on a finer scale. In my study, small-scale habitat heterogeneity, and specific habitat features were critical variables determining richness and abundance of reptiles, and the negative impact of the weed, in this case, occurred mainly because it reduced habitat heterogeneity. I recommend that managers should strive to maintain natural environments with high habitat heterogeneity and with specific habitat features, such as native grass, leaf litter, and bare ground because it is apparently habitat microstructure that benefits the assemblage.

CHAPTER 3: SHORT-TERM RESPONSES OF REPTILE ASSEMBLAGES TO FIRE IN NATIVE AND WEEDY TROPICAL SAVANNAH

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Introduction

Land managers use fire as a management tool with the aim of reducing hazardous build-up of fine fuels in natural, recreational, and cultivated areas (Queensland Fire and Rescue Authority Act 1990). Prescribed burning often occurs in the cool, dry times of the year because fires are perceived as more destructive as the weather heats up in the spring before rains (Queensland Fire and Rescue Authority Act 1990; Kennedy and Potgieter 2003; Setterfield *et al*., 2010; Pastro *et al*., 2011; Penman *et al*., 2011; Price *et al*., 2012; Burgess *et al*., 2014; Alba *et al*., 2015). Fires for wildlife management are ignited at times when environmental conditions allow the fire to meander in the landscape and self-extinguish, and are intended to create a mosaic of burnt and unburnt habitat, which is, in turn, thought to maintain native biodiversity (Queensland Fire and Rescue Authority Act 1990).

Exotic grasses are among the worst threats to native biodiversity, because they can rapidly change ecosystem functions and services (Elton 1958; D'Antonio and Vitousek 1992; Zavaleta *et al*., 2001). Invader grasses often grow taller and denser than native perennial grasses, and can be very successful competitors (McIvor and Howden 2000; Vogler and Owen 2008; Wilsey *et al*., 2009; Foxcroft *et al*., 2010; Lindsay and Cunningham 2012; Alba *et al*. 2015). Land managers often use fire as a management tool to reduce both weed encroachment, and increased fuel loads caused by weeds (Price *et al*., 2012). However, fires fuelled by invasive grasses may burn hotter and more intensely than native grass fires, potentially creating severe fires at times when natural fires do not occur (D'Antonio and Vitousek 1992; Corbett *et al*., 2003; Setterfield *et al*., 2010). Hotter fires can consume more vegetation, which may change faunal resource dynamics, effecting food availability, shelter opportunities, and predator susceptibility of native fauna (Barnard 1987; Valentine *et al*., 2007; Pastro *et al*., 2011; Penman *et al.,* 2011; McGregor *et al*., 2014). In addition, hotter fires may increase mortality rates in small vertebrates (Griffiths and Christian 1996; Barlow and Peres 2004; Smith *et al*., 2012; Cross *et al*., 2015). Repeated fires may reduce species ranges, and fire-sensitive species may become locally extinct (Parr and Andersen 2006; Driscoll and Henderson 2008; Penman *et al*., 2011; Russel-Smith *et al*., 2012). On the other hand, tropical savannah ecosystems that are shaped by natural fires are highly diverse, suggesting that the fauna of tropical savannahs are resilient to naturally occurring fires (Woinarski *et al*., 2004; Andersen *et al*., 2005; Pianka *et al*., 2012). Reptiles in these habitats are thought to be adapted to high natural fire frequency (Braithwaite 1987; Friend 1993; Trainor and Woinarski 1994; Corbett *et al*., 2003; Pastro *et al.,* 2011), and may prefer the habitat structure and composition created by fire (Braithwaite 1987; Friend 1993; Trainor and Woinarski 1994; Singh *et al*., 2002*a*; Pianka *et al*., 2012).

Typically, studies of the effects of fire compare areas with different fire histories (e.g., Driscoll and Henderson 2008; Valentine *et al*., 2012; Nimmo *et al*., 2013; Pastro *et al*., 2014). Such studies examine fire succession, and the long-term effects of fire, but are not designed to compare the effects of fire in habitats with different starting conditions. It is, however, of interest to track the same environment, before and after fire, to determine the nature and rate of recovery after fire in similar habitats with different starting conditions.

I compared replicate habitats, with similar histories, dominated by different types of native grass, or invaded by weeds, and determined the short-term influence of fire on fauna communities in these habitats, directly after burning, and approximately ten months after burning, when the cover of grass had returned to pre-fire levels. My study provides insight into the response of fauna immediately and shortly after fire, in different grassy habitats. In environments that may burn more than once per year, due to a combination of wildfire and prescribed burns, such as savannah woodlands, especially when weed-infested, determining the short-term effects of fire is highly relevant (Price *et al*., 2012).

Here I described reptile responses to fire in open woodland and savannah landscapes in northern Queensland, Australia. I used tropical savannah reptiles as my study organisms, because they are highly abundant and typically respond strongly to habitat disturbances (Braithwaite 1987; Pianka *et al*., 2012; Smith *et al*., 2013; Hacking *et al*., 2014). I compared reptile assemblage composition in native kangaroo grass (*Themeda triandra*), black spear grass (*Heteropogon contortus*), and non-native grader grass (*Themeda quadrivalvis*), before, immediately after and up to fifteen months after prescribed burning, to determine if there were detectable changes in reptile assemblage composition before, immediately after, and shortly after prescribed fire.

Methods

Study system

Study sites were located in savannah and open forest at Undara Volcanic National Park (18°19`29.92``S, 144°36`28.31``E). I used a total of 24 sampling sites with eight replicates of each habitat dominated by a particular grass, either native kangaroo grass (*Themeda triandra*), native black spear grass (*Heteropogon contortus*), or non-native grader grass (*Themeda quadrivalvis*). Briefly, the area was a grazing property until it was made a national park in 1992. At the time of my study, the entire area had not been grazed for 16 years. Black spear grass and native kangaroo grass grow together in the same land type, and I exploited patches dominated by each grass on small scales at my study sites. Grader grass grows in disturbed areas, and was common on the sides of tracks, and in previously cultivated areas at my site, but also occurred in patches closely associated with, and interspersed with the native grasses. I exploited such patches to specifically target differences in the fauna at my sites that were influenced, in particular, by burning each grass type, and that were not primarily driven by differences in other factors, such as soil type, past history or spatial location. For a more comprehensive description of sampling sites and history see Chapter 2.

Grader grass is native to India, and grows in sward emerging as a single stolon, whereas the two native grasses grow in clumps or hummocks (McIvor and Howden 2000; Keir and Vogler 2006). Grader grass can grow to 2.5 meters producing high above-ground biomass, whereas these native grasses grow to 1.5 m. A detailed habitat description has been provided elsewhere (Chapter 2), and for a more comprehensive review of grader grass characteristics and biology, see Keir and Vogler (2006).

The rangers at Undara Volcanic National Park implemented prescribed fires in April 2009 and 2010 at selected sampling sites, when environmental conditions were cool enough to allow the fire to self-extinguish in the late afternoons, creating a mixed landscape of burnt and unburnt patches. Sampling sites in the current study had been burnt on rotation every 2 years since 2002, with wildfires also occurring. A wildfire in October 2003 burned the entire park, and one in November 2008 burnt large areas of the park, including some sampling sites (Fig. 1).

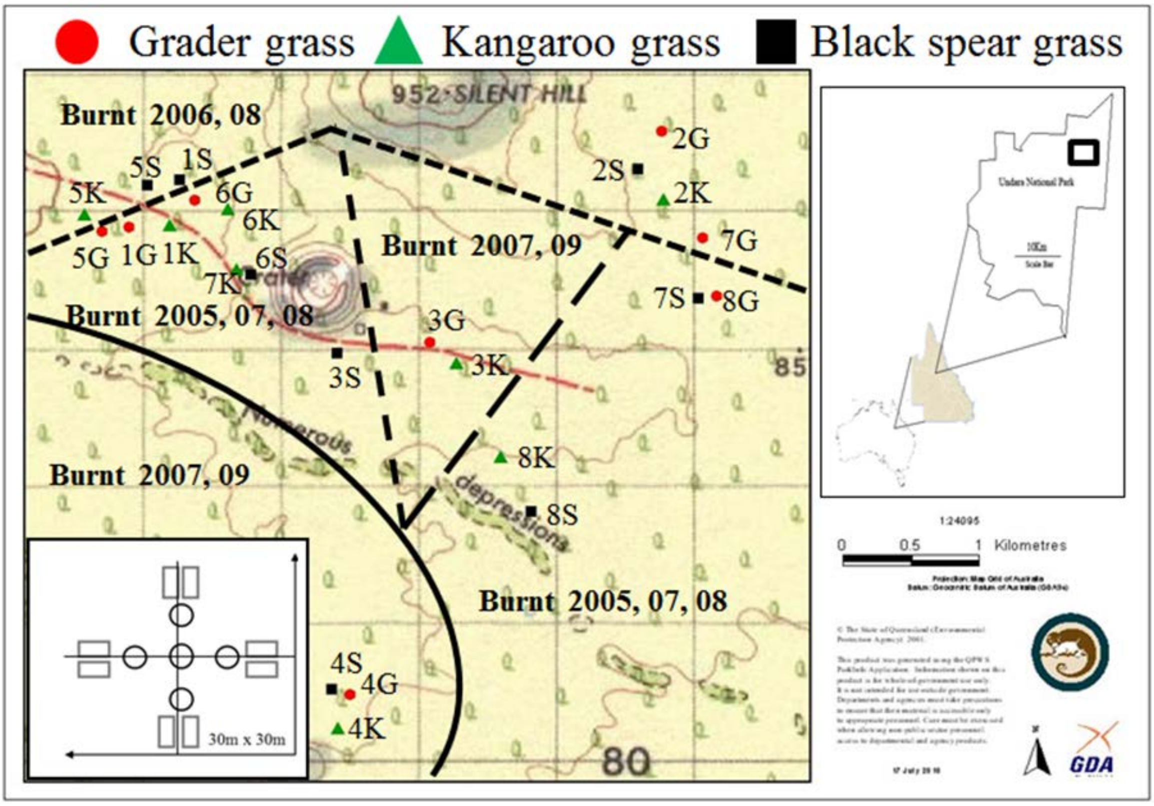

Figure 1. Location of sampling sites (50 x 50m) at Undara volcanic national park (top right corner, box indicate sampling area) and reptile trap array (30 x 30m, bottom left corner) for each site, pitfall traps (open circles), and funnel traps (boxes). Fire history of sampling sites (lines), park rangers rotationally burn selected areas in the cooler early dry season (April – May) to create a mosaic of burnt (30 – 60%) and unburnt habitats (Queensland's Fire and Rescue Authority Act 1990). Sampling sites in current study were rotationally burnt every 2 years since 2002 with wildfires in October 2003 which burn the entire park, and in November 2008 which burnt large areas of the park including some sampling sites. Prescribed and wild fires have been excluded from burning the evergreen vegetation in the depressed lava tubes (numerous depressions in map).

Survey periods and data collection

I trapped reptiles over two years (eight trapping periods) in four distinct trapping periods per year: pre-wet (21 Oct – 14 Nov 2008 and 2009), mid-wet (3 – 26 March 2009 and 2010), early-dry (14 April – 6 May 2009 and 2010), and mid-dry seasons (14 July – 12 Aug 2009 and 2010) with 19 to 21 trap-days in each season. Trapping sites were selected so at least two, and often all three, grass species occurred within 200 m of one another. I selected sites to ensure that there was no spatial clumping in particular grass types (each site had at least 2 and usually all 3 grass types). This was possible because of the highly heterogeneous nature of the grasses growing in that area, and because all three grasses were widely represented in the area.

I monitored seasonal changes in vegetation cover and in structural complexity before, during, and after fire. I conducted habitat surveys for each sampling site in each trapping period, using four 50–metre transects at each site, spaced 16.6 m apart, and habitat variables were recorded in linear centimetres on this transect. At each sampling occasion, I recorded the cover of burnt area, dominant grass (total number of cm of grader, kangaroo, or black spear grass intercepting the 50 m tape on all 4 transects, converted to % cover), of mixed grasses (calculated by summing the % cover of all other grass species), broad-leaf vegetation (% cover of herbaceous plants and legumes), leaf litter, logs, rocks, exposed soil, and canopy cover above the transect.

I used a 30 x 30 m trapping grid at each of the 24 survey sites (Fig. 1). Five pitfall traps (20l, straight-sided buckets) were placed in the ground with the lip level with the ground's surface, with one centre bucket and four 'arms' (Fig. 1). Traps were spaced 10-m apart and connected *via* a drift fence (50-cm high UV resistant fibreglass drift fence, Cyclone™), which crossed every pitfall trap, and extended a further 5 m beyond the last pitfall trap on each 'arm' of the cross. To reduce desiccation risk and exposure of captured animals, a moistened sponge and a piece of cloth were placed inside each pitfall trap, and the bottom of each trap was lined with a 5-cm layer of leaf litter. Eight funnel traps (dimensions, 180W x 730L x 170H mm) were arranged at each site. Funnel traps were placed on both sides of the drift fence on each arm of the cross, against the 5 m of drift fence projecting past the last pitfall trap on each arm, approximately 2 m from the end, with a shade cloth covering the funnel trap. To prevent small vertebrates in traps being attacked by ants, I used ant sand (Antex, 2g/kg Bifenthrin) as a deterrent, sprinkled around the mouth of the pitfall trap and underneath funnel traps. All traps were checked and cleared twice daily, in the early morning (5:30 – 8:30) and in the late afternoon (16:00 – 18:00), and captured reptiles were identified to species using Wilson (2005).

Statistical analyses

Habitat composition

To describe habitat composition before and after fire I compared the percent cover of each of the dominant grasses (grader, kangaroo, and black spear grass), mixed grass (all other grass species combined), burnt area, broad-leaf vegetation, logs and branches, rock, leaf litter, bare ground, and tree canopy cover among sites. I classified sites that had not been burnt for 2 years prior to the prescribed burning as unburnt, and sites immediately after they were burned as burnt, and in revegetated areas up to 15 months after fire as revegetated. Prior to statistical analysis, I relativised habitat data by dividing the cover of each variable in cm by the maximum cover of that variable at any sampling site, and compared these values using MANOVA with Wilk’s lambda as the test statistic, followed by ANOVAs and Tukey’s HSD *posthoc* tests when significant differences were detected in habitat cover among the sampling sites (SPSS V.20).

Reptile assemblage composition

I described the reptile assemblage composition in unburnt, burnt, and revegetated sites for each dominant grass type (grader, kangaroo, and black spear grass). To reduce the influence of rare species, I excluded those with less than 12 captured individuals. I standardised trapping effort at all sites to individuals sampled per 100 trap nights, and to reduce the statistical influence of common species, prior to statistical analysis, numbers of individuals captured for each species were relativised by dividing the abundance of each reptile species by the maximum abundance of that species caught at any sampling site. Reptile species used in all statistical analyses are listed in Table (1). To determine whether reptile richness and abundance varied among treatments I used generalized linear models (GLZM) with Gaussian-error distribution, identity link function and followed significant differences with pairwise least significant difference (LSD) comparisons (SPSS V.20).

Table 1. Untransformed catch numbers of 18 common reptile species among unburnt (G, K, S), burnt (GB, KB, SB), and revegetated (GR, KR, SR) – grader, kangaroo, and black spear grass habitats to illustrate trends in species composition with significant indicator species $P < 0.05$*, $P < 0.01$** in bold and indicator species approaching significance $P = 0.0846$^ in italic.

Species	**Unburnt**			**Burnt**			**Revegetated**		
	G	K	S	GB	KB	SB	GR	KR	SR
Amalosia rhombifer	0	3	2	1	2	2	0	1	1
Carlia schmeltzii	13	36	32	0	10	3	9	16	12
Carlia vivax	14	13	12	2	2	5	14	9	6
Cryptoblepharus adamsi	0	11	4	0	2	1	0	9	0
Ctenotus taeniolatus	3	4	11	1	2	3	2	9	12
Delma tincta	1	3	5	0	0	2	4	1	2
Demansia psammophis	4	8	6	0	1	1	2	0	3
Diporiphora australis	3	10	5	0	6	3	1	7	1
Gehyra dubia	3	1	3	2	0	1	1	2	0
Glaphyromorphus cracens	5	**16****	11	0	0	0	6	3	4
Heteronotia binoei	0	5	4	1	3	0	1	3	2
Lygisaurus foliorum	5	**33****	19	0	6	2	4	17	9
Menetia greyii	2	10	8	5	4	1	11	5	8
Morethia taeniopleura	3	**18***	13	1	1	0	2	6	3
Proablepharus tenuis	1	7	5	0	0	1	3	**10****	4
Pseudonaja textilis	2	5	8	0	0	0	***9***^	1	3
Strophurus williamsi	0	3	2	3	2	0	2	0	0
Varanus scalaris	0	**10****	3	0	0	1	0	0	0

I used the statistical package PC-ORD to explore reptile assemblage composition (McCune and Mefford 1999). Reptile composition and habitat variables were relativised by maximum (as above) with habitat treatment (unburnt, burnt, revegetated) as the category, and quantitative habitat variables were: percent cover of dominant grass, mixed grass, leaf litter, logs, rock, exposed soil, burnt area, and canopy cover. I used Multiple Response Permutation Procedures (MRPP) to create a non-parametric, rank-transformed Sorensen (Bray-Curtis) distance matrix among reptile assemblages in unburnt, burnt, and revegetated grader, kangaroo, and black spear grass treatments. The MRPP produces an A-statistic from chance-corrected within-group agreement and a p-value for each pairwise comparison. I followed this with non-metric multidimensional scaling (NMDS) to show the differences in reptile assemblage composition among sampling sites ($r^2 < 0.20$) when significant ($P < 0.05$) differences were detected. For the NMDS, I used the autopilot “slow and thorough” with Sorensen distance measures, dimensionality was determined by Monte Carlo test (9999 permutations, significance test of stress in relation to dimensionality of the number of axes in final analysis). I extracted axis and cumulative scores by using Sorensen (Bray-Curtis) dissimilarity indices with original end point selection, city-block projection geometry and calculation of residuals. To illustrate reptile assemblage compositional trends among treatments, I constructed bi-plots from NMDS sites and species scores. Finally, I investigated the responses of specific reptiles to treatments; I used the indicator species analysis with Monte Carlo tests of significance of observed maximum indicator values for reptile species with 9999 permutations and random number seed in PC-ORD (McCune and Mefford 1999).

Results

Habitat composition

I detected significant variation in habitat variables among unburnt, burnt, and revegetated sites in each grass type (MANOVA $\lambda = 0.001$, $P < 0.001$, untransformed means ± SE, Table 2).

Table 2. Mean untransformed reptile abundance and richness, and averaged percent cover of habitat variables in unburnt (G, K, S), burnt (GB, KB, SB), and revegetated (GR, KR, SR) grass sites and all statistics were performed on relativized data ± 1SE.

	Unburnt			Burnt			Revegetated		
	G	K	S	GB	KB	SB	GR	KR	SR
Reptile									
Abundance	14.75±0.75	32.67±2.88	25.50±4.48	2.67±0.80	8.20±3.31	6.50±2.50	11.83±2.27	19.80±2.48	17.50±5.33
Richness	7.25±0.48	11.83±0.95	10.33±1.36	1.83±0.54	4.60±1.44	4.75±1.80	6.83±0.98	7.00±1.00	7.75±1.44
Burnt				67.15±13.53	72.82±4.91	64.69±7.72			
Dominant Grass	46.29±4.31	55.71±5.26	48.14±3.59	5.39±3.58	7.83±4.99	12.44±2.72	82.04±3.41	56.75±5.72	50.64±2.11
Mixed Grass	42.56±3.17	19.37±3.07	33.78±4.17	9.39±4.41	1.55±0.72	2.31±0.10	11.57±2.72	28.53±6.09	36.06±5.18
Broad leaf	1.72±0.72	1.00±0.39	1.47±0.80	1.81±1.17	0.01±0.01	0.02±0.02	4.27±1.28	2.45±0.63	0.90±0.45
Leaf litter	2.61±1.15	14.81±2.87	11.14±1.98	5.37±3.47	15.71±3.52	13.99±8.37	0.14±0.01	3.40±0.63	2.41±0.48
Rock	1.51±0.74	0.08±0.04	0.59±0.27	0.99±0.58	0.51±0.46	4.56±2.81	0.57±0.41	0.38±0.33	3.60±2.26
Log	0.33±0.20	1.27±0.31	0.78±0.17	0.25±0.21	1.16±0.23	0.71±0.12	0.13±0.09	1.31±0.14	0.78±0.13
Bare ground	4.98±0.61	7.76±2.22	4.08±1.30				1.28±0.49	7.18±1.70	5.59±2.25
Canopy	11.41±8.43	29.91±3.78	25.64±4.70	6.21±3.81	31.35±3.39	20.71±1.94	2.74±1.41	26.62±4.75	13.95±1.79

Obviously, there was significantly more burnt area at burnt sites than at unburnt and revegetated grass sites (ANOVA $F_{8,37} = 99.005$, $P = 0.001$), but more interestingly, the burnt area was greater in burnt grader than in burnt black spear grass sites (Tukey's HSD, $P < 0.05$). Dominant grass cover varied significantly (ANOVA $F_{8,37} = 38.340$, $P < 0.001$); revegetated grader grass sites had significantly higher grader grass cover than unburnt grader grass sites (Tukey's HSD, $P < 0.05$, Fig. 2). Similarly, there was significantly higher mixed grass cover in unburnt than in revegetated grader grass habitats (ANOVA $F_{8,37} = 17.625$, $P < 0.001$, Tukey's HSD, $P < 0.05$, Fig. 2), whereas the percent cover of dominant and mixed grass cover in the two native grass sites did not differ between unburnt and revegetated sites.

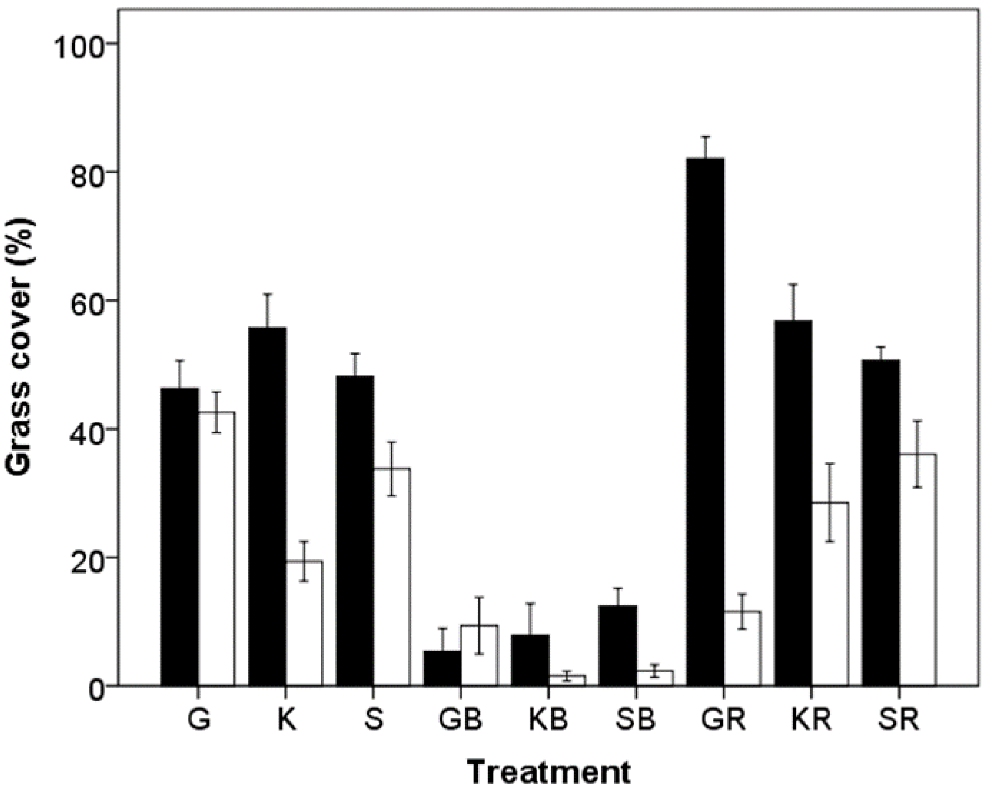

Figure 2. Mean grass cover (%) in dominant grass (black), and in mixed grass (white bars) cover in unburnt, burnt, and revegetated grader (G, GB, GR), kangaroo (K, KB, KR), black spear (S, SB, SR) grass habitats while MANOVA analysis was performed on relativised habitat data, and error bars ± 1SE.

In other habitat variables, the percent cover of logs in the different grass sites differed significantly (ANOVA $F_{8,37} = 6.321$, $P < 0.001$), there was a higher cover of logs in unburnt, burnt, and revegetated kangaroo grass sites than in burnt and revegetated grader grass sites (Tukey's HSD, $P < 0.05$). But more importantly, before burning there were no significant differences in the percent cover of logs among grader, kangaroo, and black spear grass sites. The reduction of logs in grader grass suggests that it burns at higher temperatures than native grasses. The cover of leaf litter (ANOVA $F_{8,37} = 4.322$, $P = 0.001$) and bare ground (ANOVA $F_{8,37} = 5.172$, $P < 0.001$) were significantly higher in unburnt kangaroo grass sites than in revegetated grader grass sites (Tukey's HSD, $P < 0.05$). Typically, for most variables that differed, habitat variables in black spear grass were intermediate to kangaroo grass and grader grass, and not significantly different from kangaroo grass, or either grass. Percent cover of broad leaf vegetation, (ANOVA $F_{8,37} = 1.755$, $P = 0.118$), rock (ANOVA $F_{8,37} = 2.071$, $P = 0.071$), and canopy (ANOVA $F_{8,37} = 0.471$, $P = 0.869$) did not differ among grass sites.

Reptile abundance and richness

I trapped for a total 27,972 trap days, and I captured a total of 800 individuals from 48 species including 9 families. I selected the 18 most numerous reptile species (range of abundances 12 – 131, $n = 731$) to describe the reptile assemblages (Table 1). Lizards were most numerous and represented 90% of all reptiles captured, and 74% of all captures were lizards in the family Scincidae, with skinks in the genus *Carlia* the most commonly captured species across all sampling sites. *Carlia schmeltzii* was the single most numerous species, followed by *Lygisaurus foliorum*, and then *C. vivax* (Table 1).

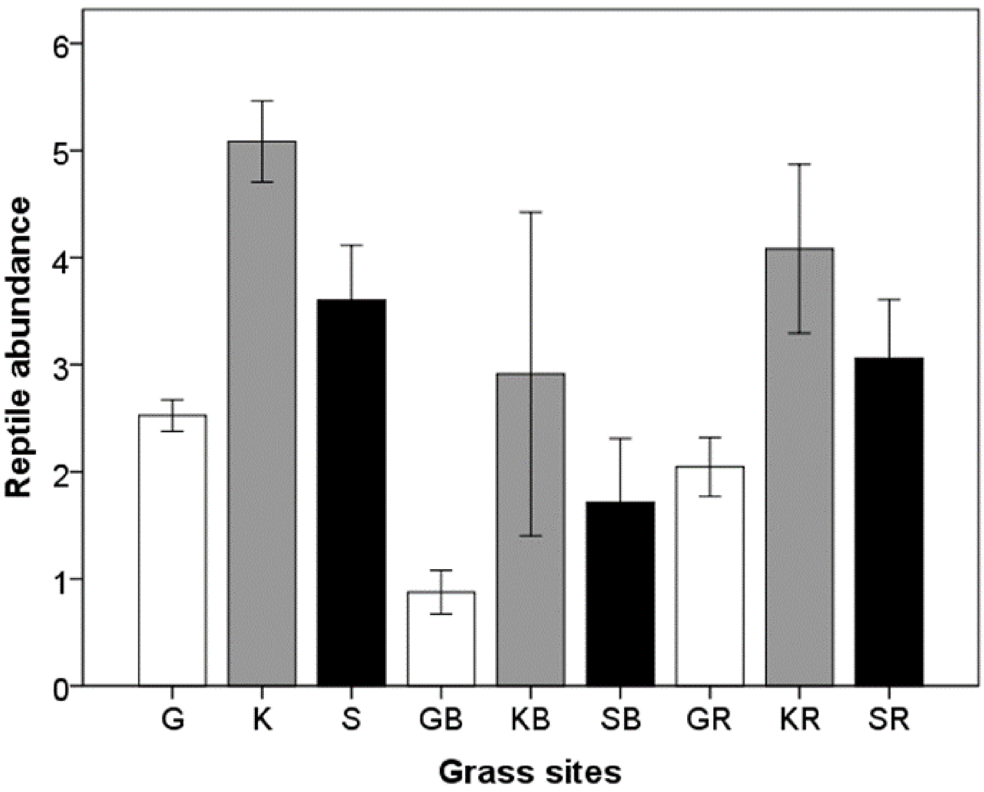

Figure 3. Untransformed average reptile abundance (GZLM analysis was performed on relativised by maximum reptile abundance data) in unburnt (G, K, S), burnt (GB, KB, SB), and revegetated (GR, KR, SR) habitats in grader (white), kangaroo (grey bars), and black spear (black bars) grass with error bars ± 1 SE.

I detected significant differences in reptile abundance among unburnt, burnt, and revegetated grass sites (GZLM Wald x^2 = 29.566, *df* = 8, 37 $P < 0.001$, Fig. 3). There were no significant differences among the burning states in richness of reptiles (GZLM Wald x^2 = 12.066, *df* = 8, 37 $P = 0.148$). Immediately after burning, abundances of reptiles were significantly reduced in the different grass types compared to their unburned state, except grader grass, in which abundance was very low initially, and for which the trend for reduced abundance was only marginally significant (pairwise comparisons, unburnt vs burnt kangaroo grass, LSD, $P = 0.007$, unburnt vs burnt black spear grass LSD, $P = 0.029$, and approached significance in unburned vs burned grader grass sites LSD, *P* = 0.055, Fig. 3). I did not detect any significant differences overall in reptile abundances between unburnt and revegetated or burnt and revegetated sites in any grass type (LSD, *P* > 0.05).

Reptile assemblage composition

Differences in assemblage composition of reptiles among grader, kangaroo, and black spear grass habitats prior to burning were described elsewhere (Chapter 2). Reptile assemblage composition varied significantly among the different grass types and in response to burning and revegetation. I detected significant differences in reptile community structure in unburnt, burnt, and revegetated grasses (MRPP: A = 0.1740, *P* < 0.001). In grader grass sites, which were overall depauperate, the reptile assemblage composition differed significantly between unburnt and burnt (A = 0.133, *P* = 0.025), but not in revegetated grader grass sites, which were similar to, and overlapped both the unburnt and burnt assemblages. Similarly, the reptile assemblage in unburned black spear grass sites was significantly different from burnt sites (A = 0.148, *P* = 0.002), but revegetated sites were similar to the unburnt sites. The reptile assemblage composition in unburnt kangaroo grass sites were significantly different from burnt (A = 0.143, *P* = 0.002), and revegetated (A = 0.101, *P* = 0.044) sites. Cross comparisons showed that the reptile assemblage composition in unburnt kangaroo differed significantly from that in grader grass (A = 0.139, *P* = 0.016), but not black spear grass. Interestingly, there were no differences detected in reptile assemblage composition among the different grass sites just after they were burned (*P* > 0.05). After revegetation, reptile assemblages differed significantly between kangaroo and grader grass sites (A = 0.194, *P* = 0.011), while the spear grass sites were intermediate. Similar to reptile abundance, the reptile assemblage in unburnt kangaroo grass sites was similar to the other native grass (unburnt black spear grass sites $P = 0.822$), but differed significantly from that in all other grass states ($P < 0.05$).

I found a stable, three-dimensional NMDS solution accounting for 65.68% of the variance (first axis = 30.90%, second axis = 17.68%, and third axis = 17.11%) with a final stress of 0.180 (Fig. 4a and b). Unburnt and revegetated grass formed two distinct groups, while there were no clear patterns among burnt grass sites, which appeared more scattered, indicating high variation in the reptile composition among the burnt grass sites (Fig. 4a). Unburnt and revegetated native grasses grouped more clearly than did grader grass sites.

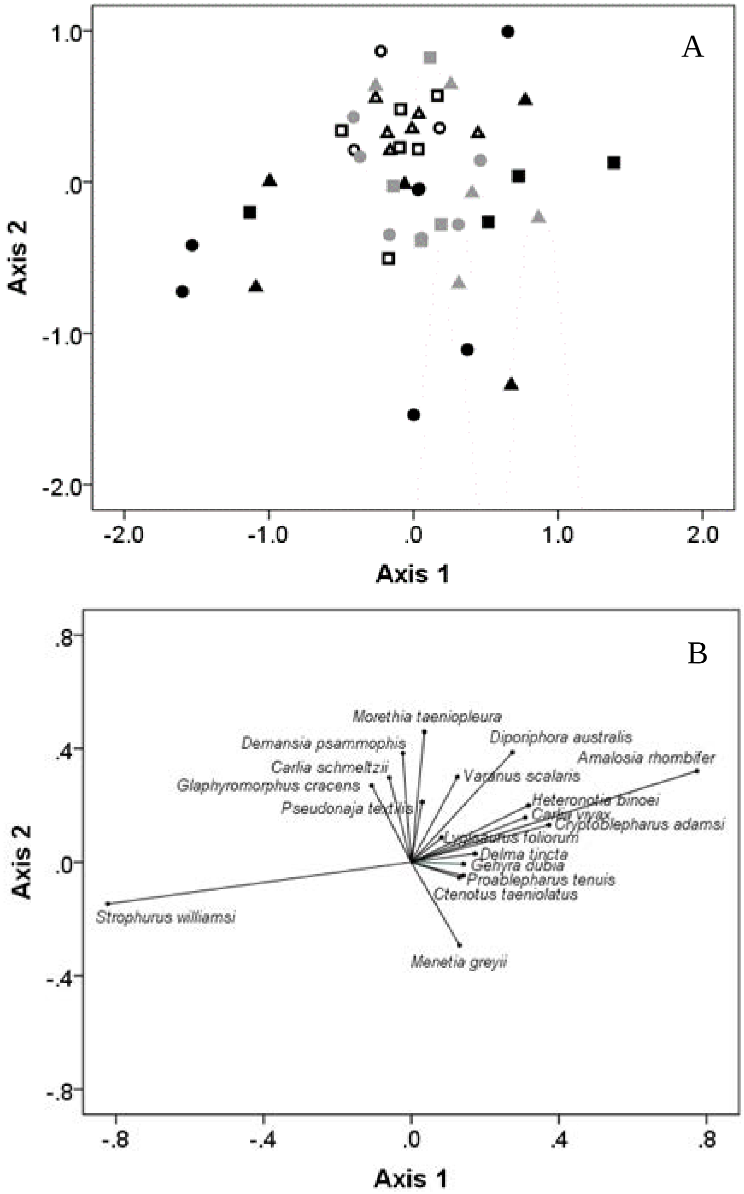

Figure 4. Two dimensional NMDS ordination (stress = 0.180) with the 18 reptile species (data relativised by maximum). (A) Open symbols = unburnt grass habitats, filled black symbols = burnt habitats, and filled grey symbols = revegetated grass habitats with grass symbols, circles = grader, triangles = kangaroo, and squares = black spear grass, (B) correlations ($r^2 > 0.20$) with the 18 reptile species.

Indicator species associated with unburned and burned habitats

The indicator species analysis indicated that I captured more reptiles in unburnt than in burnt and revegetated grass sites, and that reptiles were on average more strongly associated with native than invasive grasses. Reptile species *Glaphyromorphus cracens*, *Lygisaurus foliorum*, *Morethia taeniopleura*, and *Varanus scalaris* were significantly associated with unburnt kangaroo grass habitats, while *Proablepharus tenuis* was significantly associated with revegetated kangaroo grass sites (Table 1 and 3). The eastern brown snake *Pseudonaja textilis* was the only reptile that showed a strong association to grader grass and approached significance as an indicator of revegetated grader grass sites (Table 1 and 3). *G. cracens*, *L. foliorum*, *M. taeniopleura* and *V. scalaris* were encountered more than 40% more frequently in unburnt kangaroo grass habitats than in revegetated kangaroo grass habitats, and encountered more than 75% more frequently in unburnt compared to burnt kangaroo grass sites (Table 1). *P. tenuis* was the only lizard significantly associated with revegetated kangaroo grass, and was encountered 50% more frequently in revegetated than in unburnt kangaroo grass sites with an 80% higher encounter rate in revegetated compared to burnt kangaroo grass sites (Table 1).

Although differences were not statistically significant, comparing unburnt, burnt, and revegetated grass sites I detected higher numbers of *Carlia vivax* and *Gehyra dubia* in unburnt grader grass, whereas *Carlia schmeltzii* and *Demansia psammophis* were detected in greater numbers in unburnt kangaroo grass.

In burnt grass sites, I captured more *Strophurus williamsi* in burnt grader grass, whereas *Diporiphora australis* and *Heteronotia binoei* were more abundant in burnt kangaroo grass while the gecko *Amalosia rhombifer* was detected more frequently in burnt black spear grass sites.

Finally, in revegetated grass sites, here I detected more of the legless lizard *Delma tincta* and *Menetia greyii* in revegetated grader grass; whereas the skinks *Cryptoblepharus adamsi* and *Ctenotus taeniolatus* were found in higher numbers in revegetated kangaroo grass sites.

Table 3. Indicator species (relativized by maximum) analyses with observed indicator value (IV), mean indicator value from randomized groups (± 1 SD) at level of significance with species significantly associated with unburnt kangaroo* grass habitats, one species significantly associated to revegetated kangaroo^ habitats with one species§ approaching significant level in revegetated grader grass habitats.

Species	IV	Mean ± SD	*P*-value
*Glaphymorphus cracens**	35.2	16.2 ± 4.81	**0.0005**
*Lygisaurus foliorum**	28.5	17.2 ± 4.10	**0.0099**
*Morethia taeniopleura**	30.9	16.4 ± 5.03	**0.0145**
Proablepharus tenuis^	39.8	17.6 ± 6.10	**0.0066**
Pseudonaja textilis§	25.3	16.4 ± 6.01	*0.0836*
*Varanus scalaris**	59.8	18.0 ± 9.43	**0.0017**

Discussion

Reptiles were more abundant in native grasses that had been unburnt for 2 years, than in similar sites invaded by grader grass. The lowest abundances of reptiles were observed in burnt grader grass sites, but burning reduced the abundance of reptiles in all grass sites. Some species returned, as revegetation occurred, to abundances similar to their pre-burning levels, but many remained absent or less abundant even after revegetation in this study. Overall abundances recovered to pre-fire levels in revegetated grasses. I found, however, that reptile community composition changed with fire, and remained different, especially in kangaroo grass sites, even after revegetation.

Habitat structural effects of burning

The percentage cover of dominant and mixed grass was similar in all the unburnt grass habitats, in burnt grass sites, and in the two native grasses after they were revegetated. However, grader grass cover was higher, and mixed grass cover lower, in revegetated than in unburnt grader grass sites, indicating that grader grass comes back vigorously after fire, replacing other grasses. In my study, I observed that during fires, flames in grader grass reached higher than flames in native grass (pers. obs.). There was no difference in percent cover of logs among unburnt grader, kangaroo, and black spear grasses, but the percent cover of logs was reduced in grader grass post-burning. This suggests that fires in grader grass habitats may have been hotter in the weed than in native grass sites, consuming more logs. Similarly, fires in invasive gamba grass (*Andropogon gayanus)* are hotter than those in native grasses, causing greater damage to woody vegetation which reduces the availability of refuges such as logs and tree hollows for fauna (Setterfield *et al*., 2010).

Reptile assemblage patterns in relation to prescribed fire

I found that reptile abundances varied greatly among the different burning treatments, which was interesting, because my study sites have been burnt every 2 years and at times even more often, when there was wildfire. Thus, the reptile assemblage in my study area was probably biased towards reptile species that are less sensitive to frequent fires. If my assemblage was completely composed of fire-insensitive species, however, I should have seen little change in abundance and species composition of the reptile communities after fire (e.g., McCoy *et al*., 2013). Vegetation structure is often correlated with reptile abundance, and therefore the responses of reptiles to fire may have been driven by their responses to vegetation structural change (Valentine and Schwarzkopf 2008; Valentine *et al*., 2012). At least some reptiles inhabiting naturally fire-prone systems may prefer the habitat structure and composition created by frequent grass fires (Braithwaite 1987; Friend 1993; Trainor and Woinarski 1994). Pianka *et al*., (2012) identified that the central netted dragon (*Ctenophorus nuchalis)* increased rapidly after fire, while abundances of the sympatric military dragon (*Ctenophorus isolepis)* decreased as a result of reduced vegetation cover after fire. Singh *et al*., (2002*a*) demonstrated that lizard species in fire-prone systems were resilient to fire-induced structural modification of the habitat, as long as the preferred structures remained.

In my study system, Tommy Round-head dragons (*Diporiphora australis*) declined the least (40%) in burnt native grass sites, suggesting that they are relatively tolerant to prescribed burning. Similarly, Bynoe's geckos (*Heteronotia binoei)* had similar capture rates in unburnt, burnt and revegetated kangaroo grass habitats, and their abundances were low in grader and black spear grass sites, regardless of burning state. However, most other species in my study declined much more than 40% after burning, and they did not return to unburnt abundances as vegetation cover returned. Decline without complete recovery nearly a year after fire suggests that these reptile species may always have relatively small populations in habitats with frequent fire.

Other studies, examining longer post-fire periods, found increasing abundances of some species with increasing time since fire (Letnic *et al*., 2004, Valentine and Schwarzkopf 2008; Valentine *et al*., 2012; Nimmo *et al*., 2013; Smith *et al*., 2013). Valentine *et al*., (2012) detected higher abundances in the common dwarf skink *Menetia greyii* in habitats from which fire had been excluded for more than sixteen years. In the current study, abundances of *M. greyii* did not vary significantly among unburnt, burnt, and revegetated grasses. In my study, northern soil-crevice skinks (*Problepharus tenuis*) were the only species that increased significantly in revegetated kangaroo grass after fire, and it is not clear why.

Prescribed fires often reduce accumulated leaf litter deposits, and species that are strongly correlated with leaf litter often occur in lower abundances after fire (Braithwaite 1987; Friend 1993; Singh *et al*., 2002b; Legge *et al*., 2008; Valentine and Schwarzkopf 2008; Price *et al*., 2010; Martin and Murray 2011; Valentine *et al*., 2012; McCoy *et al*., 2013). In my sites, leaf litter was reduced by up to 75% between unburnt and revegetated native grass sites. Leaf-litter-associated skinks such as mulch skinks (*G. cracens*), litter skinks (*L. foliorum*), and fire-tailed skinks (*M. taeniopleura*) were significantly associated with unburnt kangaroo grass sites, and declined between 50 and 80% in revegetated native grass sites compared to their original densities in this study. This response of some reptiles to changes in habitat structure might be followed by other species, for example, specialist lizard predators such as the yellow-faced whip snakes (*Demansia psammophis)* were most common in unburnt kangaroo grass sites, much reduced in burnt sites, and absent in revegetated kangaroo grass sites which may have been driven by lower lizard abundances at these sites (Cogger 2014). Mott *et al*., (2010) reported that the spotted-tree monitor (*Varanus scalaris)* was absent from sampling sites after burning, similar to this study which also showed much reduced *V. scalaris* abundances in burnt and revegetated native grass sites. Reduced numbers of lizard predators such as snakes and monitors may be due to a combination of altered habitat properties and lower overall prey abundance after prescribed burns.

Eastern brown snakes (*Pseudonaja textilis)* were the only snake species associated with grader grass, and they increased by 75% in revegetated grader grass sites, while these snakes declined 60 to 80% in the two revegetated native grass sites after burning.

Eastern brown snakes were the most common snake species we captured, and they apparently actively select sites with higher densities of mice (Shine 1989; Whitaker and Shine 2003). Revegetated grader grass sites have higher seed loads than unburnt grader grass sites (Vogler and Owen 2008). Eastern chestnut mice (*Pseudomys gracilicaudatus*) were abundant in revegetated grader grass (Chapter 4), which may explain why I detected higher numbers of brown snakes in these locations.

The most abundant lizard in the current study was the robust rainbow skink (*Carlia schmeltzii),* and they occurred in greater numbers in unburnt kangaroo grass sites than in unburnt grader and black spear grass sites. The sympatric tussock rainbow skink (*Carlia vivax)* was the most common skink in grader grass. This species has been reported to be closely associated with closed forest (Singh *et al*., 2002*a*). However, I observed tussock rainbow skinks most in unburnt and revegetated grader grass compared to the native grass habitats. Grader grass, with its dense growth structure, may reduce solar radiation reaching the ground in a similar way to closed forest habitats, creating favourable habitat for these lizards. In contrast, robust rainbow skinks declined more than 70% after burning in kangaroo grass and their numbers were reduced by more than 55% in revegetated kangaroo grass sites. Similarly, tussock rainbow skinks reduced their abundances by 85% after burning in grader grass, but in contrast to robust rainbow skinks, these skinks returned to their previous numbers as grader grass sites became revegetated. This suggests that tussock rainbow skinks are more fire-tolerant than robust rainbow skinks, even though they both persist after fire. Striped skinks (*Ctenotus taeniolatus*) declined with more than 80% in burnt spear grass habitats, but returned to similar abundances with emerging vegetation. Interestingly, this species also increased in abundance in revegetated kangaroo compared to unburnt kangaroo grass habitats. Skinks in the genus *Ctenotus* are active at high diurnal temperatures (Cogger 2014), but burnt sites may be too hot for them to persist.

Reptiles and prescribed fire management

Land managers use prescribed fires to reduce weeds and lessen the impact from wildfires (Price *et al*., 2012). Repetitive and frequent fires may increase the size of burnt areas (Alba *et al*., 2015), and frequent (1 < 2 years) fires change the vegetation structure (Burgess *et al*., 2014; Griffiths *et al*., 2015). Many studies report that reptile abundance and richness are unaffected by fires, whereas other studies report that habitats that are burnt frequently have lower reptile abundance and richness, and even fire-insensitive reptiles are often detected in higher abundances in habitats with longer time since fire (Woinarski *et al*., 2004; Perry *et al*. 2012; McCoy *et al*., 2013). I found that reptile abundance and richness were similar between unburnt and revegetated sites. More importantly, however, I detected a significant difference in reptile assemblage composition between unburnt and revegetated native grass sites, demonstrating that to detect the influence of fires, especially in fire-adapted communities, it may be important to analyze community structure as well as abundance and richness. Importantly, I found that the community structure of reptiles was still different 15 months after fire from 2 years after fire, and therefore it may be beneficial to allow longer inter-fire intervals to allow community structure to recover more fully when repeated fires are implemented for management. The weed I studied was encouraged by fire, and frequent burning was not beneficial for weed reduction in my study.

Conclusion

The reptiles inhabiting grader grass were a depauperate subset of the species inhabiting native grasses; no reptile species were significantly associated with unburnt, burnt, or revegetated grader grass. Reptile abundances were also lower in grader grass, regardless of burning state, compared to the two native grass habitats. The lowest reptile abundance of any treatment occurred in burnt grader grass sites, and revegetated grader grass returned to the same low abundances as prior to burning. Native grasses had significantly higher reptile richness and abundances than grader grass, in all states of burning, and overall abundances of reptiles in native grass sites returned to similar levels after revegetation had occurred. All burnt grass sites had lower reptile abundance than unburnt or revegetated grass sites. The habitat composition in burnt sites differed most dramatically from unburnt and revegetated grass sites, which was most likely the reason reptiles were less abundant there. In contrast to abundance, reptile assemblage composition in native kangaroo grass did differ between unburnt and revegetated grass sites. Four species were significantly associated with unburnt kangaroo grass and many species were detected in reduced abundances in the two native grasses after revegetation. I found no evidence that burning the weed, grader grass created a more hospitable habitat for reptiles. Instead, I found that burning grader grass simply allowed it to flourish, and to support the same depauperate community of reptiles present in grader grass left for longer periods. The main drawback of the current study was that the area has been burnt so frequently that it is difficult to draw inferences regarding reptile assemblage composition in longer unburnt savannah and open woodland habitats (> 2 years).

Even in these extremely fire-prone, often-burnt habitats, however, reptile numbers in native grasses declined after burning, and failed to return with revegetation to levels I measured after 2 years without burning, suggesting that longer periods without burning may be beneficial to reptile assemblages, even in very fire-prone habitats. The responses of reptiles to burning in all the habitats seemed to be plausibly driven by changes in habitat structure, although this hypothesis should be tested with experiments manipulating habitat structure

CHAPTER 4. MAMMAL RESPONSES TO FIRE IN A NATIVE SAVANNAH INVADED BY A WEEED (GRADER GRASS, *Themeda quadrivalvis*)

Publication submitted as: Abom, R., Schwarzkopf. L., (*Submitted*). Mammal responses to fire in a native tropical savannah invaded by a weed (grader grass, *Themeda quadrivalvis*). *Journal of Applied Ecology*.

Introduction

Both fire and weeds are major, non-independent forces shaping vegetation composition and structure in naturally fire-prone tropical savannahs (D'Antonio and Vitusek 1992; Foxcroft *et al*., 2010; Lindsay and Cunningham 2012; Alba *et al*., 2015) Land managers use fire to reduce fuel build-up, which is thought to reduce the impact of wildfires on flora, fauna, and the built environment (Queensland's Fire and Rescue Authority Act 1990; Price *et al*., 2012). Invasive weeds increase the fuel load, causing fires to burn hotter and more intensely than do native grass fires (Vogler and Owen 2008; Setterfield *et al*., 2010; Russel-Smith *et al*., 2012). An increase in fire intensity at times when natural fires do not occur may delay flowering events and reduce insect availability, which may negatively impact small vertebrates (Corbett *et al*., 2003; Radford and Andersen 2012; Kwok and Eldridge 2015). Intense grass fires may also increase the area burned, and hotter burns can reduce the availability of shelter sites such as logs, hollows and tree trunks (Setterfield *et al*., 2010; Haslem *et al*., 2011; Russel-Smith *et al*., 2012; Tng *et al*., 2014; Chapter 3). More intense and frequent fires open the understory vegetation structure in savannahs and open woodlands (Burgess *et al*., 2014; Alba *et al*., 2015), and fauna that shelters in dense grasses may be more susceptible to fire (Barlow and Peres 2004; Smith *et al*., 2013).

Mammals may be sensitive to frequent fires (Pardon *et al*., 2003; Andersen *et al*., 2005; Francl and Small 2013; Griffiths and Brook 2014; Kelly *et al*., 2014; Griffiths *et al*., 2015; Mendonça et al. 2015), and gradually decline with repeated burning, or suddenly collapse in abundance, with a slow recovery after fire (Pardon *et al*., 2003; Griffiths and Brook 2014; Griffiths *et al*., 2015; Mendonça *et al*., 2015). Some rodent species avoid burnt habitats by moving to unburnt sites (Clarke and Kaufman 1990), and therefore occur in lower abundances directly after fire, returning to pre-fire levels with emerging vegetation cover (Vieira 1999; Kirchner *et al*., 2011). On the other hand, some mammal species prefer burnt habitats and increase in abundance following fire (Vieira 1999; Breed and Ford 2007; Bock *et al*., 2011). So, there are a wide range of possible responses to fire of different mammal species.

Changing fire regimes, in association with changing land use and weed encroachment, are suspected of contributing to declines in small and medium weight-range mammals in Australia (Johnson 2006; Griffiths and Brook 2014), but few studies have examined the response to fire of mammal communities in tropical savannahs, in Australia, or elsewhere.

Here I investigate mammal responses to fire in an Australian native savannah partially invaded by a noxious weed: grader grass (*Themeda quadrivalvis*). I compared replicate habitats, with similar histories, dominated by different types of native grasses, or invaded by a grassy weed, to quantify the short-term influence of fire on mammal communities in these habitats directly after burning, and more than a year after burning, when the cover of grass had returned to pre-fire levels. My study provides insight into the resilience of tropical savannah mammal populations immediately and shortly after fire in different habitats, in environments that burn very frequently (often more than once per year).

Methods

Study system and sampling periods

Undara Volcanic National Park (18°19`29.92``S, 144°36`28.31``E) covers an area of 66,000 ha, and is situated 850 m above sea level, approximately 420 kilometres northwest of Townsville, Queensland.

I trapped small mammals (5g - 3.5kg) over eight trapping periods (from 11 to 21 days long) between October 2008 and July 2010 (Table 1). In total, I surveyed 24 sampling sites per trapping period, eight sites each, and each site was dominated by a particular grass: invasive grader grass (*Themeda quadrivalvis*), native kangaroo grass (*Themeda triandra*), or black spear grass (*Heteropogon contortus*). I trapped over two years, with four distinct trapping periods per year: in the pre-wet (21 Oct – 14 Nov 2008 and 2009), mid-wet (3 – 26 March 2009 and 2010), early-dry (14 April – 6 May 2009 and 2010), and mid-dry seasons (14 July – 12 Aug 2009 and 2010).

Table 1. Untransformed mammal captures in mammal abundance, richness, and individual mammal species. Average habitat cover in percent of unburnt grader (G), kangaroo (K), black spear (S), burnt (GB, KB, SB), and revegetated (GR, KR, SR), all statistics were performed on relativized data, by dividing each variable (mammals and habitat variables) by the maximum of that variable at any sampling site, ± 1SE.

	Unburnt			**Burnt**			**Revegetated**		
	G	**K**	**S**	**GB**	**KB**	**SB**	**GR**	**KR**	**SR**
Mammal Abundance	101	241	252	58	70	59	138	48	60
Mammal Richness	6	6	10	7	4	7	6	5	5
Rufous bettong	21	18	52	33	37	29	14	34	27
Northern brown bandicoot	42	163	150	13	27	22	49	6	12
Eastern chestnut mouse	24	37	25	1		1	58	2	13
House mouse	8	14	12	4		1	6		2
Tropical short-tailed mouse	2	3	4	5	3	4	1	2	
Common planigale	4	6	3	2		1	10	4	6
Brush tail possum			3		3	1			
Stripe-faced dunnart			1						
Feral cat			2						

Table continue on next page…

Rabbit			1	1					
Burn area				67.2±13.5	72.8±4.9	64.7±7.7			
Dominant Grass	46.3±4.3	55.7±5.3	48.1±3.6	5.4±3.6	7.8±5.0	12.4±2.7	82.0±3.4	56.8±5.7	50.6±2.1
Mixed Grass	42.6±3.2	19.4±3.1	33.8±4.2	9.4±4.4	1.6±0.7	2.3±0.1	11.6±2.7	28.5±6.1	36.1±5.2
Broad leaf	1.7±0.7	1.0±0.4	1.5±0.8	1.8±1.2	0.1±0.1	0.1±0.1	4.3±1.3	2.5±0.6	0.9±0.5
Leaf litter	2.6±1.2	14.81±2.9	11.1±2.0	5.4±3.5	15.7±3.5	14.0±8.4	0.1±0.1	3.4±0.6	2.4±0.5
Rock	1.5±0.7	0.1±0.04	0.6±0.3	1.0±0.6	0.5±0.5	4.6±2.8	0.6±0.4	0.4±0.3	3.6±2.3
Log	0.3±0.2	1.3±0.3	0.8±0.2	0.3±0.2	1.2±0.2	0.7±0.1	0.1±0.1	1.3±0.1	0.8±0.1
Bare ground	5.0±0.6	7.8±2.2	4.1±1.3				1.3±0.5	7.2±1.7	5.6±2.3
Canopy	11.4±8.4	29.9±3.8	25.6±4.7	6.2±3.8	31.4±3.4	20.7±1.9	2.7±1.4	26.6±4.8	14.0±1.8

Site history, grasses, and fire

All of my sampling sites were located in savannah open woodland at Undara Volcanic National Park. In addition to woodland, depressed lava tubes meander through the landscape, characterised by evergreen vine thicket vegetation similar to that found along the east coast of tropical Australia (Atkinson and Atkinson 1995). Prior to 1992, when Undara became a national park, the area was a grazing property, and some parts were used for growing vegetables. Remnants of the fields can still be seen to the east of the Yarramulla Ranger Station (at sites 2G, 7G, and 8G, Fig. 1).

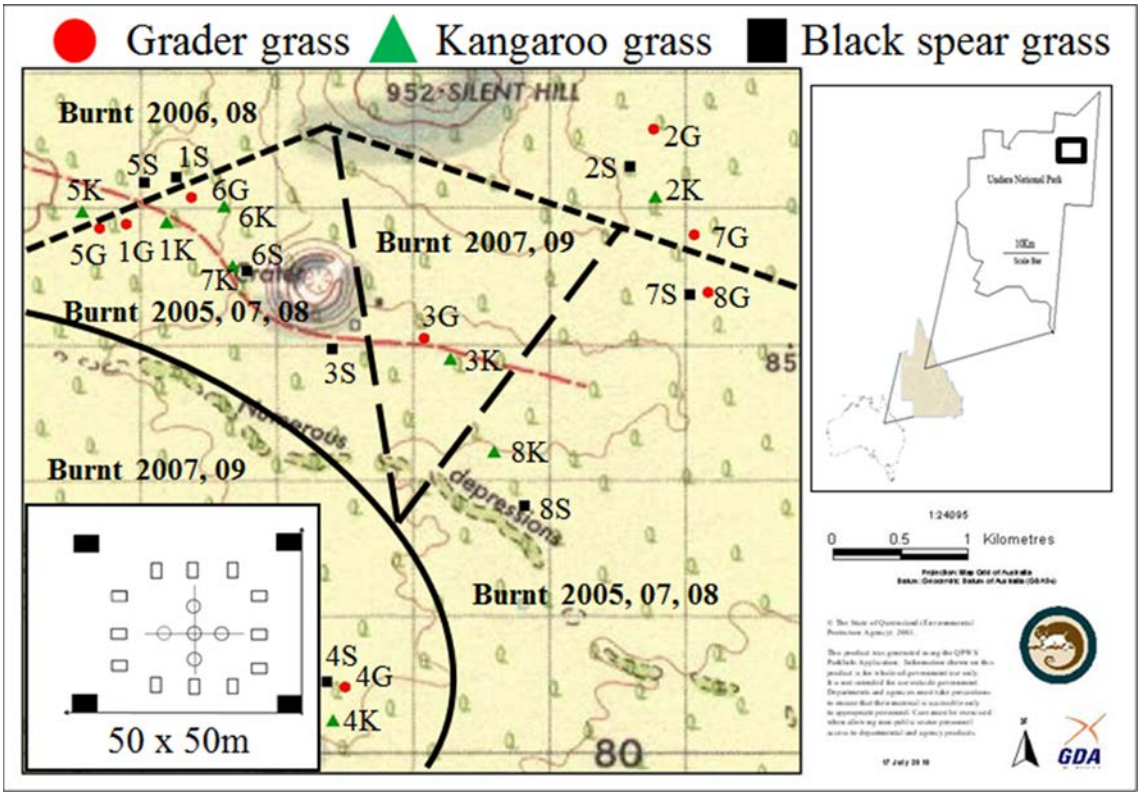

Figure 1. Location of sampling sites (50 x 50m) at Undara volcanic national park (top right corner, box indicate sampling area) and mammal trap array (50 x 50m, bottom left corner) for each site, pitfall traps (open circles, n = 5), Elliott traps (boxes, n = 12), and cage traps (filled squares, n = 4). Fire history of sampling sites (lines), park rangers rotationally burn selected areas in the cooler early dry season (April – May) to create a mosaic of burnt (30 – 60%) and unburnt habitats (Queensland’s Fire and Rescue Authority Act 1990). Sampling sites in current study were rotationally burnt every 2 years since 2002 with wildfires in October 2003 which burn the entire park, and in November 2008 which burnt large areas of the park including some sampling sites. Prescribed and wild fires have been excluded from burning the evergreen vegetation in the depressed lava tubes (numerous depressions in map).

The study site consists of mixed stands of kangaroo and black spear grass, sometimes dominated by one or the other grass, with introgressions of grader grass (see Chapter 2 for a more detailed habitat description). Sites dominated by spear grass had a higher proportion of other grasses on them than areas dominated by kangaroo grass. Grader grass was more common on roadsides and in previously cultivated areas, but had also invaded areas of native grass that appeared undisturbed. Trapping sites were selected so at least two, and often all three grass species occurred within >100 m of one another (Fig. 1). I selected sites to ensure that there was no spatial clumping of particular grass types. This was possible because of the highly heterogeneous nature of the grasses growing in that area, and because adjacent patches of all three grasses were widely represented in the area.

Grader grass is a noxious, annual grass, native to India, and is considered a major threat to natural, cultivated, and recreational habitats where it is introduced (Keir and Vogler 2006). It is a common weed in disturbed systems worldwide (Keir and Vogler 2006). Grader grass has spread rapidly throughout central and northern Australia. It is a typical invasive grassy weed, it emerges as a single stolon (up to 3m tall), is fast growing, and a prolific seeder that can germinate all year around in northern Australia (for a more comprehensive review see Keir and Vogler 2006). In contrast, native kangaroo (*Themeda triandra*) and black spear (*Heteropogon contortus*) grasses are perennials and grow in clumps or hummocks to 1.5 m in height.

To reduce weeds and lessen the impact of wildfires in the hotter pre-wet season (October - December), park rangers burn selected areas at Undara on rotation in the cooler early dry season (April – May) to create a mosaic of burnt (30 – 60%) and unburnt habitats (Queensland's Fire and Rescue Authority Act 1990). Savannah woodlands are naturally fire-prone (Foxcroft *et al.*, 2010), and Undara Volcanic

National Park is burnt at least partially by wildfires every 3 to 5 years. In the current study, sampling sites had been rotationally burnt every 2 years since 2002, with wildfires in October 2003 that burnt the entire park and in November 2008 that burnt large areas of the park including some of my sampling sites (Fig. 1). During the current study, park rangers used prescribed burns in April of 2008 and 2009 (Fig. 1) when environmental conditions were cool enough to allow the fire to self-extinguish in the late afternoons (Queensland's Fire and Rescue Authority Act 1990).

Habitat and mammal sampling protocol

To track changes in habitat variables and vegetation cover in unburnt, burnt, and at revegetated sites, I sampled each site in each trapping period by laying four 50-metre transects transversely, spaced 16.6 m apart, and recorded each variable in linear centimetres along the transect. The four transects were combined to create a mean % cover of each variable per site. I recorded grader, kangaroo, and black spear grass cover (dominant grass), mixed grass (all other grasses combined), broad-leaf vegetation (herbaceous, legumes, and small bushes), leaf litter, logs, rocks, bare ground (space available between structure such as grass tussocks), and canopy cover above the transect.

To describe mammal composition at the sampling sites, I used pitfall traps, and baited Elliott and cage traps (Fig.1). In the centre of each sampling site, 5 unbaited pitfall (20-l straight-sided bucket) traps were deployed, with one centre pitfall trap and four arms. Traps were spaced 10 m apart and connected *via* a 0.5 m high drift fence (Cyclone mesh). I lined each pitfall trap with a 5-cm layer of leaf litter and provided a moistened sponge for water and cover to captured mammals. At each trap site I used 12 baited Elliott (W 100 x L 325 x H 100 mm) traps spaced 10 m apart encompassing the pitfall trap array, and at the outer perimeter of the trapping area, I placed four baited cage (dimensions; W 300 x L 605 x H 290 mm) traps in a square, spaced 50 m apart. Elliott and cage traps were placed in a naturally shaded area or a shade cloth was provided. I used a mixture of oatmeal, vanilla essence, and peanut butter as bait in Elliot and cage traps. I baited Elliott and cage traps every second day in the early evening (17:00-19:00) and checked, cleared, and closed the Elliott and cage traps in the early morning (04:30-06:30). Pitfalls remained open 24 hours a day and I monitored these traps twice daily, in the early morning (05:00-08:00), and in the late afternoon (16:30-18:30). Prior to release of mammals at their point of capture, mammals were identified to species level using Menkhorst and Knight (2004). I marked medium-sized mammals individually using ear clips, and we batch-marked small mammals by trimming the tip of the tail with a pair of scissors (Livingstone, SDI) to obtain DNA samples for another study, and to distinguish between captures and recaptures. Clipping tools were sterilized with an open flame between individuals.

Statistical analyses

Habitat and mammal analyses

I described the habitat composition in unburnt, burnt, and revegetated sites for each dominant grass type (grader, kangaroo, and black spear grass). Habitat variables (grader, kangaroo, black spear, and mixed grass, leaf litter, logs, rock, bare ground, burnt area, and canopy cover) at each sampling site were first averaged over the four transects per site, and then habitat variables were averaged across the number of trapping periods for which the sampling site remained in one of the three habitat states (unburnt, burnt, or revegetated), and converted to % cover, and mammal trapping data were standardised to 100 trap nights. Prior to statistical analyses, habitat variables were transformed using a relativising transformation to range between 0 and 1 by dividing each variable by the maximum cover of that variable at any sampling site. This procedure helps prevent very abundant cover variables driving the results.

To investigate patterns in habitat variables among sampling sites and habitat states, I used the statistical package PC-Ord (McCune and Mefford 1999). I used non-metric multidimensional scaling (NMDS) to explore patterns among habitats in the quantitative variables: % cover of grader, kangaroo, black spear, and mixed grass, leaf litter, logs, rock, bare ground, burnt area, and canopy cover (cut-off value $r^2 < 0.20$) in the three different categorical habitat states – unburnt, burnt, and revegetated grass sites. For the NMDS analyses, I used the autopilot "slow and thorough" with Sorensen distance measures, dimensionality was determined by Monte Carlo tests (9999 permutations, significance test of stress in relation to dimensionality of the number of axes in the final analysis). I extracted axis and cumulative scores using a Bray-Curtis (Sorensen) dissimilarity index with original end point selection, city-block projection geometry and calculation of residuals. To illustrate habitat trends among treatments, I constructed bi-plots from NMDS sites and habitat variables scores (McCune and Mefford 1999).

I described overall mammal abundance, and richness, and individual species abundance for each of the six mammal species captured on my study sites in unburnt, burnt, and revegetated dominant grader, kangaroo, and black spear grass using generalised linear models (GZLM, SPSS V.20). I constructed separate models using a Gaussian-error distribution, identity link function, and Wald-square statistics with mammals as the dependent variable, and treatment (unburnt, burnt, and revegetated dominant grass sites) as the predictor to investigate mammal distributions among sampling sites. I followed modelling with pairwise comparisons (least significant difference, LSD) of estimated means to investigate significant differences in mammals among states in grader, kangaroo, and black spear grass dominated sites.

To investigate the relationship between overall mammal abundance, overall richness, individual mammal species abundances and specific habitat attributes, I used generalised linear mixed effect models (GLMMs) in the statistical program R v2.15.2 (R Development Core Team 2012). I used relativised mammal and habitat variables (as above) with a Gaussian error distribution, identity link function, and treatment (unburnt, burnt, and revegetated dominant grader, kangaroo, and black spear grass sites) as the random factor to tease out important relationships. I employed the lmer function in the lme4 package (Bates *et al*., 2013), dredge (automated model selection) and model average function in the MuMIn package (Barton 2013) in R v2.15.2 (R Development Core Team 2012). I constructed one global model for mammal abundance and richness and one global model for each of the six mammal species, using the dredge function to select models. Model averaging with multimodel inference was used to investigate the relative importance of each habitat variable to mammals (Barton 2013). Models are ranked according to model fit using the corrected Akaike information criterion (AICc), and models within ≤ 2 ΔAICc are considered similar in support (Burnham and Anderson 2002). I tested for collinearity among the ten habitat variables, and evaluated variables by pairwise correlations. Of the 55 pairwise correlations, all the correlations were below the commonly used value ($r = 0.7$).

Results

Habitat composition

I found a stable two-dimensional NMDS solution accounting for 90.43% of the variance (first axis = 58.43%, and second axis = 32.00%) with a final stress of 0.086 for sites and habitat variables (Fig. 1A and B, mean cover % ± SE of habitat variables provided in Table 1). Sampling sites showed strong patterns in vegetation cover among dominant grass sites and states, in that unburnt, burnt, and revegetated grass sites clustered into separate groups (Fig. 2A). Unburnt and revegetated grader grass grouped away from native grass sites, and burnt grass sites clustered in three distinct groups away from unburnt and revegetated sites (Fig. 2A). The habitat variables broad leaf vegetation, and grader and mixed grass cover were more strongly associated with unburnt and revegetated grader grass sites, whereas bare ground, native grasses, leaf litter, log, and canopy cover were more closely associated with unburnt and revegetated native grass sites. Percent cover of burnt ground, as expected, was strongly associated with burnt grass sites (Fig. 2B).

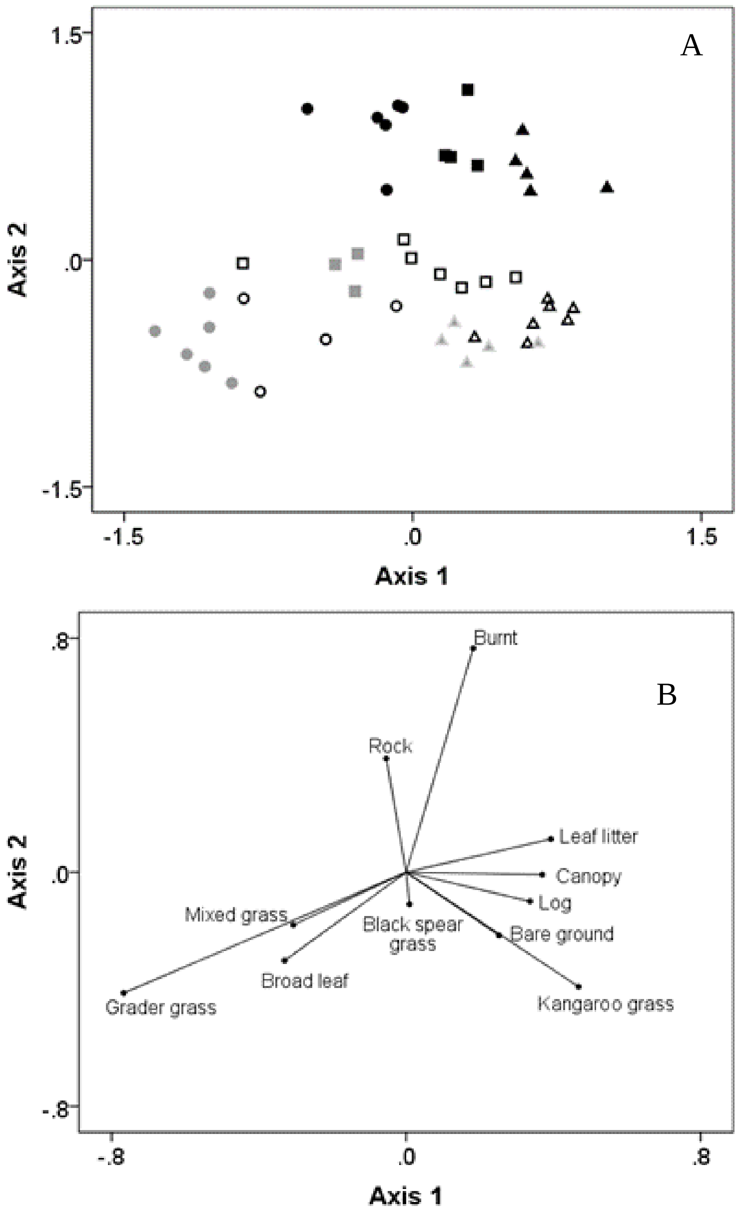

Figure 2. (A) Vegetation structure in relation to habitat variables (relativised by maximum % cover) as a two-dimensional NMDS ordination (stress = 0.086). The first axis represents 58.43% of the variation, and the second axis 32.00%. Symbols; unburnt (open), burnt (filled), and revegetated (grey) with grader = circles, kangaroo = triangles, and black spear grass = squares. (B) Habitat variables driving the NMDS results (r2 > 0.20).

Mammal assemblages and habitat variables

I sampled for a total of 24,960 trap nights, and captured a total of 1029 mammals (467 individuals, excluding recaptures) from 10 different species (untransformed catch numbers are provided in Table 1). Excluding recaptures, the eastern chestnut mouse (*Pseudomys gracilicaudatus, n* = 137), and northern brown bandicoot (*Isoodon macrourus, n* = 124) were the most common mammals, followed by the rufous bettongs (*Aepyprymnus rufescens*, *n* = 89), house mice (*Mus musculus, n* = 47), common planigales (*Planigale maculata, n* = 35), tropical short-tailed mice (*Leggadina lakedownensis, n* = 24), brush tail possums (*Trichosurus vulpecula, n* = 6), feral cats (*Felis catus, n* = 2), rabbits (*Oryctolagus cuniculus, n* = 2), and stripe-faced dunnarts (*Sminthopis macroura, n* = 1).

Movement among sites

Recaptures of marked animals indicated that northern brown bandicoots and rufous bettongs moved greater distances than small mammals, and they moved among sites. Hence, I used recaptures of these animals to examine habitat use. 49% of marked northern brown bandicoots (*n* = 181 of 371 recaptures), and 59% of marked rufous bettongs (*n* = 113 of 193 recaptures) were recaptured in sites within 5 km of their previous capture site. Northern brown bandicoots were recaptured most often in unburnt native kangaroo (*n* = 53, 29%) and black spear grass (*n* = 50, 28%) sites, and I detected bandicoots using unburnt grader grass sites only 10% (*n* = 18) of the time. Northern brown bandicoots had the lowest recaptures in burnt and revegetated grass sites (≤ 8%). Rufous bettongs were recaptured more frequently in unburnt black spear grass sites (*n* = 37, 33%) with only 6% or less recaptured in unburnt grader and kangaroo grass sites.

However, once sites had been burnt I found that rufous bettongs were recaptured more frequently in burnt (n = 14, 12%) and revegetated kangaroo grass sites (n = 18, 16%) than in similar states in grader and black spear grass (≤ 9%). In contrast, few, if any, of the small mammals, including eastern chestnut mice, house mice, tropical short-tailed mice, or common planigales were recaptured at sites other than their site of initial capture, verified using tail clips and data on size and sex of marked individuals at each site.

Responses of mammals to fire

Standardised mammal richness in unburnt, burnt, and revegetated grader and kangaroo grass sites was similar (GZLM Wald x^2 = 10.305, df = 1, 8 P = 0.244), however, mammal richness in black spear grass was lower in revegetated sites than in unburnt or burnt black spear grass sites (Table 1, Fig. 3). Overall, mammal abundances were higher in the unburnt grass sites than in burnt or revegetated grass sites. Mammal abundance was highest in unburnt black spear grass sites, and mammal abundances were significantly higher in unburnt kangaroo and black spear grass than in burnt grader grass sites, and compared to all revegetated grass sites (GZLM Wald x^2 = 16.967, df = 1, 8 P = 0.033, LSD P < 0.05). Even when the cover of grasses had returned to levels similar to those prior to burning, overall mammal abundances did not recover, and in general, mammal abundances were between 40 and 55% lower in revegetated grass sites compared to unburnt grass sites (Table 1, Fig.3).

Abundances of northern brown bandicoots were similar in all the unburnt grass sites, and bandicoot numbers were significantly higher in unburnt native grass than in burnt and revegetated grass (GZLM Wald x^2 = 34.435, df = 1, 8 P < 0.001, LSD P < 0.05,

Table 1, Fig. 2). In contrast, rufous bettong abundances increased at all burnt grass sites, with the highest abundances detected in burnt kangaroo grass, compared to unburnt grass sites (GZLM Wald $x^2 = 22.546$, $df = 1, 8$ $P = 0.004$, LSD $P < 0.05$), and with similar abundances in native grasses once the grass cover returned, but they were detected in much lower abundances in revegetated grader grass sites (Table 1, Fig. 3).

Differences in abundances small mammals among grasses before burning approached significance, including eastern chestnut mice (GZLM Wald $x^2 = 14.847$, $df = 1, 8$ $P = 0.062$) and tropical short-tailed mice (GZLM Wald $x^2 = 14.171$, $df = 1, 8$ $P = 0.077$). Interestingly, eastern chestnut mice were most abundant in unburnt grader grass, and reached their lowest abundances in all burnt grass sites. Abundance of eastern chestnut mice returned to pre-fire levels in grader grass, once the grass had regrown, but did not return to prior abundances in revegetated native grass. In contrast, abundances of the tropical short-tailed mouse were higher in burnt grasses than in unburnt and revegetated grasses (Table 1, Fig. 3). I did not detect any significant trends in the house mouse (GZLM Wald $x^2 = 12.384$, $df = 1, 8$ $P = 0.135$) or in the common planigale (GZLM Wald $x^2 = 8.790$, $df = 1, 8$ $P = 0.360$). House mice and planigales were most common in unburnt grasses. Planigales returned to revegetated grader and kangaroo grass sites, however, house mice abundance did not recover with emerging grass cover (Table 1, Fig. 3).

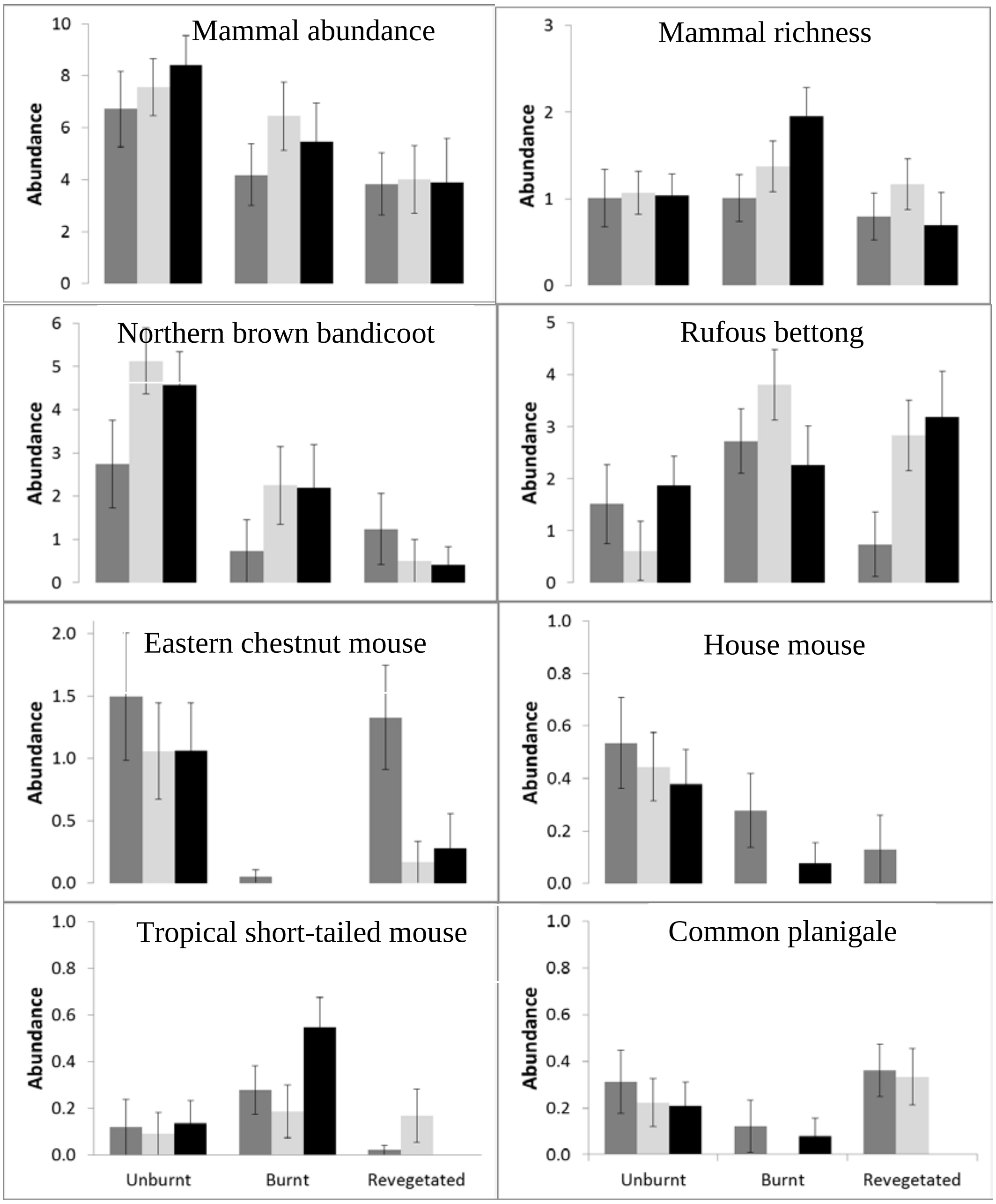

Figure 3. Estimates of mean mammal abundances (untransformed and standardised to 100 trap nights) (GZLM) in grader (grey), kangaroo (pale), and black spear (black bars) grasses ± SE, zero values = no animals captured, and note that y-axis values vary among figures.

Possible reasons for responses to fire: habitat features influencing mammal abundance and richness

Overall, I found that models including two or more habitat variables showed very little support, and therefore I compared models with one habitat variable, with treatment included as a random factor. The model selection indicated that leaf litter cover was the most supported single variable explaining mammal abundance (w_i = 65%), and richness (w_i = 99%, Table 2) differences among treatments. Critical variables varied among mammal species. Treatment alone was the most important factor explaining rufous bettong (wi = 29%), and house mouse (w_i = 22%) abundances, although broad leaf vegetation, mixed grass, and leaf litter also influenced house mouse abundance ($\Delta i \leq 2$, Table 2). Broad-leaf vegetation was strongly and positively related to abundances of eastern chestnut mice (w_i = 54%), and common planigales (w_i = 99%). Abundance of northern brown bandicoots was best explained by models including the variables bare ground, leaf litter and treatment, and the tropical short-tailed mouse preferred habitats with increased cover of rock, leaf litter, and bare ground ($\Delta i \leq 2$, Table 2).

Table 2 Model output for overall mammal abundance, richness, and individual species abundances, with treatment (unburnt, burnt, and revegetated dominant grader, kangaroo, and black spear grass sites) included as a random effect. Models with Δi ≤ 2 are displayed with the number of parameters (K), log likelihood (LogLik), corrected AIC (AICc), rank according to best model (ΔAIC_C), and model weight (*wi*).

Target	Models	K	LogLik	AICc	ΔAIC_C	*wi*
Mammal abundance	Leaf litter + (treatment)	4	1.8402	5.2719	0	0.6464
Mammal richness	Leaf litter + (treatment)	4	32.5801	-56.2079	0	0.9938
Rufous bettong	Treatment	3	-4.202	14.9622	0	0.2871
	Broad leaf + (treatment)	4	-3.7265	16.4054	1.4432	0.1395
Northern brown bandicoot	Bare ground + (treatment)	4	-1.7299	12.4123	0	0.3418
	Leaf litter + (treatment)	4	-2.1879	13.3281	0.9159	0.2162
	Treatment	3	-3.6592	13.8765	1.4643	0.1643
Eastern chestnut mouse	Broad leaf + (treatment)	4	0.445	8.0623	0	0.5408
House mouse	Treatment	3	-7.9604	22.4788	0	0.2203
	Broad leaf + (treatment)	4	-6.803	22.5583	0.0795	0.2117
	Mixed grass + (treatment)	4	-7.1885	23.3293	0.8504	0.144
	Leaf litter + (treatment)	4	-7.6158	24.1839	1.705	0.0939
Tropical short-tailed mouse	Rock + (treatment)	4	0.8831	7.1862	0	0.2236
	Treatment	3	-0.5196	7.5973	0.4111	0.1821

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	Leaf litter + (treatment)	4	0.578	7.7964	0.6101	0.1648
	Burn area + (treatment)	4	0.4248	8.1027	0.9165	0.1414
Common planigale	Broad leaf + (treatment)	4	5.205	-1.4577	0	0.9889

The model averaging results of the relative importance of each habitat variable on mammal assemblages indicated that, in general, mammal abundance and richness increased in habitats with higher cover of leaf litter. Mammal abundances also increased with bare ground cover, and mammal richness increased in sites with higher cover of rocks (Fig. 4). The northern brown bandicoot favoured sites with more bare ground and leaf litter cover (Fig. 4). Small mammals such as planigales, house, and eastern chestnut mice increased in abundance in habitats with higher broad leaf and grass cover, in contrast, rufous bettong numbers declined in these habitats (Fig. 4). Interestingly, the tropical short-tailed mouse was the only species that showed a positive association with burned area. In contrast, abundances of the eastern chestnut mouse and planigales were much reduced in burnt grass habitats, as well as in sites with higher canopy cover (Fig. 4).

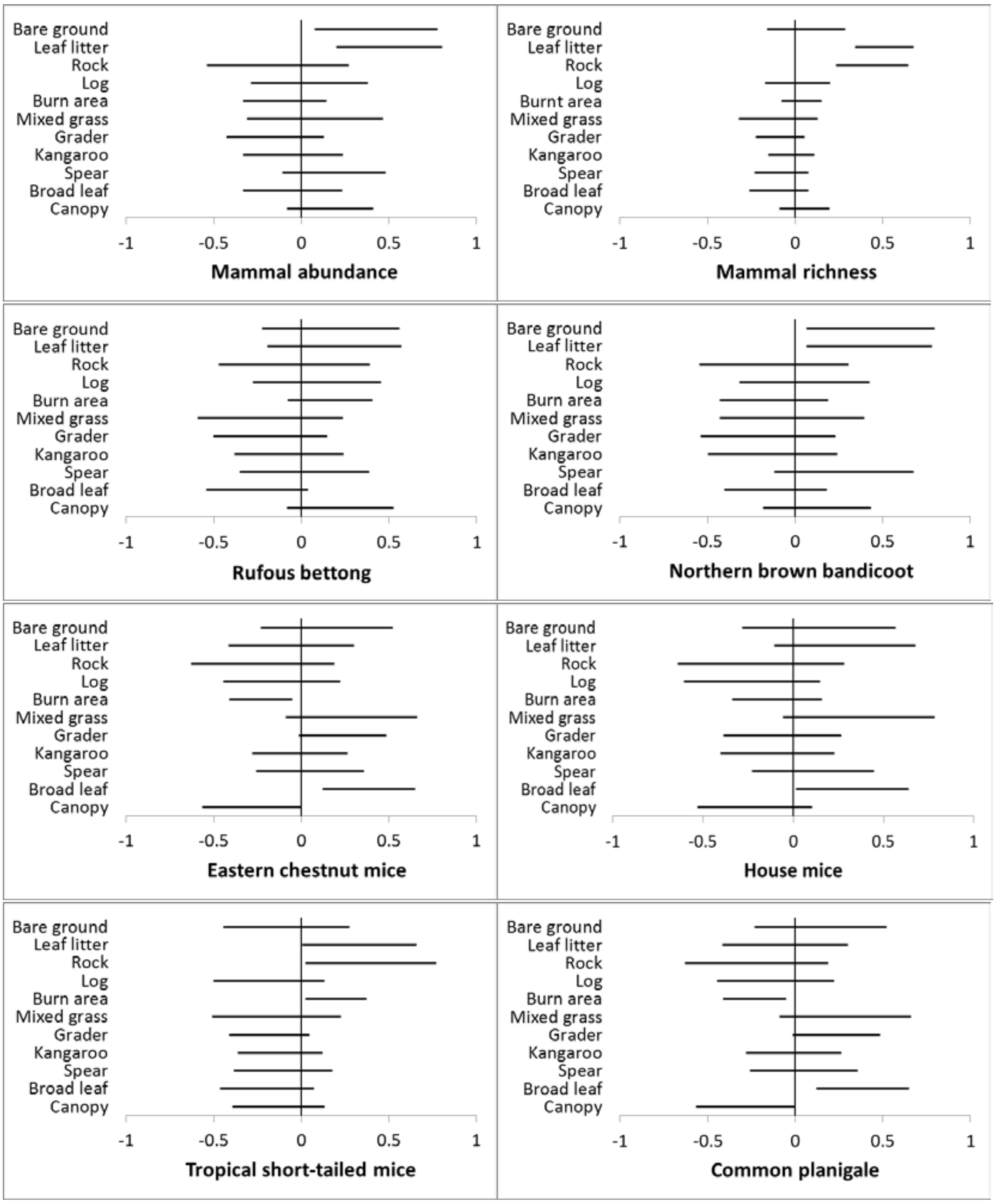

Figure 4. Model average coefficient estimates with 95% confidence intervals. Habitat variables that do not overlap zero indicate factors with high influence.

Discussion

Mammal species richness remained similar in unburnt, burnt, and revegetated grass sites, whereas mammal abundance was more variable among dominant grass sites and states. I captured more mammals in unburnt grasses than in burnt grasses, and the lowest abundance of mammals was recorded in revegetated grasses fifteen months after burning. The interaction between fire and weeds did seem to homogenize the habitat, as the weeds grew back as a more complete monoculture (Chapter 3), and fire in weeds did remove more habitat features, such as logs and leaf litter, than it did in native grass. These observations are all consistent with previous studies, but my focus on individual species showed that the habitat changes wrought by fire seemed to discourage only some mammal species, whereas others were equally abundant in weeds after fire and grass regeneration.

How did fire influence habitat?

Unburnt, burnt, and revegetated dominant grass habitats were distinguishable in terms of habitat variables. Broad-leaved vegetation, grader and mixed grass cover were strongly associated with unburnt and revegetated grader grass sites, respectively, whereas native grasses, bare ground, leaf litter, log and canopy cover were associated with unburnt and revegetated kangaroo and black spear grass sites. Rocks were more visible in burnt areas, and grouped with burnt grass sites. Interestingly, the habitat composition of unburnt grader grass was more variable than in revegetated grader grass sites, indicating that grader grass grew back as a purer stand, and therefore that such sites were homogenized by fire. In contrast, the habitat composition in native grass sites changed little following fire, indicated by the grouping of unburnt and revegetated native kangaroo and black spear grass sites. Other studies investigating invasive grass growth after fire have also found that that invasive grasses grow back more densely than native grasses, which reduces plant diversity and habitat heterogeneity in native habitats invaded by non-native weeds (Vogler and Owen 2008; Lindsay and Cunningham 2012; Alba *et al.*, 2015; Chapter 3). The clearing of grasses (native and invasive) by fire promotes the establishment of weeds, and has positive effects on weed proliferation (Foxcroft *et al.*, 2010; Setterfield *et al.*, 2010; Alba *et al.*, 2015; Chapter 3). Invasive grasses with higher dead standing biomass burn hotter than native grasses, and these hotter fires simplify the savannah by consuming low understory vegetation, and fallen logs which provide structure and hollows used by many animals (Setterfield *et al.*, 2010; Haslem *et al.*, 2011; Russel-Smith *et al.*, 2012; Tng *et al.*, 2014; Chapter 3).

How did fire and weeds influence mammals?

Overall, mammals preferred unburnt grass sites and were detected in higher abundances in these habitats, which was interesting, because my sampling sites have been burnt every two years since 2002, and at times more often, when there have been wildfires. Some species increased in abundance following fire, however, suggesting that these species preferred the habitat structure created by the fire. Bettongs were positively influenced by fire, perhaps because fire allowed easier access to buried food, such as truffles (Vernes and Pope 2001; Pope *et al.*, 2005). Short-tailed tropical mice also increased after fire, although the reason for this is unknown. They may move more in habitats created by fire than they do in undisturbed habitats (Moro and Morris 2000; Kutt and Kemp 2005). These mice were detected in reduced numbers after vegetation regrew.

Medium-sized mammal species, like the northern brown bandicoot, had a strong preference for unburnt native grass habitats and were strongly linked to native grass habitats characterised by a moderate amount of bare ground, and lots of leaf litter. Bandicoot numbers declined in burnt areas, and their abundances declined further in revegetated grasses, possibly due to the reduction in cover of leaf litter. Other studies have shown that the northern brown bandicoot is sensitive to frequent and large scale fires (Pardon *et al.*, 2003; Woinarski *et al.*, 2004; Griffiths *et al.*, 2015). The bandicoot population at the Kapalga fire experiment declined with increased fire frequency from about three animals per 100 trap nights to one bandicoot in 7000 trap nights, and even after five years of fire exclusion these populations had not recovered (Pardon *et al.*, 2003). Reduced numbers of bandicoots may have been caused by high fire-induced mortality at the time of fire, higher post-fire deaths, or emigration to unburnt habitats (Pardon *et al.*, 2003). A similar population decline of northern brown bandicoots was described earlier by Friend (1990) at Kapalga in the mid-1980s, which was later confirmed to be due to late dry season fire (Pardon *et al.*, 2003). In my study, the prescribed fires were ignited in the early dry season (April 2008 and 2009) and a wildfire occurred in the late dry season (October 2008), which burned parts of Undara. My northern brown bandicoot population behaved very similarly to those at Kapalga (Friend, 1990; Pardon *et al.*, 2003). Bandicoots were initially abundant (~5 individuals per 100 trap nights, Fig. 3) in unburnt grass habitats, and experienced ~ 50% lower capture rates in burnt grasses, decreasing to less than one individual per 500 trap nights in sites in which the vegetation had regrown after the fire. Like the bandicoot population at Kapalga, bandicoots at Undara did not collapse rapidly, instead the population declined gradually over fifteen months (after May 2009 to July 2010) until bandicoot numbers were very low.

Small mammals showed mixed responses to fire. Common planigales, eastern chestnut mice and house mice were detected in higher abundances in unburnt grass sites with more broad-leaved vegetation. Planigales and chestnut mice were associated with grader grass cover. Although planigale, chestnut and house mice numbers were much reduced in burnt grass sites, only planigales and chestnut mice were negatively associated with burnt area, and returned with emerging grass in revegetated sites. House mice, on the other hand, almost disappeared once habitats had been burnt.

Conclusion

Tropical savannahs are highly diverse and naturally fire-prone systems (Foxcroft *et al*., 2010). I found, as have other studies, that fire in weeds changes the structure, and reduces plant biodiversity in these habitats (Setterfield *et al*., 2010; Haslem *et al*., 2011; Russel-Smith *et al*., 2012; Burgess *et al*., 2014; Griffiths *et al*., 2015). Land managers use prescribed fires with the intention of reducing weeds, and lessening the impact from wildfires on fauna (Price *et al*., 2012). This approach may not be successful for fire sensitive mammals (Griffiths and Brook 2014). For example, by the end of the current study, northern brown bandicoots almost completely disappeared from my sampling sites, most likely because there was reduced suitable habitat for bandicoots, which may increase the risk of local extinction (Pardon *et al*., 2003; Griffiths *et al*., 2015). On the other hand, some mammals appeared to prefer the habitat created by fire. In my study, rufous bettongs and tropical short-tailed mice were most common immediately after burning, becoming less abundant as vegetation returned. Finally, some mammals returned to their previous abundances in the weed, but not in native grass, while others returned to their previous abundances in native grass, but not in the weed. Here I suggest that prescribed burns in naturally fire-prone systems may reduce overall mammal abundance, and if the conservation goal is to avoid overall reductions in abundance, I recommend that areas be burnt more irregularly, potentially allowing a more diverse vegetation assemblage and structure to be established (Parr and Anderson 2006; Burgess *et al*., 2014; Griffiths *et al*., 2015). On the other hand, I found that the responses of individual species to fire in weeds was idiosyncratic and some species may prefer burned areas. Thus, it is important to identify which species are more sensitive to frequent fires, to establish fire regimes which retain species diversity based on multiple mammal species responses (Litt and Steidl 2011; Kelly *et al*., 2015).

CHAPTER 5. NATIVE MAMMALS PERCEIVE A MORE ACCURATE LANDSCAPE OF FEAR THAN INTRODUCED SPECIES

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Introduction

Predation is a strong force influencing most aspects of life for prey animals (Lima and Dill 1990). Time of day, season, moon radiance, habitat structure and vegetation height, distance to shelter, predator odours, and predator abundance may all influence activities because of their influence on the perceived risk of predation (Kotler *et al*., 1994; Bouskila 1995; Jacob and Brown 2000; Abramsky *et al*., 2002; Ylönen *et al*., 2002; Jacob 2008; Lima and O'Keefe 2013). Because predation risk has such a profound influence on activity, avoiding predation can be costly. Time spent avoiding predators may influence fitness because foraging or mating success is reduced (Lima and Dill 1990). For example, skinks (*Carlia* sp.) can distinguish between, and avoid, dangerous, specialist predacious goannas (*Varanus scalaris*), compared to a more generalist congener (*V. varius*) (Lloyd *et al*., 2009). Similarly, juvenile anemonefish (*Amphiprion percula*) can distinguish between predatory and herbivorous fish using chemosensory cues (Dixson *et al*., 2012). Thus, although animals alter their behaviour to avoid predators, they are also adept at minimising the costs of predator avoidance.

Many rodent species avoid open microhabitats, because they are perceived as areas with higher predation risk, and therefore they forage under and around natural structures to reduce detection (Dickman 1992, Jacob and Brown 2000, Mandelik *et al*., 2003, Powell and Banks 2004, Stokes *et al*., 2004, Pastro and Banks 2006, Breed and Ford 2007, Jacob 2008, Strauss *et al*., 2008; Fraschina *et al*., 2009; Abu Baker and Brown 2010, Dickman *et al*., 2010; Fanson *et al*., 2010, Hinkelman *et al*., 2012). There are, however, some exceptions; some desert rodents (e.g., *Gerbillus pyramidum, Dipodomys deserti* and *D. merriami*) prefer to forage in open sites rather than under cover (Kotler *et al*., 1993, Bouskila 1995). The variation among rodents in preferred foraging habitat may be driven by differences in perceived predation risk. Rodents threatened by snakes may avoid cover, whereas those preyed upon by birds may avoid open spaces (Kotler *et al*., 1992, Bouskila 1995, Abramsky *et al*., 2002, Embar *et al*., 2014).

Long-term evolution in a particular environment with predators likely shapes the landscape of fear, and therefore determines the antipredator behaviour of many species. Appropriate antipredator behaviour may influence the success of invasive species (Dickman 1992), and the urban concentration of some invasive species may be driven by inappropriate responses to predators in the predator-filled natural environment (e.g., Cisterne *et al*., 2014). Few studied quantify and compare the drivers of antipredator behaviour in native and introduced species, but this information can be useful to determine the risks of successful invasion of native environments (Zozaya *et al*., 2015).

Perceived risk of predation is often measured using giving-up densities, which quantify the amount of risk a foraging animal will tolerate before leaving a productive foraging patch, by determining the amount of food left in the patch when the animal ‘gives up’ (Brown 1988). Many studies assume that giving up densities are a measure of the level of predation, or make assumptions about the kind of habitats that are likely to cause fear (e.g., open habitats or closed habitats, depending on the prey species) (Dickman 1992, Bouskila 1995, Kotler *et al*., 1994). Many studies use experimental enclosures, stocked with known numbers of predators, to create a landscape of fear in which to conduct giving up density experiments (Kotler *et al*., 1992, Abramsky *et al*., 2002, Embar *et al*., 2014). Few studies directly examine the predator densities in different natural habitats, and then measure giving up densities, although this is a logical extension of describing a real landscape of fear.

I used giving-up density experiments to measure the perceived risk of predation of introduced house mice (*Mus musculus*) and native chestnut mice (*Pseudomy gracilicaudatus*) rodents ,in the open, and in closed, grassy habitats. I also quantified the number of predators using these habitats, as part of a wider survey. Thus, I quantified risk of predation, and determined the corresponding perceived risk of predation, in habitats for two rodent species with different evolutionary backgrounds.

Methods

Study area and sampling period

Rodent trapping, predator surveys, and foraging experiments were conducted in savannah open woodland at Undara Volcanic National Park (18°19`29.92``S, 144°36`28.31``E), approximately 420 kilometres northwest of Townsville, Queensland, Australia. I trapped rodents between October 2008 and July 2010, in eight sampling periods, in four seasons of each year (Table 1 for numbers of rodent trapped numbers) and surveyed abundance of predators (Table 1) (see Chapters 2, 3 and 4 for detailed trapping and survey protocols). Rodent foraging experiments were performed over two 10–day periods in the cooler dry season (8th – 18th – 28th of July 2011).

Table 1. Untransformed survey abundances of predatory birds, mammals, and reptiles among sampling sites (no nocturnal predatory birds were observed).

	Grass habitat			
Species	Burnt	Grader	Kangaroo	Black spear
Mice				
Mus musculus	5	14	14	14
Pseudomys gracilicaudatus	2	82	39	38
Raptors				
Elanus axillaris	1	2		1
Milvus migrans		1		
Falco berigora	6		1	
Falco cenchroides	7			
Mammal				
Felis catus				2
Snakes				
Acanthophis spp.			1	
Pseudechis australis			1	
Pseudonaja textilis		11	6	11
Pseudonaja nuchalis			1	1
Antaresia stimsoni		1	1	
Aspidites melanocephalus	1			
Boiga irregularis			2	1

Study species

There were two abundant rodent species at my study sites. Introduced, invasive house mice (*Mus musculus*) weigh 10 to 25 grams, are omnivorous, and can be easily recognised by their musky odour (Menkhorst and Knight 2004; Van Dyck and Strahan 2008). Eastern chestnut mice (*Pseudomys gracilicaudatus*) are much larger (45-115g), and feed on a variety of seeds, fungi, plant material, and invertebrates (Luo *et al*. 1994; Menkhorst and Knight 2004; Van Dyck and Strahan 2008). The critical predators for rodents at my sites were eastern brown snakes (*Pseudonaja textilis*), which are large, fast moving snakes that feed predominantly on rodents (Shine 1989).

Foraging arenas

I investigated rodents' perceived risk of predation using giving-up densities in the field. I used foraging trays placed under cover of grass and in the open (one metre from grass cover). At open sites, grass was cut using a grass trimmer (STIHL®, model FS 50 C, Australia), and left at a uniform height of 15mm, whereas in grassy sites grass was 1-1.5 m high. After preliminary experiments with seeds and mealworms, I found both rodent species preferred mealworms. I determined the density of mealworms required to achieve accurate measures of giving-up densities, by mixing the bait with a substrate (vermiculite, Proganics^{TM}). Mixing the bait with the vermiculite prevented rodents consuming all the food offered, and allowed me to quantify the mass of mealworms remaining when the perceived predation risk outweighed the benefits of time spent foraging in the arenas (Fig. 1).

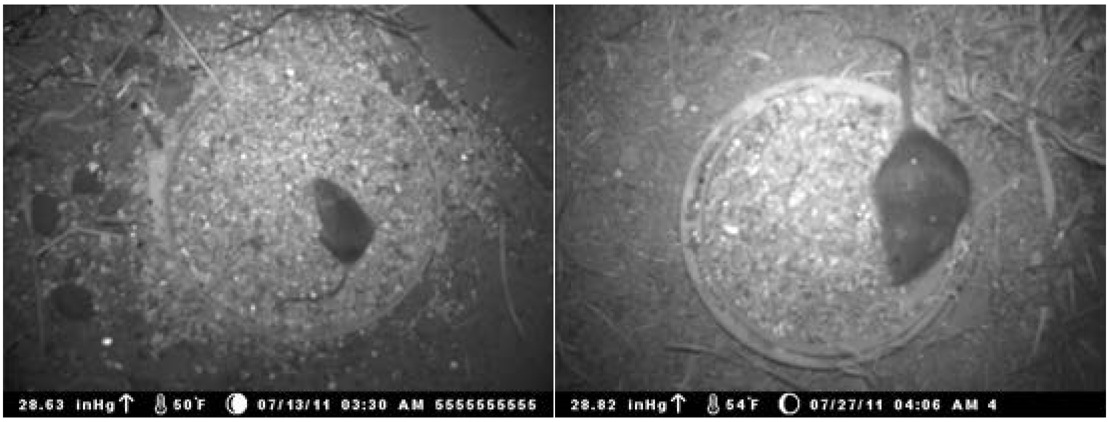

Figure 1. Foraging house mice (*M. musculus* - left) and Eastern chestnut mice (*P. gracilicaudatus* - right) in the giving-up density experimental arenas. Sizes of the two species are relative (*M. musculus* is much smaller than *P. gracilicaudatus*).

To create foraging arenas, I secured a circular wire-mesh tube (0.5 metre in diameter, and 0.8 m high, mesh size, L 80 x H 60 mm) to the ground using four 150 mm u-shaped metal pegs. This allowed rodents a 360° degree entry and exit to and from the feeding arena, while also allowing natural light to penetrate. In this area, foraging trays (55 mm deep, and 175 mm in diameter) were set into the ground and levelled. The arenas excluded brown bandicoots *(Isodon macrurus)*, and rufous bettongs (*Aepyprymnus rufescens)* from entering foraging arenas.

A total of 32 foraging arenas were established and baited with 20 mealworms (approximately 5.5 grams) mixed with one litre of vermiculite. I placed each bait tray in the feeding arena at dusk (17:30 – 18:30), and collected them just before dawn (05:30 – 06:30) to prevent small birds from consuming or disturbing food in the bait trays. All sites were unmonitored for two days prior to the start of the experiment, to allow rodents to become familiar with the arenas and to start feeding there, and then monitored for ten consecutive days during the experiment.

To verify which rodent species were visiting the foraging arenas at night, I used digital game cameras with infrared motion sensors (Moultrie®, model 160, Alabster, AL, USA). I mounted 8 game cameras each night on a rotational schedule to cover each bait tray 5 times over the course of the experiment. I secured game cameras 0.6 m above the bait tray, using two one-metre glass-fibre rods (10 mm in diameter) and cable-ties (Crescent™). Game cameras were adjusted to include the bait tray and the foraging arena in the picture (Fig. 1). I set the cameras to take one initial still picture followed by a 6 sec video.

Statistical analysis

I converted the number of mealworms consumed to grams, and square root transformed the grams of mealworms consumed, to use as my target variable, with 3 predictor variables: distance to cover (= 0 under grass, or 1 in the open), rodent species (eastern chestnut or house mice), and total eastern brown snake abundance in that habitat, determined from trapping surveys. I determined the influence of each predictor variable using multimodel inference using information theory (Akaike's Information Criterion corrected for small sample sizes, AICc, Burnham and Anderson 2002). I used the lmer function in the lme4 package (Bates *et al*. 2013) and the dredge function in the package MuMIn (automated model selection, Barton 2013) in the statistical program R v2.15.2 (R Development Core Team 2012). My global model had grams of food consumed as the target variable with and all three predictors (distance to cover, mice species, and eastern brown snake abundance). The dredge function on the global model included all possible models, to tease out which predictors were more important determinants of the amount of food consumed. Models were ranked according to model fit in the corrected

Akaike information criterion (AICc). Models with ΔAICc ≤ 2 were considered highly supported (Burnham and Anderson 2002). I tested for collinearity between pairs of all three variables, using pairwise correlations. Collinearity was weak and of the pairwise correlations, no correlations were above the commonly used value ($r = 0.7$).

Results

I conducted the foraging experiment over a total of 320 experiment/nights. I had 69 samples of foraging, with a total of 33 *Pseudomys gracilicaudatus*, and 36 *Mus musculus* foraging observations. A model including interaction effects between distance to cover and rodent species, and distance to cover and eastern brown snake abundance was the most strongly supported model ($w_i = 58\%$ Table 2, and giving-up density predictions, Appendix Fig. A1 and A2). The second best model had 3 times less support ($w_i = 18\%$) than the most supported model ($\Delta AIC_C = 2.36$), and thus I provide statistics of the most supported model. Eastern brown snake abundance had the strongest significant support in the top model influencing rodent foraging behaviour, followed by mice species, distance to cover x eastern brown snake abundances, distance to cover, and distance to cover x mice species (Table 3).

Table 2. Model output of mealworms consumed (SQRT transformed) by mice as the target variable and predictors distance to cover (under cover of grass and in the open), snake (mean abundance of eastern brown snakes), mice species (eastern chestnut and house mice), and interaction effects. Models are displayed according to model fit with number of parameters (K), log likelihood (logLik), corrected AIC (AICc), and rank according to best model (ΔAIC_C), model weight (*wi*).

Intercept	Distance to cover	Snake	Mice spp	Distance to cover * Snake	Distance to cover * Mice spp	Snake * Mice spp	Distance to cover * Snake * Mice spp	K	LogLik	AICc	ΔAIC_C	w_i
2.34	+	-0.30	+	+	+			7	-21.33	58.49	0	58.50
2.36	+	-0.31	+	+	+	+		8	-21.23	60.85	2.36	18.00
2.40	+	-0.30	+	+				6	-24.03	61.42	2.93	13.50
2.35	+	-0.31	+	+	+	+	+	9	-21.18	63.41	4.92	5.01
2.39	+	-0.30	+	+		+		7	-24.03	63.90	5.40	3.93
2.19	+	-0.23	+		+			6	-27.17	67.69	9.20	5.88E-03
2.29	+	-0.28	+		+	+		7	-26.21	68.25	9.75	4.46E-03
2.23	+	-0.20	+					5	-32.75	76.45	17.95	7.39E-05
2.20	+	-0.29		+				5	-33.54	78.03	19.54	3.35E-05
2.30	+	-0.24	+			+		6	-32.36	78.08	19.59	3.27E-05
2.29		-0.27	+			+		5	-38.04	87.02	28.53	3.73E-07

Table continue on next page…

2.16		-0.21	+		4	-39.23	87.08	28.59	3.63E-07
1.96	+	-0.18			4	-43.13	94.88	36.39	7.32E-09
1.76	+		+		4	-49.08	106.78	48.29	1.91E-11
1.71	+		+	+	5	-48.20	107.36	48.86	1.43E-11
1.80		-0.18			3	-50.75	107.87	49.38	1.11E-11
1.60	+				3	-53.22	112.82	54.33	9.35E-13
1.66			+		3	-53.95	114.27	55.78	4.52E-13
1.44					2	-59.24	122.66	64.17	6.81E-14

Table 3. The best model output for predictor variables and interaction effects to explain foraging behaviour (the number of grams of mealworms left in foraging trays, or giving up densities) in native eastern chestnut and introduced house mice in a natural grassland.

Models	Estimate	Std Error	t value	Pr(>|t|)	*P* <
(Intercept)	2.339	0.102	23.045	< 0.001	0.001
Distance to cover	-0.555	0.221	-2.503	0.015	0.05
Snake Abundance	-0.298	0.035	-8.421	<0.001	0.001
Rodent species	-0.288	0.102	-2.820	0.006	0.01
Distance to cover * Snake Abundance	0.208	0.061	3.409	0.001	0.01
Distance to cover * Rodent species	-0.450	0.199	-2.267	0.027	0.05

Eastern chestnut mice consumed more mealworms at forging stations than did house mice. At sites from which eastern brown snakes were absent, both species of rodent consumed more mealworms under the cover of grass than from foraging arenas in the open. However, with increasing eastern brown snake abundance at sampling sites, reduced their foraging under cover of grass (Fig. 2). As brown snake abundance increased, eastern chestnut mice shifted their foraging behaviour to consume more mealworms in the open than under the cover of grass (Fig. 2). Interestingly, house mice consumed fewer mealworms under the cover of grass at sites with higher eastern brown snake abundance, but never shifted to forage more in the open (Fig. 2).

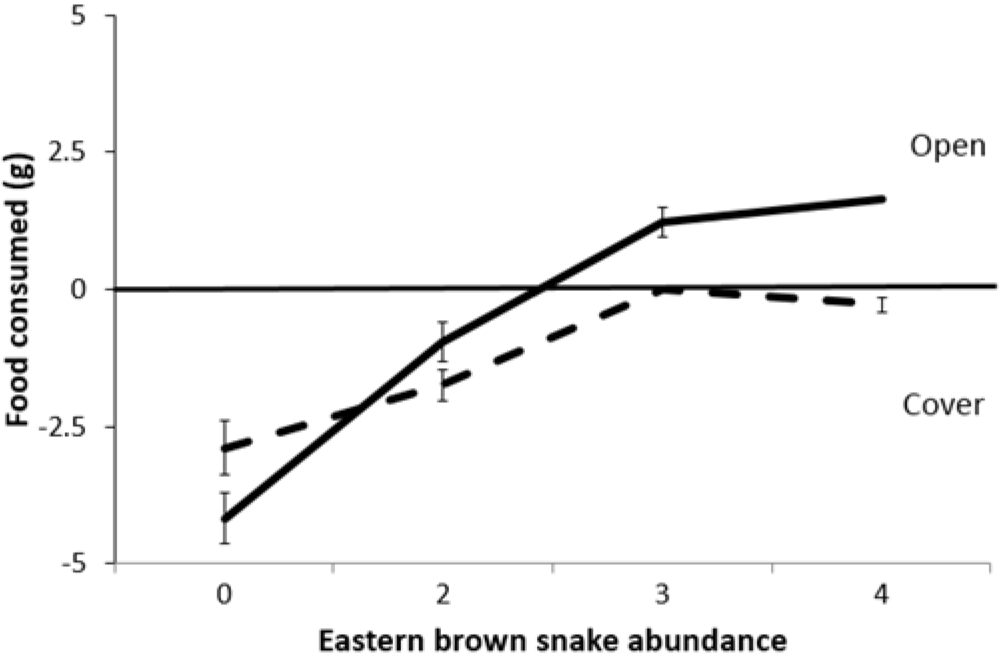

Figure 2. Mean relative differences in grams of mealworms consumed by introduced house mice (*M. musculus* – broken line) and native eastern chestnut mice (*P. gracilicadatus* - solid line) under cover (below), and in the open (above the 0 consumption line) (error bars ±1SE), illustrating the shift shown by Eastern chestnut mice from foraging under cover to foraging in the open as snakes become more numerous in the habitat.

Discussion

My experiments demonstrated that, in the absence of snakes, both native eastern chestnut mice, and introduced house mice preferred to forage under cover. However, as the perceived (and likely actual) risk of predation from snakes increased, the strategies of the native and the introduced species diverged. Eastern chestnut mice responded to an increased perceived risk of predation from snakes by shifting to foraging in the open, whereas the introduced mice never made this shift, they simply reduced food intake when under cover. My experiments also suggested that, overall, native eastern chestnut mice were bolder when foraging than introduced house mice, because on average, eastern chestnut mice consumed more mealworms than did house mice.

It was surprising that snakes, rather than nocturnal predatory birds such as owls, appeared to be driving the perceived risk of predation of rodents in my study area. Southern boobook owls (*Ninox boobook*), and barking owls (*Ninox connivens*), are present in the area, but I did not detect any during my surveys, suggesting they were not very numerous, at least at the time of my study. Given the low density of nocturnal predatory birds, the response of the native chestnut mice, of shifting to foraging in the open, was appropriate to the actual level of risk in the habitat. In comparison, the response of house mice was less appropriate. In general, *Mus musculus* use dense vegetation to avoid predators (Dickman 1992), and many smaller rodent and marsupial species tend to avoid open areas (Mandelik *et al*. 2003; Stokes *et al*. 2004; Strauss *et al*. 2008; Dickman *et al*. 2010). I suggest that the response of *Mus musculus* in my study was indicative of a generalised antipredator response in house mice, rather than a specific response to avoid nocturnal raptors present in the area.

The greater boldness of the native species, overall, and in the context of increased predation, is interesting because the success of introduced species is often attributed to greater boldness (Chapple *et al*. 2012). I found, however, that the native rodent was bolder than the introduced species, and this bold behaviour appeared to be more appropriate to acquiring food in a low nocturnal bird predation environment. Inappropriate antipredator responses may be responsible for lowered fitness of invasive species (Sih *et al*. 2010). In general, *Mus spp.* do not change their feeding behaviour with the exposure to odours from unfamiliar mammalian predators (Dickman 1992; Powell and Banks 2004; Strauss *et al*. 2008; Shapira *et al*. 2012), and so do not seem to have very flexible antipredator strategies. In my study, however, house mice reduced their food intake with increasing number of eastern brown snakes, suggesting that the house mice avoided these predators, so they showed some flexibility in foraging strategies, although not as much as the chestnut mice. In my study, introduced mice were considerably less abundant in the study area than native mice (Table 1), suggesting that they may experience lower fitness in this environment. Perhaps the generalised fear response of house mice in novel environments is initially successful, but prevents flexible behaviour in response to native predators in native environments. Similar observations were made in experiments comparing native and introduced house geckos (Cisterne *et al*. 2014). In that study, a generalised fear response of introduced geckos was useful in urban environments, but apparently less successful in native environments.

In general, grassland rodents tend to avoid open areas (Dickman 1992; Jacob and Brown 2000; Powell and banks 2004; Pastro and Banks 2006; Jacob 2008), while desert rodents, which occur in more open habitats, tend to avoid riskier areas under cover where snakes could lie in ambush (Kotler *et al*. 1992; Kotler *et al*. 1993; Bouskila 1995). Such generalisations depend on the species and the environment to which they are exposed. It is very unusual, however, for rodents to entirely shift their behaviour from foraging undercover to foraging in the open, as I observed in eastern chestnut mice. For example, several rodent species (gerbils, *Gerbillus allenbyi, G. pyramidum* and kangaroo rats *Dipodomys deserti*) reduce their foraging behaviour under cover when exposed to snakes in experimental enclosures, and increase it again when snakes are removed (Kotler *et al*., 1993; Bouskila, 1995; Embar *et al*. 2014), but none completely changed their behaviour to foraging in the open.

At my study sites, large rodent eating snakes may have been the major agent of predation for rodents in grassy habitats (Shine 1989). Unlike the ambush predators used in most experiments on rodent foraging behaviour (Bouskila 1995, Kotler *et al*. 1993, Embar *et al*. 2014) eastern brown snakes actively hunt their prey (Shine 1989; Cogger 2014), making them fierce predators with the ability to pursue their prey in grass, where other predators, such as mammals, may not be successful (Shine 1989; Hughes *et al*. 2010; McGregor *et al*. 2014). It is unclear how rodents in my study detected eastern brown snakes. One plausible possibility is that both species may have been able to detect the scent of snakes, as occurs in some other rodents (Bouskila (1995). Eastern chestnut mice have likely coevolved with eastern brown snakes, and may, therefore, have developed alternative foraging tactics in grasslands with high snake activity.

The complete shift, from foraging more under cover to foraging more in the open shown by eastern chestnut mice, suggests that they may be able to assess the relative danger from snakes and from nocturnal birds. It would be interesting to conduct enclosure experiments exposing these mice to various densities of both predators, to learn more about their assessment of the relative risks from these two types of predators. Exposing house mice to similar experiments may reveal if our suggestion is supported that they lack flexibility in foraging behaviour compared to native species.

Conclusion

It is critical that individuals identify and respond specifically to particular threats to avoid predation. Native eastern chestnut mice have achieved this with an unusually high degree of plasticity in their foraging tactics, allowing them to choose foraging sites with fewer predators. In contrast, introduced house mice simply reduced their foraging activities at sites with higher abundance of snakes, indicating a more generalised response to predators. Differences in the antipredator responses of these two rodent species may contribute to their relative fitness in this environment.

CHAPTER 6. GENERAL DISCUSSION

Human mediated disturbances such as the spread of non-native grasses beyond their natural range pose a grave threat to native flora and fauna (D'Antonio and Vitousek 1992). It is, however, critical to understand these disturbances and how they impact native ecosystems, to effectively manage native systems invaded by non-native species, to reach management and conservation goals. I worked in an area that was particularly well suited to determine the effects of weeds and fire, and their interaction, on fauna. My study site was relatively small, and the community structure of species on my sites was similar. Also, weeds and native grasses grew side-by-side in many areas of my site, so I could directly compare the influence of the different grass types on community structure, without confounding spatial autocorrelation among sites. My study was relatively rare in that it examined the influence of weeds on fauna, not only describing the effects on assemblage composition, but trying to determine the mechanisms causing effects, wherever possible. It is the first to investigate the effects of grader grass (*Themeda quadrivalvis*) on native faunal diversity. I also examined the influence of fire in these small-scale, replicated native and weed-invaded habitats, describing the short-term effects of fire and recovery of grass cover on reptile and mammal composition. Finally, I investigated rodents' landscape of fear in relation to actual predator abundances in tropical savannah and open woodlands of northern Australia.

Impacts of invasive weeds on reptile diversity

Annual non-native grasses are among the worst threats to native ecosystems, because they can rapidly alter the ecosystem that they invade (D'Antonio and Vitousek 1992).

Reptile richness and abundance was significantly higher in native-grass dominated savannah than in savannah invaded by grader grass (*Themeda quadrivalvis*) (Chapter 2). To tease out the reasons reptile richness and abundance were significantly lower in grader grass sites than in native grasses, I investigated grass temperatures, food availability, predator abundance, and habitat structure (Chapter 2). My results showed that grass temperatures, food availability, and predator abundances did not differ between weeds and native grass, although predator abundance was slightly higher in native grass. Thus reptiles were not richer or more abundant because in native grass because of thermal, food, or predator avoidance advantages over reptiles in weeds. The habitat structure did differ among grasses (Chapter 2), however, in that grader grass grows in dense swards, whereas native grasses grow in a clumping or hummock structure. Native grass also had higher cover of leaf litter, and logs (although there were no significant differences in canopy cover among grasses), and exposed soil than detected in grader grass (Chapter 2). The higher diversity in habitat structure in native grasses was positively associated with higher reptile abundance and richness (Chapter 2). Thus, the loss of habitat heterogeneity, and the uniform habitat structure in sites invaded by grader grass caused lowered reptile richness and abundance in weedy sites. Given that grader grass has spread rapidly over most of central to northern coastal Queensland and across most of northern Australia, and has the potential for further spread (Keir and Vogler 2006), it should be a high priority to manage this invasive weed. An understanding of its effects on faunal composition, as well as on individual species, is important for implementing appropriate management decisions. My work suggests that it is the transformative effect of grader grass on the ecosystem that causes its impact on reptiles. The uniform habitat structure provided by the weed is low quality for reptiles, and they avoid entering it (Hacking *et al*., 2014).

Weeds are often controlled by fire, and at Undara, fire is used to suppress grader grass. There is, however, and unfortunate feedback loop between weeds and fire. Grassy weeds can cause fires to be hot and intense, which can help create the open, disturbed conditions that promote the weeds (including grader grass) in the first place. The low structural complexity caused by weeds, and promoted by fire used to control weeds, appears doubly detrimental to reptile communities using grasslands.

Reptile and mammal responses to frequent burns

Savannahs are high fire-prone, but also highly faunally diverse ecosystems, which suggests that fauna in tropical savannahs are resilient to naturally occurring fires (Woinarski *et al*., 2004; Andersen *et al*., 2005; Foxcroft *et al*., 2010; Pianka and Goodyear 2012). To reduce the buildup of invasive weeds in savannahs, land managers often use fire (Setterfield *et al*., 2010; Price *et al*., 2012; Russel-Smith *et al*., 2012). I assessed the use of fire, and quantified reptile and mammal responses in unburnt (not burnt for 2 years), newly burnt, and in revegetated (up to 15 months after burning) grader and native grass sites (Chapters 3 and 4).

Native grass habitat types and burning states were similar, but unburnt and revegetated grader grass sites were quite different from native grasses (Chapters 3 and 4). These differences occurred because there was significantly higher grader grass cover in revegetated than in unburnt grader grass, which did not occur in the native grasses (Chapters 3 and 4). Many lizards with specific arboreal and terrestrial habitat requirements (tree hollows, leaf litter) were associated with unburnt native grass, especially kangaroo grass (Chapter 3). Many fewer litter-dwelling skinks occurred in burnt and revegetated kangaroo grass, while the arboreal goanna disappeared from such sites (Chapter 3). Similarly, northern brown bandicoots (*Isoodon macrourus*) were strongly associated with leaf litter, and their abundance was much reduced after burning, and they too almost completely disappeared by the end of the study (Chapter 4). House mice (*Mus musculus*) also almost disappeared towards the end of the study, although the cause of their disappearance is unknown (Chapter 4). Rufous bettongs (*Aepyprymnus rufescens*) and tropical short tailed mice (*Leggadina lakedownensis*) favoured habitat created by fire, possibly because burning allowed easier access to buried food (Vernes and Pope 2001; Pope *et al*., 2005; Chapter 4). In contrast, Eastern chestnut mice were captured in lower abundances, and eastern brown snakes (*Pseudonaja textilis*) were absent from burnt grass habitats (Chapters 3 and 4). Interestingly, both these species returned with returning grader grass cover, and eastern brown snakes were detected in higher abundances in areas with higher abundances of eastern chestnut mice (Chapters 3 and 4). Grader grass, with its fast growth and high seed availability probably provided chestnut mice with an abundant food source, and chestnut mice were far less abundant in revegetated native grasses than in revegetated weedy sites (Chapter 4). Similarly, eastern brown snake abundance was 3 times lower in revegetated black spear grass and 9 times lower in revegetated kangaroo grass sites than abundances detected in revegetated grader grass sites (Chapter 3). Shine (1989) reported that adult eastern brown snakes may follow their prey. My study may confirm that eastern brown snakes actively seek and remain in areas with higher prey abundances (Chapters 3 and 4).

I found no evidence that burning grader grass created a more hospitable habitat for reptiles or mammals, with the exception of eastern chestnut mice and eastern brown snakes. Instead, I found that burning grader grass simply allowed it to flourish, and to support the same depauperate community of fauna present in grader grass left unburnt for longer periods. Both reptile and mammal abundances were highest in unburnt and much lower in burnt grass sites. Unlike mammals, reptiles tended to return with returning grass cover, although not to pre-fire abundances. Agamid lizards are often described as early successional species with rapid increase in population numbers following fire (Pianka and Goodyear 2012). However, in the current study the dragon, *Diporiphora australis* declined slightly in their numbers following fire (Chapter 3). It seems that reptiles are slightly more resilient to the short-term effects of burning than many mammals. One could argue that my study sites have been burnt so frequently (≤ 2 years between fires), that I could only survey reptile species that are fire resilient, but the extremely high fire frequency at Undara is not untypical of many managed savannah habitats. In my study, reptiles were never associated with burnt grass sites, in that almost all reptiles declined in their abundances after burning (Chapter 4), suggesting some effect of fire on even these, apparently highly resistant, species.

Rodents' landscape of fear

The most common rodent predator at my study sites was the eastern brown snake. I did survey for feral cats (*Felis catus*), other reptiles that consume rodents, and for diurnal and nocturnal raptors (Chapters 2 to 5). I only detected two feral cats, however, and snakes other than the eastern brown snake were detected in low abundances, and most diurnal raptors were detected in burnt sites with low rodent abundance, and I did not observe any nocturnal raptors during my study (Chapters 2 to 5). The results from Chapters (3 and 4) showed that higher eastern brown snake abundances were associated with higher eastern chestnut mice abundances in revegetated grader grass, and interestingly, both species were detected in much lower abundances in revegetated native grasses.

Predation has a profound impact on foraging strategies of prey, because survival of captured prey is extremely low (Lima and Dill 1990). Time of day, season, moon radiance, habitat structure and vegetation height, distance to shelter, predator odours, and predator abundance may all influence prey activity, because of their influence on the perceived risk of predation (Kotler *et al*. 1994; Bouskila 1995; Jacob and Brown 2000; Abramsky *et al*. 2002; Ylönen *et al*. 2002; Jacob 2008; Lima and O'Keefe 2013). I described eastern chestnut and house mice foraging tactics in relation to abundances of actively hunting, eastern brown snakes. I established a giving-up density foraging experiment in the field to investigate foraging behaviour in the native eastern chestnut (*Pseudomys gracilicaudatus*) and the introduced house mice (*Mus musculus*). Both rodents foraged almost exclusively under grass cover when brown snakes (*Pseudonaja textilis*) were absent (Chapter 5). Eastern chestnut mice, however, changed foraging activities when brown snakes were present. Chestnut mice foraged less under cover and more in open sites as brown snake abundance increased. House mice did not show this foraging shift in relation to increasing eastern brown snake abundance, instead house mice simply reduced their foraging activity when snakes were present (Chapter 5). As introduced house mice responded to high snake abundance by reducing rather than changing their foraging activity, the shift in foraging behaviour from closed to open in eastern chestnut mice may be a result of co-evolution of predators and prey. Dickman (1992) demonstrated that *Mus domesticus* retreat into denser vegetation when threatened by predators. Feral cats, for instance, have higher capture success in open sites with less vegetation and in burnt grass habitats (McGregor *et al*. 2014). Brown snakes can, however, follow their prey in dense vegetation, which may reduce the effectiveness of the predator avoidance tactics used by the introduced house mouse. This scenario is plausible, because house mice were detected in much lower abundances than chestnut mice (Chapter 4).

Management Implications

The weed I studied was encouraged by fire, and frequent burning did not reduce its occurrence (Chapter 3). Instead, I suggest that reducing fire frequencies in areas invaded by this weed will allow for the reestablishment of native grasses, because unburnt grader grass sites had a higher cover and variety of native vegetation than did revegetated grader grass sites after burning (Chapter 3 and 4), suggesting that when unburnt, the grader grass is eventually outcompeted by other grasses. Isolating and excluding fire in weed infested areas, and re-seeding native plants may reduce the impacts of invasive weeds (Keeley 2001; Cione *et al*., 2002; Milton 2004; Vogler and Owen 2008; Setterfield *et al*., 2014; Yelenik *et al*., 2015).

Overall, faunal abundances were lower in weed infested sites than in native savannah, with much reduced faunal abundances in both native and invaded savannah, following the use of fire, whereas faunal abundances remained lower in revegetated than in unburnt sites. Hence, it may be beneficial to wildlife to increase the time between prescribed fires (> 5 years) to allow the habitat structure as well as the faunal community to recover (Yates *et al*., 2008).

Weed establishment in Australia is one of the leading causes of habitat degradation, and weed establishment increases the natural fire frequency in invaded habitats, allowing them to flourish under the new conditions they create. This, coupled with land managers’ attempts to remove weeds by using fire, especially at Undara, will increase the pressure on native habitats and their inhabitants. One argument is that if burning frequency is reduced, fires become more intense when they do occur (Murphy and Russell-Smith 2010; Price *et al*., 2012), however it is also possible to argue that excluding fire allows for the reestablishment of native vegetation, which will reduce fuel load and hence reduce fire frequency and intensity over time (Cione *et al*., 2002). It is however a challenging debate, because fire-prone grassland systems are shaped by high natural fire frequency (Foxcroft *et al*., 2010), so frequent fire is not supposed to be detrimental. In any case, decisions to burn weeds should include an awareness of the likelihood of enhancing certain species while discouraging others, and conservation decisions should be based on an awareness of fire sensitive species in a multiple species response.

Future Directions

My study was conducted over two years, and this allowed me examine various different weather conditions and vertebrate assemblage states, but the relationship between community assemblages and habitat is dynamic, and dependent on many biotic and abiotic factors. It would, therefore, be interesting to resume the vertebrate survey, and conduct it over a longer period, to determine whether the patterns I observed, or inferred, are robust.

One drawback of my study was that the area has been burnt so frequently that it was difficult to draw inferences regarding reptile and mammal composition in longer unburnt savannahs and open woodlands, determining faunal responses to less frequent fire. Most of reptile and mammal species in my study were negatively impacted by the changes in habitat structure created by the weed and high fire frequency (≤ 2 years). In keeping with this, more experiments examining habitat structure in native and weed-infested savannah with both short and longer fire return frequency should be conducted. I found that the revegetation of grader grass after fire promoted higher eastern chestnut abundance, and increased rodent densities were coupled with increased abundances of eastern brown snakes. It would be interesting to determine if this correlation was a cause and effect relationship, for example by radiotracking snakes while continuing to survey rodents, and determining snake movements in relation to rodent abundances, or by radiotracking both snakes and rodents, and determining their movements in relation to one another. Another interesting avenue that could be explored if radiotracking both groups would be the capture success of rodents by snakes, to determine if increased foraging success of snakes increases fear in rodents. Studying rodent and eastern brown snake movements using radiotelemetry in savannah systems before and after burning, would provide information on their relative home range sizes, and overlap under changing environmental conditions. Most studies of the influence of snake foraging on mice use ambush hunters such as vipers and rattlesnakes in arid zones (Daly *et al*., 1990; Kotler *et al*., 1992; Kotler *et al*., 1993; Bouskila 1995; Embar *et al*., 2014), and so do not examine the landscape of fear generated by active predators. Other experiments use as their predators mammals like foxes and feral cats, which have reduced mobility, and likely reduced prey capture success in dense weedy habitats (Dickman 1992; McGregor *et al*., 2014).

It would also be interesting to investigate the mechanisms driving the responses of the mice that I observed, for example by determining their responses to chemical cues and odours from reptile predators, perhaps using fresh shed skins from snakes as stimuli. Other chemical cues to investigate would be faecal pellets from stressed rodents, to investigate if fear in other rodents of the same or different species (for example using faecal pellets and urine as stimuli) would alter rodents’ foraging activity in a high quality patch with higher predator abundance.

In my foraging study, small mammal abundances were positively associated with the presence of shrubs, and negatively associated with tree canopy cover (Chapter 4), and the causal link between these structures and abundance of rodents could be quantified by manipulating habitat structure, say by shrub removal, and then use foraging trials to determine if habitat structure without shrubs is perceived to be more frightening by savannah rodents (Mandelik *et al*., 2003; Stokes *et al*., 2004).

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APPENDICES

Appendix 1.

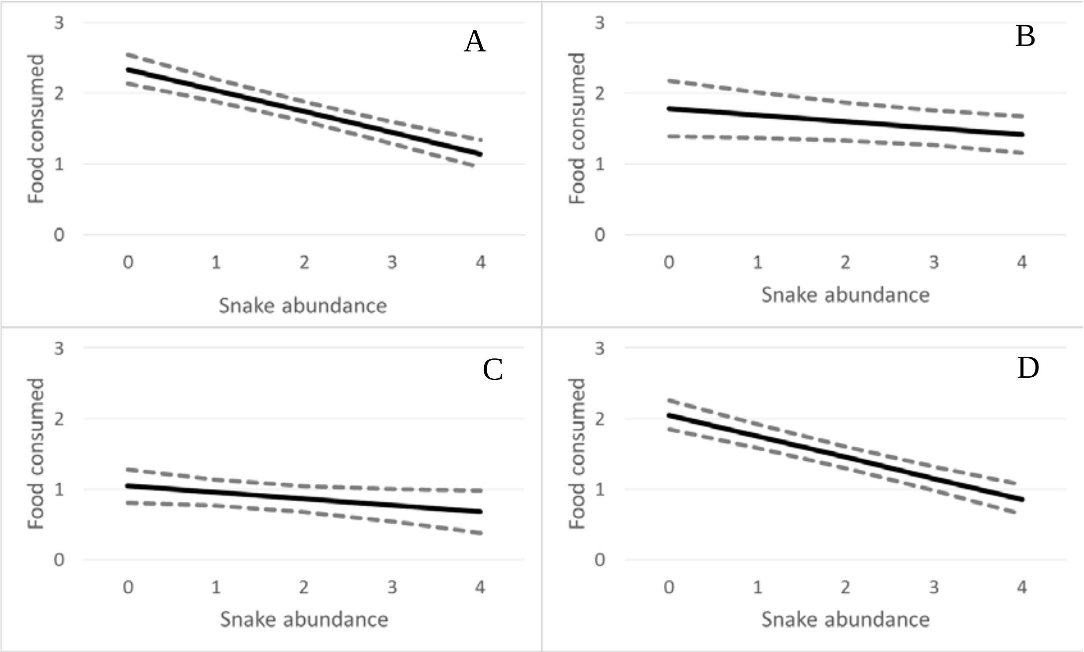

Figure A1. Predicted mealworms consumed (square root transformed) by eastern chestnut mice under grass cover (A), and in the open (B), and by house mice under grass cover (C) and in the open (D) with 95% confidence intervals (dotted line).

Appendix 2.

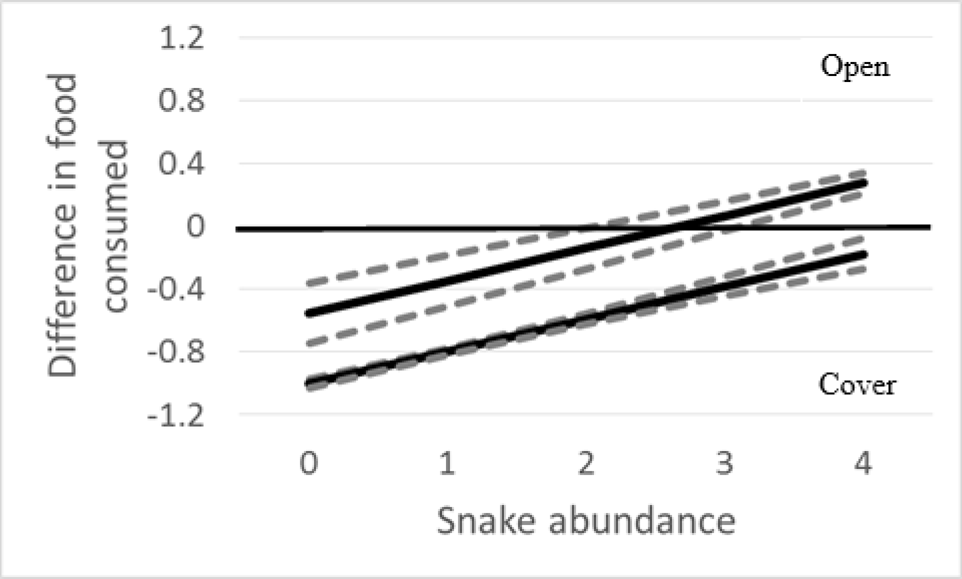

Figure A2. Predicted difference in mealworms consumed (square root transformed) by rodents in grams (SQRT), eastern chestnut (top line), and house mice (bottom line) with 95% confidence levels (dotted lines).

Appendix 3.

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