Faunal community structure and predator relationships in Uluṟu Kata Tjuṯa National Park, central Australia

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Abstract

This thesis focuses on the main habitat types at Uluṟu-Kata Tjuṯa National Park (UKTNP), in central Australia, and examines how and why native species are distributed throughout the system. ‘Top down’ and ‘bottom up’ processes are examined, with a spotlight on the role of predation in driving the dynamics of the vertebrate community and the subsequent effects on the diversity, abundance and distribution of native prey.

Over the course of nine chapters and using a combination of long term historical, and contemporary data, this study examines the diversity of fauna contained within the different areas of UKTNP and which species play particular roles in defining fauna assemblages. A range of inputs into a typical desert system, informed by the literature review of Chapter Two, are examined for their effect on fauna including rainfall, fire, the role of the apex predator, the influence of the apex predator on smaller predators, the structure of the vegetation community and the food resources available. Conclusions and management recommendations are contained within the final section of the thesis.

Authorship attribution statement

Chapter Four of this thesis is published as Bennison, K., Godfree, R. and Dickman, C.R., 2018. Synchronous boom–bust cycles in central Australian rodents and marsupials in response to rainfall and fire. *Journal of Mammalogy*, *99*(5), pp.1137-1148. I organised and co-analysed the data and wrote the drafts of the manuscript.

Statement of originality

This is to certify that to the best of my knowledge; the content of this thesis is my own work. This thesis has not been submitted for any degree or other purposes.

I certify that the intellectual content of this thesis is the product of my own work and that all the assistance received in preparing this thesis and sources have been acknowledged.

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I have been stomping around the bush measuring things, sitting at a desk writing things or thinking about things to do with this study for so long that it feels like an old friend. And, as is the case with old friendships, it has introduced me to many amazing people along the way.

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Chapter One

Introduction

One third of the world's land area is desert. The deserts of Australia make up a significant proportion of this area, with up to 70% of our continent classified as either arid (<250 mm rain annually) or semi-arid (250–500 mm rain annually).

This PhD contributes to our understanding of the drivers of ecological community structure in the semi-arid deserts of central Australia. The study location is Uluṟu-Kata Tjuṯa National Park (UKTNP) – a twice World Heritage listed National Park located 320 km south-west of Alice Springs in the Northern Territory.

Using historical and contemporary observational data and results obtained from experimental manipulations, my study looks closely at the main habitat types and how and why native species are distributed throughout the system. ‘Top down’ and ‘bottom up’ processes are examined, with a spotlight on the role of predation in driving the dynamics of the vertebrate community and the subsequent effects on the diversity, abundance and distribution of native prey.

Overview

The six data chapters of this PhD pose the following broad questions:

i. Are there consistent patterns between vegetation types and fauna assemblages in the semi-arid regions of central Australia?
ii. Do rainfall and fire forge consistent patterns in faunal communities?
iii. Does the apex predator, the dingo, regulate the smaller introduced predators, the feral cat and European red fox, in unbaited semi-arid areas of central Australia? Do the relationships vary in different habitat types and/or different seasons?

iv. How does dingo presence affect native species? Do native species fear dingoes? Or feel protected by their presence?

v. What else drives diversity and abundance of native species in local areas? Is it a function of local microhabitat variation?

To explore these questions and examine the basis on which they are proposed, this PhD has nine chapters: one is an introduction to the study and the study site, one is primarily a review chapter, six chapters present primary data and the final chapter concludes the study. A brief synopsis of these chapters, and of the study location, is presented below.

Chapter One- Introduction

Chapter One describes the study site including its biotic and abiotic components such as resident species and weather patterns as well as the components of management relevant to the thesis. The chapter also introduces the study and broadly outlines the questions the study sets out to answer within the context of the area. Additionally, this chapter briefly outlines the structure of the thesis and the individual chapters.

Chapter Two- Literature review

The second chapter is the review chapter, providing a brief summary of desert systems throughout the world, and in Australia. It sets the scene by summarising the key drivers of ecological community structure. It also examines the collective evidence for the existence of apex predator effects, directing a spotlight in particular towards the Australian context which involves the dingo, red fox and feral cat, and describes the complexity and controversy that attend the debate about how dingoes may affect the smaller species.

Chapter Three - Historical habitat use and spatial distribution of native vertebrates at Uluṟu-Kata Tjuṯa National Park

Using a 16-year data set that remains largely unanalysed, this chapter begins the journey to understand the structure of faunal assemblages at UKTNP, while later chapters explore the drivers behind these structures. By examining the relationship between habitat/vegetation communities and faunal assemblages, this chapter investigates the extent to which habitat creates consistency in faunal community structure. It also provides a comprehensive historical baseline and gives perspective to later chapters.

Chapter Four - Synchronous boom-bust cycles in central Australian rodents and marsupials in response to rainfall and fire

This chapter examines the temporal impact of rainfall and fire on a faunal group that can respond quickly to desert resource pulses – the mammals. This chapter is crucial to informing discussion in later chapters.

Chapter Five - Historical habitat use and spatial distribution of native vertebrates in the three contemporary study habitats at Uluṟu-Kata Tjuṯa National Park

Using the same 16-year data set, this chapter focuses on faunal community structure and species occurrence patterns in the three habitats focused on for the rest of this study – *Triodia basedowii* (hard spinifex) grassland and *Acacia aneura* and *Eucalyptus* spp. woodlands. Faunal and habitat associations identified in Chapter Three are examined more closely in these three habitats and are used for comparison and reference with the contemporary study sites to understand the influence of the vegetation community in determining faunal communities, as compared to other drivers of faunal assemblages.

Chapter Six - Spatial and temporal relationships between a top predator and mesopredators at Uluṟu-Kata Tjuṯa National Park

This chapter focusses on the relationships between dingoes and foxes and dingoes and cats at UKTNP. Using remote photography and occupancy analyses, the influence of dingo activity on fox and cat activity and spatial and temporal distributions across seasons is investigated, as is the relationship with environmental variables such as habitat, water availability and track placement.

Chapter Seven - The influence of dingoes on the foraging intensity of small mammals at Uluṟu-Kata Tjuṯa National Park

In this chapter, giving-up densities (GUDs) are used to examine whether dingo activity or lack thereof, influences the behaviour of native species. GUDs are used to examine the effect of stable, predictable dingo presence on the foraging choices of small mammals in spinifex grasslands at UKTNP.

Chapter Eight - The drivers of faunal community structure at Uluṟu-Kata Tjuṯa National Park and the influence of rainfall, habitat, predator activity and other environmental variables

Using observational data from fauna and flora surveys, this chapter Investigates the influence of local microhabitat variation in structuring vertebrate assemblages in the study habitats at UKTNP.

Chapter Nine - Conclusion and management recommendations

Finally, this chapter integrates and summarises the key findings from the data chapters and makes recommendations for the management of feral animals and native vertebrate populations at UKTNP that arise from the data.

The study location - Uluṟu Kata Tjuṯa National Park

UKTNP covers 1325 km^2 and welcomes approximately 300,000 visitors annually from Australia and around the world (UKTNP unpublished data). The Muṯitjulu Aboriginal Community is located within the Park and is home to around 150-200 A<u>n</u>angu (Pitjantjatjara- and Yankunytjatjara-speaking Aboriginal people). *Tjukurpa* (A<u>n</u>angu Law and culture) describes the creation of the natural world and structures the relationships and responsibilities A<u>n</u>angu have to it (Uluṟu - Kata Tjuṯa Board of Management and Parks Australia 2000). Historically, both Uluṟu and Kata Tjuṯa were economically important locations for A<u>n</u>angu (Layton 1989). Reliable water sources dictated traditional travelling routes, and resources available within the Park were enough to permit large gatherings of A<u>n</u>angu during favourable seasons (Layton 1989).

Inalienable freehold title to the Park was granted to Aṉangu in 1985 (Uluṟu - Kata Tjuṯa Board of Management and Parks Australia 2000). The area was then leased back to the Commonwealth to be run as a national park (Uluṟu - Kata Tjuṯa Board of Management and Parks Australia 2000). A Board of Management with a majority of Aṉangu traditional owners was established by legislation and continues to manage UKTNP for the protection of its natural and cultural values (Uluṟu - Kata Tjuṯa Board of Management and Director of National Parks 2010).

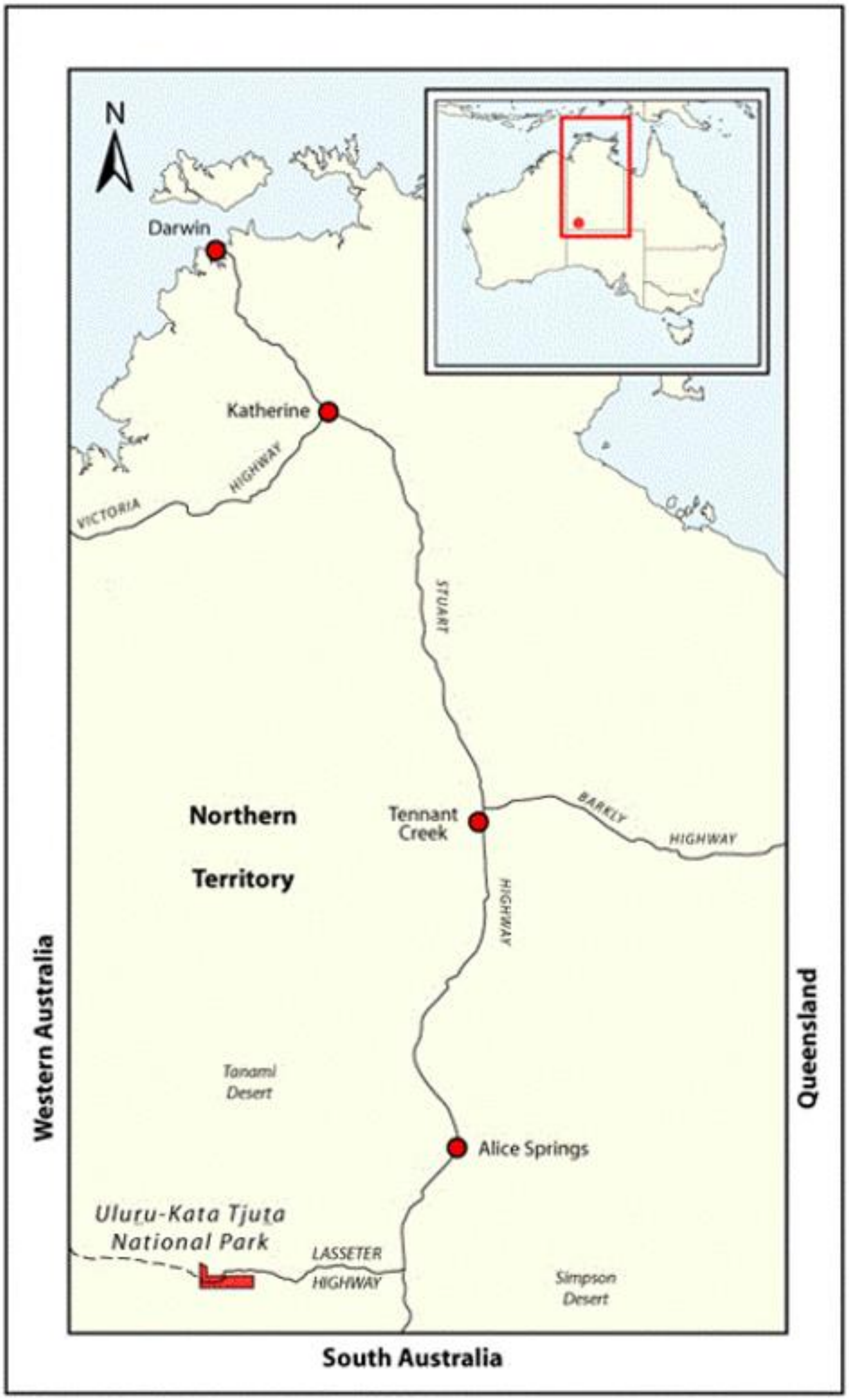
Climate

UKTNP is semi-arid, receiving an average of 290 mm of rain annually. While significant rainfall can occur at any time, the majority occurs in the warmer months associated with monsoonal weather patterns to the north (Reid *et al.* 1993). Rain events can also be extremely patchy across the desert landscape.

Unlike rainfall, temperature at UKTNP is quite predictable (Reid *et al.* 1993). The summer months experience hot days and mild to warm nights, with an average of 43 days above 40 degrees Celsius between October and April (Bureau of Meteorology 2017). Typically, cool to mild days and cold nights occur in winter, and frosts are not unusual (Bureau of Meteorology 2011, Reid *et al.* 1993.

Geology and landforms

UKTNP is situated within the Amadeus Basin geological region (English 1998a, Sweet and Crick 1992). The sandstone monolith Uluṟu and the conglomerate domes of Kata Tjuṯa rise to 340 m and 500 m above the surrounding plain, respectively, and are the Park's most significant topographic features (Uluṟu - Kata Tjuṯa Board of Management and Parks Australia 2000). They formed approximately 550 million years ago from material associated with the erosion of ancient mountains to the west (Sweet and Crick 1992). Although Uluṟu and Kata Tjuṯa visually dominate the landscape, dunefields and sandplains cover most of the Park (English 1998a, Johnson and Burbidge 2008, Reid *et al.* 1993, Uluṟu - Kata Tjuṯa Board of Management and Parks Australia 2000). The dunes reach heights of up to 13 m (Sweet and Crick 1992). In addition to these sand deposits, clay-rich red earths are found in both outwash areas associated with Uluṟu and Kata Tjuṯa and in dune swales across the greater Park (English 1998a, b).



The study area at Uluṟu - Kata Tjuṯa National Park in the southwest of the Northern Territory showing locations of major towns and (inset) location within Australia.

Flora and fauna

Consistent floristic patterns are found within the Park's sand dune and sandplain habitats (Buckley 1981). Vegetation is sparse on dune crests, and dense stands of thryptomene (*Aluta maisoneuveii*) occur on the midslopes (Buckley 1981, English 1998b). Lower dune slopes are dominated by spinifex (*Triodia* spp.), whilst the clayey sands of the outer swales support tussock grasses (Buckley 1981). The relatively higher soil moisture and greater microhabitat diversity associated with Uluṟu supports greater plant diversity than the surrounding sandplain and dune environments (Kerle 1995). Perennial grasses and sedges are found at semi-permanent waterholes, and water courses are lined with bloodwoods (*Corymbia opaca*; Kerle 1995). Kata Tjuṯa, where the complexity of the rock domes provides a wide variety of habitat types, is more floristically diverse than Uluṟu (Kerle 1995). The dominant woodlands in the national park comprise dense stands of mulga (*Acacia aneura*), especially on the heavier soils of the dune swales (Buckley 1981, English 1998b), and sizeable areas of mallee eucalypts (*Eucalyptus* spp.) also occur (Kerle 1995).

Twenty-one native and five introduced mammal species are found at UKTNP, as well as 178 bird species (Commonwealth of Australia 2019). With 77 species present, UKTNP has recorded a a richer diversity of reptiles per unit area than any other location within the Australian arid/ semi-arid zone (Reid *et al.* 1993). Dingoes (*Canis dingo*) are not controlled in the park, making UKTNP one of the few regional areas in Australia where dingo populations are left unhindered and relatively intact (Allen *et al.* 2011). The lack of dingo control reflects the wishes of A̲n̲angu (the local Aboriginal people) in a jointly managed park. As the dingo is an important ancestor in the region's creation stories and valued as a companion by Aboriginal communities, it has been protected, rather than controlled, in and around the park (Director of National Parks 2010).

Study sites

Historic

Chapters Two, Three and Four of this study involve analyses of a large data set spanning 16 years. Surveys were conducted at eight sites within the national park in 1994, 1995, 1997, 1999, 2000, 2002, 2004, 2006, 2008 and 2010 originally by the Commonwealth Scientific and

Industrial Research Organisation (CSIRO) and later by staff of the national park who replicated the sampling methods of CSIRO to maintain consistency. The sites were chosen to be representative of the major vegetation communities in the park, including soft and hard spinifex grasslands (*Triodia pungens* and *T. basedowii*, respectively), mulga (*Acacia aneura*), mallee (*Eucalyptus* spp.) and *Acacia ammobia* woodlands, drainage lines around Uluṟu and Kata Tjuṯa, and spinifex sand plain.

Contemporary

The contemporary study sites used for this study were within UKTNP boundaries. Four sites were randomly placed in each of the three major habitat types in the park—hard spinifex grasslands (*T. basedowii*), mulga (*A. aneura*) woodlands and mallee (*Eucalyptus* spp.) woodlands. Each site was in an interdune swale to negate the confounding effects of dune vegetation and topography, and each site was situated next to a vehicle track. Each site had two sub-sites, one located directly adjacent to a vehicle track and the other at least 1.5 km from the track.

Chapter Two - Literature Review: Drivers of ecological community structure in global and Australian deserts

1. Global deserts

Geographical extent and variety

Deserts occupy approximately a third of the world's land surface and occur on all continents. They are fundamentally differentiated from other ecosystems by their low rainfall and high potential evapotranspiration and are generally characterized by a lack of perennial vegetation (Mares 1999, Whitford 2002). The location of deserts across the globe depends on their latitude and their location according to the major global wind patterns; most deserts are found between 15° and 35° latitude, both north and south of the equator and within the southeastern and northeastern trade winds belt (Calow 2009). However, there is also a great variety of deserts around the world, in terms of climate, topography, dominant landforms and biota. They can occur below sea level or at high altitudes, along the coast or in the heart of a continent and can be very hot (>50 °C) or very cold (-40 °C) at their extremes (Mares 1999, Ward 2016).

The lack of rainfall in deserts is caused by a range of predictable climate processes that deny precipitation to these areas. The most common is caused by a desert's proximity to the tropics (sub-tropical deserts). Heated, moisture-laden air in the tropics rises and as it does the air cools and drops this moisture as tropical heavy rain. The cooler and drier air then moves away from the equator towards the poles and descends again with very low levels of humidity at around 30° north and south latitude. This process of global air movement is responsible for the widespread subtropical deserts, including those of northern and southern Africa, Australia and temperate North and South America (Mares 1999, Ward 2016). Aridity can also be triggered by cool offshore currents in coastal areas reducing the moisture carrying capacity of the chilled air that eventually reaches the coast. The moisture condenses as fog as it encounters land and causes dense fog banks along the coast, leaving little moisture available to fall as rain. These fog deserts include the Atacama Desert in Chile, the Namib Desert in southwestern Africa and the Baja desert in North America (Ward 2016, Mitchell *et al.* 2019). Rain shadows caused by mountain ranges or other geographical impediments can also cause enough aridity to produce deserts on the leeward slopes, and this process is responsible for deserts in North and South America, India and Afghanistan. Deserts located within vast continents can also be denied rainfall as moist air from the sea loses moisture on its journey across the land, resulting in inland deserts such as some in Central Asia and Australia and the Gobi Desert in China and Mongolia (Mares 1999, Ward 2016). Finally, in the freezing deserts of the Arctic and Antarctic, the extreme cold of the air prevents moisture condensing and therefore it cannot fall as rain (Mares 1999). In some deserts, a combination of several of these factors leads to reduced rainfall (Ward 2016).

Desert landscapes are generally characterized by either sand and sand dune systems, saline dominated soils or rock/stone dominated areas. Desert soils are characterized by low levels of nutrients and close resemblance to the underlying rock from which they form (Mares 1999). They are usually also low in organic matter, reflecting the general absence of vegetation above ground, with this organic matter concentrated in the first few centimetres of topsoil. The areas directly underneath and immediately surrounding patches of vegetation are generally higher in moisture and organic matter; these create small areas of fertility in otherwise austere and unproductive landscapes (Ward 2016).

Drivers of ecological community structure in global deserts

Virtually all ecological communities, including those inhabiting deserts, are structured by both 'top down' and 'bottom up' processes. When upper trophic levels have important influences on the rest of the community the effects are termed 'top down' and include mechanisms such as predation, competition, herbivory and human-made land uses including grazing by domestic livestock. When community structure is influenced primarily or even just for transient periods by the availability of resources such as nutrients, light, nesting sites, rainfall or decomposition and primary production rates, the effects are understood to be under the influence of ‘bottom up’ processes (e.g., Letnic *et al.* 2011a).

Bottom up processes in desert communities

Rainfall

Deserts are generally classified as hyperarid, arid or semi-arid depending on their average rainfall and often on the precipitation to evapotranspiration (P/ET) ratio (Whitford 2002). Hyperarid deserts have no season that is commonly associated with rainfall and on average receive less than 25 mm annually. Their P/ET ratio is <0.03. Arid deserts receive between 25 and 250 mm of rain annually and have a P/ET ratio of 0.03 – 0.19, while semi-arid deserts receive between 250 and 600 mm of rain annually and have a P/ET ratio of 0.20 – 0.49. Arid and semi-arid deserts are also characterized by long droughts (Mares 1999) and pulse rainfall (Mares 1999, Huxman *et al.* 2004, Schwinning *et al.* 2004, Sponseller 2007). Semi-arid areas exhibit moderate levels of consistent grass/shrub growth (Mares 1999).

Rainfall in deserts is highly variable (Ward 2016), both seasonally and spatially. Rainfall in the 'right' season can trigger a pulse of biological activity including plant growth, flowering and seeding (Vidiella *et al.* 1999, Brown 2002, Lotan and Izhaki 2003, Schwinning and Sala 2004, Davis *et al.* 2015, Li *et al.* 2015, Huang and Zhang 2016, Ward 2016). Rain that falls out of season may not cause this activity as annuals may be adapted to seasonal growth and can be morphologically unable to respond to rainfall outside their growing season (Brown 2002, Li *et al.* 2015, Ward 2016, Nafus *et al.* 2017), or the effect may vary according to landscape features (Li *et al.* 2013). The biological effect of a rainfall event may also be influenced by antecedent soil moisture levels and the grouping of plants, with different plant functional groups responding to the water differently due to 'the physiological and morphological readiness of the plant for water-uptake and growth' (Reynolds *et al.* 2004).

Desert rainfall patterns and their effect on water availability are an extremely important shaper of desert biotic communities. Rain potentially affects the abundance and distribution of fauna species that rely on ephemeral water sources (Hamilton 1985, Hamilton and Tilson 1985, Tilson and Henschel 1986, Hervert and Krausmann 1986, Kleuver *et al.* 2017), causes vegetation composition to differ depending on the amount of rain (Schwinning and Sala 2004) and promotes species that are tolerant to drought in low rainfall years (Baez *et al.* 2013).

Primary productivity and primary consumerism

The structure, composition and abundance of vegetation—which forms the primary productivity of deserts—influences the consumer species that rely upon it (Lhotan and Izhaki 2003, Ayal 2007, Nafus *et al.* 2017), providing both a food source and refuge. The level of plant growth triggered by rainfall influences the faunal community in many ways. These include, *inter alia*, restricting the abundance of primary and secondary consumers (Baez *et al.* 2006), influencing ant species richness (Davidson 1977) and the population dynamics of many other invertebrates (Kwok *et al.* 2016), and determining apex predator presence (e.g., birds and mammals in open areas, lizards in low vegetation and snakes and larger lizards in tall, dense vegetation, Ayal 2007). The timing of rainfall can also be an important factor. It is linked, for example, to juvenile growth in desert tortoises (Nafus *et al.* 2017) and mule deer (Heffelfinger *et al.* 2018).

In years of heavy rainfall, herbivore numbers may be too low to completely exploit the short-lived phases of high primary productivity caused by individual rainfall events, and excess vegetation falls to the ground as litter (Ayal 2007). This litter is gradually broken down by macrodetritivorous arthropods, perhaps explaining the higher biomass of macrodetritivores to all other animals in deserts (Ayal 2007). Macrodetritivorous arthropods are diverse in deserts and, together with ants, are the largest consumers of plant products (Whitford 2002) and the major energy conduit between plants and most desert predators (Whitford 2002). Termites are the most common macrodetritivores in deserts globally (Whitford 2002).

Nutrients

Nutrients in desert soils can affect the level of primary productivity in desert systems, altering plant growth and community structure and, in turn, the abundance and composition of consumer species that rely on green plants. The size of desert fruits (Lotan and Izhaki 2013), number of predatory and herbivorous insects (Schade *et al.* 2003) and the area of fertility around desert shrubs (Vinton and Burke 1995, Schlesinger *et al.* 1996, Schlesinger and Pimanis 1998) are determined by nutrient availability. Rainfall events also affect the availability of nutrients in desert soils, driving the cycling of carbon and other nutrients (Austin *et al.* 2004, Huxman *et al.* 2004) and levels of nitrogen leaching (Austin *et al.* 2004).

Top down processes in desert communities

Predation

The openness of the landscape makes predation a significant top down influence on desert ecological communities and ecosystem structure. It has driven diverse adaptations of prey species that enable detection and evasion of predators in the absence of places to hide (Krebs 1972, Calow 2009, Ward 2016). Predation can affect communities by direct loss of individuals through mortality and by the behavioural and lifecycle responses of prey that are catalyzed by the constant risk of predation (Kotler 1984, Taraborelli *et al.* 2003, Tabeni *et al.* 2012, Kotler *et al.* 2016). The most abundant predators in most deserts are arachnids and small reptiles (Ayal 2007) which prey largely on termites, ants and other invertebrates. Larger (secondary) predators generally include small mammals, birds, larger reptiles and, after rain, frogs. Except for frogs, this guild is relatively mobile and consequently its constituent species have access to a large range of prey options, including also the smaller predators and the invertebrates they prey upon (Ayal 2007).

Potential prey species use a range of strategies to reduce their risk of predation in deserts around the world. These include spending more time in burrows or refuge areas in the presence of predators (Nafus *et al.* 2015) or hiding in densely vegetated areas. Many nocturnal species preferentially forage in ‘covered’ microhabitats even if these offer poorer quality resources (Rosenzweig and Winakur 1969, Hughes *et al.* 1994, Kotler *et al.* 1994, Cowlishaw 1997, Bisceglia *et al.* 2011, Tabeni *et al.* 2012, Roschlau and Scheibler 2016), or avoid activity in the most brightly lit times of the night or under the lightest phases of the moon to reduce their risk of being detected by predators (Kotler 1984, Daly *et al.* 1992, Hughes *et al.* 1994, Brown *et al.* 1988, Upham and Hafner 2013). Exceptions to these general responses may occur during times of resource shortage such as in winter or when food caches are low (Myer and Valone 1999), or among diurnal species that visually detect danger (Schooley *et al.* 1996).

Morphological adaptations of desert species may also be driven by predation. In mammals, for example, these adaptations can range from larger body size to reduce predation risk (Kotler 1984), larger auditory bullae to hear predators at greater distances and thus increase the time available for escape (Kotler 1984, Kotler *et al.* 2016), bipedal locomotion to allow jumping, zig zag movements and increased speed to more effectively flee from predation (Kotler 1984, Taraborelli *et al.* 2003, Tabeni *et al.* 2012, Kotler *et al.* 2016), cheek pouches to increase the efficiency of foraging trips and reduce the number needed for maintenance (Kotler *et al.* 2016) and, in other vertebrates, development of camouflage (Nafus *et al.* 2015).

Herbivory/Frugivory/Granivory

Herbivory (the consumption of vegetative material), frugivory (the consumption of fruits) and granivory (the consumption of seeds) are considerable top down shapers of desert ecological communities. For desert animals, plants and their seeds and fruits are critically important, either directly (for primary consumers), or indirectly (for secondary consumers) (Mares 1999). On the one hand, the level of consumption of a plant species may affect its abundance and distribution and potentially lead to the complete removal of the species from the ecosystem. It may restrict commonly consumed species to areas inaccessible to herbivores (McAuliffe 1986, Ward and Saltz 1994), reduce plant biomass (Davis *et al.* 2015) or affect the distribution of invasive flora species such as woody weeds (Ryerson and Parmenter 2001). On the other hand, propagules of many plant species are dispersed by animals in the different trophic groups. Their success in both dispersal and subsequent germination may depend upon being consumed (Letnic *et al.* 2000, Dennis 2007).

Herbivory offers resources to consumers in the form of leaves, sap, flowers, stems, nectar and pollen, all providing varying nutrient and energy values. Roots also may be consumed, supporting diverse subterranean species (Mares 1999, Davidson *et al.* 2012). As growth in deserts is usually slow and linked to rainfall pulses (Austen *et al.* 2004), plants have developed adaptations to reduce their risk of herbivory. Defense strategies include the production of toxic chemicals and physical defenses like spines and thorns (Bucher 1987, Mares 1999). Some plant species use a combination of mechanisms to reduce their chance of being eaten (Mares 1999).

However, the defense mounted by an individual species can be inconsistent and dependent on the age of the plant (Rohner and Ward 1997) or ambient temperature (Kurnath *et al.* 2016). Herbivores may differ in their tolerance for defensive phytochemicals, both seasonally (Karasov 1989) and geographically (Borruel *et al.* 1998).

Seeds are an important food for many desert animals because they are abundant and provide a concentrated source of energy, nutrients and water (Mares 1999, Ward 2016). In addition, because seeds decompose very slowly, they can be stored by animals for use during winter or during periods of drought when other food sources are scarce, and many seeds remain in the soil and thus are available to granivores for years (Mares 1999, Vander Wall and Longland 2005). The most abundant desert granivores usually are ants, birds, and rodents (Mares and Rosenzweig 1978, Brown *et al.* 1979, Mares 1999), although marsupials can be important seed removers in Australia (Mills and Letnic 2018). Seeds are also consumed by desert insects other than ants, including weevils, moth larvae, and sucking bugs (Mares 1999).

Granivores and the dynamics of granivory vary amongst the world's deserts, and seed production can fluctuate enormously from year to year (Brown *et al.* 1979). Rodents remove 86% of the total seed production in North America but less than 1% in South Africa (Kerley and Whitford 1994), while ants are the main granivores in South Africa and South America (Kerley and Whitford 1994). Rates of seed consumption are higher in North America than in South America (Kelt *et al.* 1996). In both regions seeds are eaten at low rates by birds compared with ants and rodents. The dominant granivore can vary seasonally (de Casenave *et al.* 1998, Marone *et al.* 2000), and granivory rates often differ between different microhabitats in the same area (Marone *et al.* 2000). Heteromyid rodents dominate granivory in North America, foraging near burrows and locating subterranean seed by olfaction up to 20 cm underground and caching seed in moist soil pockets (Mares 1999, Jorgensen 2001). The relative lack of rodents in South American deserts (and complete absence of rodents specialised for feeding on seeds) is a phenomenon much discussed- with the extinction of specialized seed-eating rodents hypothesized by some (Mares and Rosenzweig 1978) and dismissed by others (Marone and Horno 1997, Taraborelli *et al.* 2009).

Many species of harvester ants are found in deserts (Davidson 1977, Capinera 2011). Most species forage during the day in cooler seasons and become crepuscular or nocturnal during hot weather (Mares 1999) and show short- and longer-term responses to rainfall (Gibb *et al.* 2018). Each individual ant collects one seed at a time and brings it back to the colony's nest for storage and they will either forage singly or in groups (Mares 1999, Capinera 2011). In contrast to harvester ants, which remain *in situ* for long periods, most granivorous desert birds are migrants that arrive to exploit periods of high seed production (Mares 1999); however, a few granivorous species are desert residents. Granivorous birds forage diurnally in deserts. They are adept at locating patches of seeds, and their mobility allows them to move between new patches rather than rely on storage of seeds, as do ants and rodents (Mares 1999).

Granivory is an important top down influence on the structure of desert communities. It alters vegetation composition and structure, often reducing the abundance of adults of favoured seed species and promoting species not targeted by granivores. Granivores affect the germination and survival rates of seeds, removing seeds both from the surface (Reichman 1979, Abramsky 1983) and from the soil seed bank (Abramsky 1983). As prey, the presence and abundance of granivores also reduces or increases populations of their consumers (Inouye *et al.* 1980, Thompson *et al.* 1991, Heske *et al.* 1993, 1994, Perrin and Boyer 1994, Price and Joyner 1997).

Compared to herbivory and granivory, frugivory is less common in deserts as the flora of desert ecosystems is generally not characterized by fleshy-fruited species compared with other biomes (for example 15%, 7% and 2% of species respectively in South Africa, Australian and Israeli deserts produce fleshy fruit: Dennis 2007). Correspondingly perhaps, frugivory features less in the literature as a driver of vegetation community structure for desert communities. However, where there are fruits, frugivorous species are implicated in determining the spatial structure, patchy distribution and levels of abundance of fruiting species (Bates 1992, Aukuma and Martinez del Rio 2002, Tews *et al.* 2004 in Dennis 2007, Green *et al.* 2009, Luna *et al.* 2016) including cacti, the genus *Acacia* and many mistletoes (Dennis 2007). Common frugivores in deserts include mammals (ungulates, canids, rodents and bats), birds, and some lizards and tortoises (Dennis 2007, Rojaz-Martinez *et al.* 2015) with some species selecting which fruit to eat based on fruit size (Luna *et al.* 2016).

Competition

Competition can be defined as "*two species using, or seeking to use, the same limited resource"* (Krebs 1972). Competition can lead to exclusion, where one species dominates one or more others, limiting the population sizes of the subordinate species or forcing them from a previously shared area altogether (Callow 2009). In these situations, selective pressure may drive behavioural or morphological adaptations that reduce direct competition and facilitate resource partitioning (the differential use of resource types). Partitioning effectively expands the number of niches available and allows otherwise similar species reliant on the same resources to co-exist (Krebs 1979, Callow 2009, Ward 2016). Conversely, the removal of a superior competitor can expand the resources available to inferior competitors and allow them to grow in number, a process called 'competitive release' by Hardin (1960) and later commentators (e.g., Callow 2009).

Competition is a top down driver of structural differences in desert communities. Competition from one species to the detriment of another has been demonstrated in desert grasslands (Brown and Heske 1990, Heske *et al.* 1993, Brooks 2000, Brooks *et al.* 2001), shrublands (Carrick 2003, Schleicher *et al.* 2011) and among granivores (Brown *et al.* 1979, Davidson *et al.* 1984, Brown and Munger 1985, Heske *et al.* 1994, Abramsky *et al.* 2001), carnivores (Walker *et al.* 2007) and herbivores (Marshall *et al.* 2008). Behavioural or morphological adaptations to minimize competition have been widely demonstrated in deserts, including via temporal partitioning (Abramsky *et al.* 2001), prey selection (Walker *et al.* 2007), root depth differences among similar shrubs (Carrick 2003), differences in body size affecting seed size choice (Brown *et al.* 1975, Davidson 1977, Samson *et al.* 1992), preferential microhabitat use (Brown *et al.* 1979, Mares 1999), the use of torpor (Brown *et al.* 1979), the utilisation of different size seeds (Brown *et al.* 1975, Davidson 1977, Brown *et al.* 1979, Brown and Munger 1985, Heske *et al.* 1994, Mares 1999) and different harvesting strategies (Brown *et al.* 1972). Although much research focused on the importance of competition from the 1970s to the 1990s, attention to this top down process has diminished in recent years as the importance of other processes has been recognised, as noted in recent reviews of desert mammals by Fox (2011), Kelt (2011) and O'Connell and Hallett (2019).

Introduced species

When introduced species establish in desert systems, the flow-on effects can alter the structure of ecological communities by displacing native species, disrupting nutrient cycling and changing fire patterns and behaviour (Rogstad *et al.* 2009). Invasive species intrusion in deserts has been shown to reduce resource availability for native fauna (Marshall *et al.* 2008, Drake *et al.* 2016, Gill *et al.* 2018) and change the composition of flora (Barrows *et al.* 2009, Schachtschneider and February 2013, Chambers *et al.* 2017). Similar effects have been documented in riparian and marine communities (Kennedy *et al.* 2005).

Invasive species are commonly implicated in altering desert fire regimes and thereby directly affecting the structure of desert communities (e.g., Schlesinger *et al.* 2013). Encroachment of invasive grasses increases fuel loads and fuel connectivity across deserts where fuel loads should be naturally low and patchy (Brooks and Pyke 2002, Rogstad *et al.* 2009, Lambert *et al.* 2010, Klinger and Brooks 2017) and the subsequently altered fire regime can promote the establishment of invasive species (Rogstad *et al.* 2009, Klinger and Brooks 2017, Gill *et al.* 2018), particularly in the first few years post fire (Gill *et al.* 2018).

The introduction of grazing animals to desert systems is another potential top down process that has been found to alter the structure of desert ecological communities (Asner *et al.* 2004), including in Mongolia (Wesche *et al.* 2010), the United States of America (Ryerson and Parmenter 2001, Rogstad *et al.* 2009), Argentina (Bucher 1987, Peinetti *et al.* 2011), Mexico (Kerley and Whitford 2000, Bender and Piasecke 2015, Espinoza *et al.* 2017) and China (Zhang *et al.* 2018). Low levels of grazing can occasionally be beneficial to native communities by reducing weeds (Germano *et al.* 2012), increasing native plant cover (Bender and Piaseke 2015), helping to maintain open habitats preferred by some fauna species (Ponce-Guevara *et al.* 2016) and reducing the risk of wildfire (Chambers *et al.* 2017). However, overgrazing is generally detrimental to native species communities because of reduced vegetation cover (Espinoza *et al.* 2017, Zhang *et al.* 2018) and increasing woody weed abundance (Asner *et al.* 2004, Rogstad *et al.* 2009, Ponce-Guevara *et al.* 2016), although these effects are sometimes dependent on the dominant plant species (Ryerson and Parmenter 2001) or species of grazing herbivore (Pienetti *et al.* 2011).

2. Australian deserts

Geographical extent and variety

Australia is the second driest continent in the world (only Antarctica is drier), with 70% of the mainland receiving less than 500 mm rainfall annually (Mares 1999). Deserts in Australia are distributed across most of the inland and are found in the Northern Territory, Queensland, Western Australia, South Australia and New South Wales. Defined as areas receiving on average less than 250 mm rainfall a year, there are 10 deserts in Australia—the Great Victoria, Great Sandy, Tanami, Gibson, Little Sandy, Simpson, Strzelecki, Sturt Stony, Tirari and Pedirka—covering a combined total of 1 371 000 km^2 (Geoscience Australia, 2019). Multiple factors converge on the Australian continent to reduce precipitation and produce deserts, including its position at subtropical latitudes and the vastness of the continent- circulating air has generally lost most of its moisture by the time it reaches the centre (Morton *et al.* 2011).

Drivers of ecological community structure in Australian deserts

<u>Bottom up processes in Australian desert communities</u>

Rainfall

Rainfall is a powerful shaper of Australian desert systems as the pulse rainfall generally stimulates growth of perennial plants, the germination and growth of annual plants, and subsequent flowering and seeding (Nano and Pavey 2013). Floods produced by distant, off-site, rainfall can trigger similar growth events (Letnic and Dickman 2010). Rainfall-driven pulses of productivity are a primary determinant of the abundance of primary consumers, including many herbivores and detritivores such as termites (Abensperg-Traun 1994). Increased productivity also drives short-term increases in the abundance of other primary and secondary consumers, including mammals (Newsome and Corbett 1975, Masters 1993, Southgate and Masters 1996, Dickman *et al.* 1999a, 2001, 2010, 2011, Letnic 2003, Letnic *et al.* 2004, Letnic *et al.* 2005, Breed and Ford 2007, D'Souza *et al.* 2013, Greenville *et al.* 2013, Pavey and Nano

2013), invertebrates (Paltridge and Southgate 2001, Letnic *et al.* 2004, Kwok *et al.* 2016), birds (Paltridge and Southgate 2001, Pavey and Nano 2013, Tischler *et al.* 2013), frogs (Paltridge and Southgate 2001) and reptiles (Dickman *et al.* 1999b). Highly mobile species such as birds can move into areas within days after rainfall (Tischler *et al.* 2013); some species of small mammals make directed movements of several kilometres to access fresh resources (Dickman *et al.* 1995, Letnic 2002) after rain. Although rainfall is a powerful driver of productivity increases, the responses by consumers are sometimes inconsistent. Several studies have shown that rainfall does not always trigger increases in populations of mammals (Masters 1993, Dickman *et al.* 1999a, Paltridge and Southgate 2001, Letnic 2003, Letnic *et al.* 2004) or reptiles (Paltridge and Southgate 2001), especially if populations are constrained by other factors (e.g., predation) or are at such low density that rapid responses are precluded (Dickman *et al.* 1999a).

Primary productivity and primary consumerism

The structure and abundance of vegetation—forming the primary productivity of deserts—influences the composition of faunal communities in Australia's arid areas. Plant species richness and cover can influence the abundance of many vertebrate species, including small mammals (Letnic *et al.* 2005, Letnic and Ripple 2017), limiting the population growth of some species (Predavec 2000), affecting herbivore numbers (Letnic and Ripple 2017), and sometimes influencing populations of secondary consumers such as insectivores via complex interactions with other environmental factors (Greenville *et al.* 2016).

Among invertebrates, termites are common primary consumers in Australian deserts. Their abundance can affect the structure and numbers of insectivorous species living in local areas by providing an important food source. For example, termites form part of the diets of many lizards (Colli *et al.* 2006, Pianka and Goodyear 2012, Abensperg-Traun 1994) and some mammals (Abensperg-Traun 1994), with their importance in the diet in some cases being influenced by fluctuations in season (Abensperg-Traun 1994) or the activity levels of foraging species (Bergallo and Rocha 1994). Morton and James (1988) proposed that termite diversity underpins the very high richness of lizard species in arid Australia and this hypothesis was subsequently tested in the Brazilian Cerrado, an arid savannah in central Brazil. While lizards ate large amounts of termites in this study, there was no partitioning of this resource by different lizard species (Costa *et al.* 2008) Pianka (1989) also disputed the Morton and James hypothesis and suggested that suites of other factors are also important including the mosaic effect on habitat diversity driven by fire.

Fire

Fire can affect the composition of ecological communities in Australia's desert systems. In spinifex dominated habitats in central Australia, fire removes above-ground vegetation with return intervals of around 20 – 30 years (Latz 1995) varying with fire severity (Wright and Fensham 2017). These often large scale events (e.g., covering thousands of square kilometres) are followed by post-fire recovery involving a predictable succession of plant species, beginning with herbs and grasses, followed by spinifex which becomes dominant again after 5 – 10 years when enough rain has fallen (Latz 1995, Allen and Southgate 2002, Southgate and Carthew 2008, Nguyen *et al.* 2015). Fire affects the abundance of small mammals and other small vertebrates by the removal of food resources but even more by providing free passage through the landscape for carnivorous predators and reducing refuge and hiding areas (Sutherland and Dickman 1999, Letnic *et al.* 2013, McDonald *et al.* 2016). Fire also reduces the abundance of invertebrates (Pianka and Goodyear 2012) and some reptile and mammal species while increasing the abundance of others (Pianka and Goodyear 2012, Letnic 2002, 2003, Masters 1993, Letnic *et al.* 2004, McDonald *et al.* 2016).

Top down processes in Australian desert communities

Predation

Among mammals, the three most important predators in structuring Australian desert systems are the dingo (*Canis dingo / familiaris*), the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*). While all three species are introduced, the dingo has been present for approximately 3500-4000 years (Dickman 1996a, b, Burrows *et al.* 2003, Burrows 2018). The cat and fox are more recent arrivals (Burrows *et al.* 2003), the cat being introduced around 200 years ago (Dickman 1996a, b) and the red fox in 1871 (Dickman 1996a, b). The three species are widespread and have overlapping diets (Paltridge 2002, Pavey *et al.* 2008, Woinarski *et al.* 2018) although dingoes tend to eat larger items more frequently (Paltridge 2002, Spencer *et al.* 2014) while foxes and cats consume smaller prey preferentially (Martin *et al.* 1996, Paltridge 2002, Spencer *et al.* 2014).

These species have been widely demonstrated to influence the composition of desert ecosystems. Feral cats are linked to a decline in abundance or the local or complete extinction of many arid zone mammal species (Short and Smith 1994, Dickman 1996b, Short *et al.* 1999, Risbey *et al.* 2000, Burrows *et al.* 2003, Johnson 2006, Woinarski *et al.* 2015, MacDonald *et al.* 2016, Pedler *et al.* 2016, Doherty *et al.* 2017, Greenville *et al.* 2017, Legge *et al.* 2017) and preventing their reintroduction back to areas where these species once were common (Short and Smith 1994, Christensen and Burrows 1995, Dickman 1996b, Moseby *et al.* 2011, Spencer *et al.* 2014, Clayton *et al.* 2014, Hardman *et al.* 2016). Dingoes in arid areas can suppress the abundance of herbivores, particularly introduced domestic stock (Short *et al.* 2002, Letnic and Ripple 2017, Campbell *et al.* 2019, Doherty *et al.* 2019) and macropods (Letnic and Ripple 2017, Rees *et al.* 2017, McDonald *et al.* 2018). Foxes can reduce the abundance of their mammalian prey (Dickman 1996a, Burrows *et al.* 2003) particularly as they have been found to kill in surplus of their nutritional requirements (Short *et al.* 2002). Foxes and cats in Australian deserts have also been shown to prey commonly on reptiles (Martin *et al.* 1996, Paltridge *et al.* 1997, Short *et al.* 1999, Read and Bowen 2001, Paltridge 2002, Burrows *et al.* 2003, Woinarski *et al.* 2018, Read *et al.* 2019) and cats on birds (Martin *et al.* 1996, Paltridge *et al.* 1997, Short *et al.* 1999, Read and Bowen 2001, Woinarski *et al.* 2017) and macropods (Marlow *et al.* 2015, Read *et al.* 2019). All three species can take advantage of increased prey populations by moving into an area during population booms (Pavey *et al.* 2008). Other predators in Australian deserts shown to affect the abundance or distribution of native species include raptors (Pavey *et al.* 2008, Moseby *et al.* 2011) and reptiles (Moseby *et al.* 2011).

Like deserts in other parts of the world specific traits in prey species may have resulted from selective pressure caused by carnivorous predators. This may include the bipedal gait of spinifex hopping-mice (*Notomys alexis*) which enable them to run fast and with a zig zag motion to avoid predation (Murray and Dickman 1994b).

Herbivory/Granivory

Among vertebrates, there are relatively few species of native herbivore in the deserts of Australia, with members of the kangaroo family—Macropodidae—being the most numerous, particularly the red kangaroo (*Osphranter rufus*). Macropods shape desert communities by reducing the biomass and abundance of preferred grasses (Verdon *et al.* 2016, Letnic and Ripple 2017, Rees *et al.* 2017) which in turn can limit the populations of granivores by reducing the amount of grass seed available (Rees *et al.* 2017). In contrast, granivory is common with ants the dominant granivores (Morton 1985, Kerley and Whitford 1994, Kelt *et al.* 1996, Predavec 1997), followed by birds (Morton 1985, Kelt *et al.* 1996, Predavec 1997, Franklin *et al.* 2000) and to a lesser extent, mammals (Predavec 1997, Morton 1985, but cf. Mills and Letnic 2018). Granivores in Australian deserts mostly consume grass seeds (Morton and Davies 1983) affecting their biomass and availability (Letnic *et al.* 2018); however, the types of grass eaten can depend on dietary and habitat preferences (Murray and Dickman 1994a, b) and size of the granivore (Morton and Davies 1983). Omnivores also rely on granivory as a main feeding strategy in Australian deserts, using seed seasonally when available (Murray and Dickman 1994a, b).

Introduced species

Introduced species other than the predators noted above also play a role in shaping the structure of ecological communities in Australian deserts. Introduced feral herbivores are largely found in the most productive arid areas (Southgate *et al.* 2007). Rabbits (*Oryctolagus cuniculus*) in Australia have depleted vegetation communities in many areas, affecting the extent of occurrence and occupancy of native fauna (Pedler *et al.* 2016) and flora species (Munro *et al.* 2009, Mutze 2017). Grazing by introduced camels (*Camelus dromedarius*) and cattle (*Bos taurus*) dominates the herbivore assemblage in many arid areas (Frank *et al.* 2016). Cattle grazing can alter plant species richness (Haby and Brandle 2018), and camels negatively impact the growth of many woody species of native plants (Brim Box *et al.* 2016).

3. Mesopredator release theory - international literature

Owing to the importance of top down predation in arid Australia, most notably from the region's mammalian predators (see above), and to the attention given to the effect of predation in some aspects of this thesis, I discuss in the concluding sections of this chapter a relatively recently-emerged concept in predator ecology: that of 'mesopredator release'. The theoretical framework underpinning this concept requires two or more predator species to co-occur in a local or regional area: one of these can be characterized as a dominant or top order (and usually large) predator, and the other (usually smaller) predator (or predators) as a 'mesopredator'. The concept of mesopredator release is of interest in the Australian context due to the possibility that the deleterious impacts of two recently introduced mammalian predators (the red fox and feral cat) could be reduced in the presence of the top predator (dingo). This three-species interaction has potentially important implications for management in arid systems, and these are taken up later in this thesis.

When the highest order and dominant predator is removed from an ecosystem it can lead to an increase in the numbers (or ‘release’) of lower order predators (i.e. the mesopredators). This is the mesopredator release theory (Soulé *et al.* 1988, Estes 1996, Crooks and Soulé 1999). The removal of an apex or top predator from an ecosystem can have landscape scale consequences that range from changes in carbon sequestration (Estes *et al.* 2011, Ripple *et al.* 2014) to hyper-herbivory (Ripple and Larsen 2000, Beschta 2003, Ripple and Beschta 2004, Estes *et al.* 2011, Letnic *et al.* 2012, Lyons *et al.* 2018) and changes in vegetation structure and communities (Soulé *et al.* 1988, Estes 1996, Crooks and Soulé 1999, Ripple and Larsen 2000, Beschta 2003, Ripple and Beschta 2004). The loss of a top predator can also lead to an increase in the abundance and distribution of smaller, lower order mesopredators that had hitherto been suppressed by their apex counterpart, and a consequential increase in pressure on vulnerable prey species at lower levels in the food web (Soulé *et al.* 1988, Estes 1996, Crooks and Soulé 1999) - a phenomenon that has been demonstrated in a diverse range of terrestrial and marine ecosystems around the world (Schaller 1972, Rudzinski *et al.* 1982, Mills and Biggs 1993, Palomares *et al.* 1994, Strong *et al.* 1996, Mills and Gorman 1997, Soulé *et al.* 1988, Courchamp *et al.* 1999, Crooks and Soulé 1999, Henke and Bryant 1999, Palomares and Caro 1999, Fedriani *et al.* 2000, Soulé *et al.* 2005, Estes *et al.* 2011, Ripple *et al.* 2013).

The mechanism of mesopredator release can vary. Intraguild predation (the higher order predator hunting and consuming the lower order predator) has been demonstrated in carnivores throughout the world, including among canids (Palomares and Caro 1999, Fedriani *et al.* 2000, Krofel *et al.* 2017) and felids (Palomares and Caro 1999), with the red fox being the most common victim (Palomares and Caro 1999). Coyotes (Soulé *et al.* 1988, Crooks and Soulé 1999, Henke and Bryant 1999), wolves (Soulé *et al.* 2005), feral cats (Courchamp *et al.* 1999), Iberian lynx (Palomares *et al.* 1994) and lions and hyenas (Creel 2001) are superior competitors in many situations that have been studied, denying smaller co-occurring mesopredators a share of the finite resources and thereby restricting their population sizes and distributions. Predator avoidance and temporal separation (where a mesopredator adjusts its behaviour and distribution to avoid encountering an apex predator) has been widely demonstrated amongst carnivores, including bobcats avoiding coyotes (Fedriani *et al.* 2000), cheetahs avoiding lions (Schaller 1972, Mills and Biggs 1993, Mills and Gorman 1997), arctic foxes avoiding red foxes (Rudzinski *et al.* 1982), red foxes avoiding wolves (Haswell *et al.* 2018) and little owls avoiding tawny owls (Michel *et al.* 2016).

Despite such examples, however, the ubiquity of mesopredator release is debated. It has been challenged on the grounds that much evidence is based on weak inference (e.g., Gehrt and Clark 2003, Hayward and Marlow 2014). There is, in addition, increasing recognition that the effects of top predators on mesopredators may vary over time (Piovia-Scott *et al.* 2017) and space (Newsome *et al.* 2017). Variation in the shared environment of the mesopredator and apex predator can also influence the relationship dynamic. This may include changes associated with the moon phase (Penteriani *et al*. 2013), differences in resources available to the mesopredator (Pasanen-Mortensen *et al*. 2017, Haswell *et al.* 2017) over time and with the specific identity of the interactants (Donadio and Buskirk 2006). Human induced landscape change can add further variability to the effect of predators on mesopredators with the expansion of grazing lands (Pasanen-Mortensen *et al*. 2017), changes in forest density and habitat connectivity (Kammerle *et al*. 2017) and differences in the level of hunting by humans

(Haswell *et al.* 2017) all potentially altering the ‘natural’ interplay between the apex and mesopredator.

4. Mesopredator release theory - Australian literature

Similar debate attends the concept of mesopredator release in terrestrial Australian systems, particularly with respect to the effect of the dingo in suppressing two species of introduced mesopredator, the red fox and feral cat.

Intraguild predation between dingoes and foxes and dingoes and cats has been shown in central (Marsack and Campbell 1990) and north-west (Thomson 1992) Western Australia, north-eastern Victoria and south-eastern New South Wales (Newsome *et al.* 1983). Dingoes have also been shown to eat cats in the southern Northern Territory (Eldridge *et al.* 2002, Paltridge 2002, McDonald *et al.* 2018). Dingoes have been found to restrict the abundance and distribution of foxes by successfully competing for shared resources. Dingoes prefer large mammals and foxes prefer smaller prey (Johnson 2006), but there is still considerable overlap in the diet of the two species (Paltridge 2002, Mitchell and Banks 2005, Johnson 2006) and this overlap leads to competition. Dingoes restrict the distribution and abundance of foxes (Corbett 1995, Eldridge *et al.* 2002, Glen *et al.* 2007) and cats (Corbett 1995) in central Australia by excluding them from carcasses and waterholes. Cats and foxes may avoid dingoes by using closed or heavily vegetated areas away from open tracks, or being active at different times, to reduce the risk of encountering a dingo (Edwards *et al.* 2002, Eldridge *et al.* 2002, Algar and Burrows 2004, Wang and Fisher 2012, Schroeder *et al.* 2015). Several studies report an inverse relationship between dingo and fox abundance (Jarman *et al.* 1987, Lundie-Jenkins *et al.* 1993, Smith and Quin 1996, Newsome *et al.* 1997, Kinnear *et al.* 1988, Newsome *et al.* 2001, Brawata and Neeman 2011, Letnic *et al.* 2011, 2012, Greenville *et al.* 2014, Moseby *et al.* 2018) and dingo and cat abundance (Jarman *et al.* 1987, Lundie-Jenkins *et al.* 1993, Pettigrew 1993, Gibson *et al.* 1994, Christensen and Burrows 1995, Dickman 1996a, Brawata and Neeman 2011, Brooke *et al.* 2012, Greenville *et al.* 2014, Moseby *et al.* 2018) without exploring the possible mechanism(s) behind the phenomenon.

However, conflicting or ambiguous results have also been published, suggesting that dingoes may not always exert suppressive effects on mesopredators (Catling and Burt 1995, Fleming 1996, Paltridge 1997, Newsome *et al.* 2001, Algar and Burrows 2004, Mitchell and Banks 2005, Allen *et al.* 2015, Schroeder *et al.* 2015). Some studies note that the relationship between foxes, cats and dingoes can vary with habitat, season, level of resource availability and other local situations (Glen *et al.* 2007, Claridge and Hunt 2008, Allen *et al.* 2011, Brook *et al.* 2012, Kennedy *et al.* 2012, Wang and Fisher 2012, Newsome *et al.* 2013, Greenville *et al.* 2014). Dingoes are controlled over large areas of Australia, and this may reduce their abundance to levels below which any effects they have on foxes and cats are muted or difficult to discern (e.g., Newsome *et al.* 2017).

Predation by foxes and cats is considered a key driver of native mammal decline in Australia (Johnson 2006, Woinarski *et al.* 2015) and the primary reason for the failure of many reintroduction programs (Clayton *et al.* 2014). A protective effect of dingoes on native fauna has been shown (Lundie-Jenkins *et al.* 1993, Short and Smith 1994, Short 1998, Fleming *et al.* 2001, Meek and Shields 2001, Short *et al.* 2002, Department of Natural Resources and Mines 2006, Johnson *et al.* 1996, Rees *et al.* 2018, Geary *et al.* 2018), and many researchers support the reintroduction of dingoes where they are locally extinct (Dickman *et al.* 2009, Newsome *et al.* 2015). However, other studies report no protective effect of dingoes on prey (Allen *et al.* 2014) or note that dingoes may themselves have negative effects on native fauna (e.g., Allen and Fleming 2012), and advocate caution in making changes to dingo management. In consequence, there is much interest in understanding whether foxes and cats are ‘released’ and increase predation pressure on small prey species in areas where dingo control is undertaken (Newsome *et al.* 2015). The need for scientific, controlled experimental data to test the mesopredator release hypothesis, especially in Australia, is widely acknowledged (Estes 1996, Johnson 2006, Crooks and Soulé 1999, Glen and Dickman 2005, Glen *et al.* 2007).

In the following chapters that explore relationships between the desert environment, vegetation communities and native fauna in the study region at UKTNP, I further explore the relationship between the three mammalian predators in the broader UKTNP environment.

5. Conclusion

This chapter has synthesized much of the available information on the forces that may shape fauna communities in arid zones in Australia. The interactions between these possible drivers of change are likely extremely complex, often likely to be locally specific and difficult to tease out without long term studies of flora and fauna of the area.

The chapters of this thesis attempt to do this for one arid zone area, Uluṟu Kata Tjuṯa National Park. Long term studies, albeit imperfectly designed, are available for this park and are analysed in the first 3 chapters to look for broad patterns in community structure and what the role of the top down drivers, rainfall and fire may have had in shaping these communities over time.

The later chapters use shorter studies to examine the influence of other bottom up and top down drivers on the fauna of Uluru-Kata Tjuta National Park, including the role played by predators and the local availability of resources.

Chapter Three - Historical habitat use and spatial distribution of native vertebrates at Uluru-Kata Tjuta National Park

Introduction

As shown in Chapter Two, deserts can be highly dynamic environments, influenced by a variety of top down and bottom up processes that may, in any given period, affect the range of species that occur in local and regional areas (Chapter Two). Resource pulses driven by intermittent rainfall can temporarily change the structure and species compositional profile of these areas, as can the numbers of primary consumers and varying levels of predation.

However, differences in the vegetation community and the resources they offer are also likely to influence the species composition of consumers (Morton *et al.* 2011).Deserts are also often mosaics of a range of vegetation communities including grasslands, woodlands and richer mesic areas (Burquez *et al*. 1999, Poulos and Camp 2010). These different habitats may contain a fauna community shaped wholly or partially by the inherent properties of the vegetation itself such as structural complexity and the provision of refuge areas, providing the niche requirements of the species. In this instance, the vegetation characteristics account for the makeup of the fauna community regardless, or as well as, the temporal fluctuations in top down and bottom up influences. For example, in the small mammal communities of deserts in New Mexico, habitat preferences and foraging differences shaped the community of small mammals across habitat types rather than competition between similar species (Hallett 1982). In the deserts of India, some small mammal species show preferences for particular habitat features such as interdune areas or rocky habitats, while others are more generalist (Idris 2009) with abundance, rather than community composition, changing with rainfall. In contrast, habitat type did not account for the abundance or species richness of avian fauna in the Tanami desert in Australia, rather the influence of changing seasonal conditions structured the community (Paltridge and Southgate 2001)

Given the dynamic nature of desert environments and the difficulty with differentiating the influence of habitat type versus seasonal fluctuations, short-term or 'snapshot' surveys of biota are unlikely to uncover the range of species that occur or to provide much insight into the fluctuations in species' populations or their habitat associations. Long-term monitoring is required for these purposes (Legge *et al.* 2018). A valuable potential use for long-term datasets is to allow us to see desert habitats in good times and bad, through intermittent rainfall, droughts and fire. With them, we can study the structure of resident animal populations, the influence of immigration from newly resident species arriving to exploit resource pulses, and the changeable patterns of recruitment that arise from breeding in times of plenty and times of scarcity.

Once Uluṟu-Kata Tjuṯa National Park (UKTNP) was established in 1985, the Commonwealth Scientific and Industrial Research Organisation (CSIRO) initiated a series of surveys, from 1987 to 1991, that identified and catalogued resident fauna in eight sites, chosen to reflect the range of vegetation communities in the park. After the CSIRO surveys ended (see Reid *et al.* 1993 for a summary of the original survey results) park staff and consultants continued the survey program, and eventually built a 16-year dataset. This chapter provides one of the first analyses of that dataset.

The aim of this chapter is to examine the structure of fauna communities in the mosaic of vegetation types found within the UKTNP, omitting for now the influence of environmental fluctuations. This chapter examines the relationship between fauna and individual vegetation types over time to see if the fauna community is consistent within a particular vegetation type, or if, even within the vegetation type, there are temporal changes suggesting the influence of other factors such as the top down and/or bottom up drivers of fauna community structure outlined in Chapter Two.

Using these survey data, Chapter Three investigates the following hypotheses:

H1. Animal assemblages will differ between vegetation communities at UKTNP,

H2. Vegetation type is a key determinant of the species of birds, mammals and reptiles that occur in each site at UKTNP, and

H3. Animal assemblages remain consistent within a vegetation community over time.

Methods

Study sites

Surveys were conducted at eight ~1 × 1 km sites in 1994, 1995, 1997, 1999, 2000, 2002, 2004, 2006, 2008 and 2010. Except for one survey conducted in March 1995, all surveys were carried out in spring (October and/or November). Sites were selected a priori, originally by the CSIRO's Division of Wildlife and Ecology between 1987 and 1990 for ecological surveys of the vertebrate fauna of UKTNP (Reid *et al.* 1993). Site selections were based on having 1 site in each of the park's 6 major land classes: alluvial fans at Uluṟu, alluvial fans at Kata Tjuṯa, sedimentary foothills at Kata Tjuṯa, mulga shrubland, soft spinifex, and hard shard spinifex. An additional 2 sites in the soft spinifex land class included the distinctive vegetation types of mallee (*Eucalyptus gamophylla*, *E. mannensis*, *E. socialis*, and *E. oxymitra*), and *Acacia ammobia* open woodlands. The closest distance between sites was 5 km. and including two additional distinct vegetation types, *Eucalyptus sp*. woodlands and *Acacia ammobia* woodlands (Table 3.1 and Fig. 3.1, Appendix 2).

Climate

UKTNP receives, on average, 290 mm of rainfall a year, predominantly in summer; temperatures range from below freezing on winter nights to >40 °C in summer (Bureau of Meteorology 2010). Major rainfall years (> 400 mm) were experienced in 2000, 2002 and 2010, with below average years in surveys prior to 2000 and in 2008. Wildfires occur commonly in UKTNP, and were widespread in 2002, 2004 and 2006. Climate, and the effects of rainfall and fire, are considered in more detail in Chapter Four.

Field sampling

Trapping effort for mammals and reptiles at each site consisted of 250 aluminium 'Elliott' type-A traps (33 × 10 × 10 cm) and 36 pitfall traps (20-L plastic buckets). Elliott traps were arranged in 10 rows of 25 traps, with each trap separated by 20 m. Four arrays of pitfall traps were set in each site, each arranged in a cross formation with a central pitfall bucket surrounded by four 'arms', each with two buckets spaced 5 m apart (i.e., 9 pitfall traps formed an array). A drift fence of wire mesh, 30 cm high, ran between each bucket to increase the chance of animals encountering a trap.

Table 3.1. Dominant vegetation of eight fauna survey sites, Uluṟu–Kata Tjuṯa National Park. Sites selected a priori to encompass the different land units and distinct vegetation types in the park.

Site No	Vegetation Description
1	The northern boundary of Site 1 abuts the southern edge of Uluṟu itself. The site is a complex of communities including woodlands dominated by *Acacia aneura* and *Corymbia opaca* with understories of *Themeda avenacea* and shrubs including *Santalum lanceolatum* and *Dodonaea viscosa.* Site 1 includes Ikari waterhole at the base of Uluṟu, and experiences varying levels of incursion of the weed *Cenchrus ciliaris*.
2	Dominated by extensive *A. aneura* woodland with a diverse shrub layer that includes *Eremophila gilesii, E. latrobei, Acacia kempeana, Canthium attenuatum* and *Senna* spp.
3	Dune fields dominated by *Triodia pungens* with a scattered overstorey of *Allocasuarina decaisneana* and a shrub layer including *Acacia dictyophleba*, *Thryptomene maisonneuvii*, *Grevillea eriostachya*, *Hakea divaricata*, *Rulingia loxophylla* and *Keraudrinia integrifolia*. Dune top vegetation includes *Aristida* spp., *Ptilotus* spp., *Grevillea stenobotrya*, *Eremophila gibsoni*, *Crotalaria* spp. and *Acacia* spp.
4	Dune fields dominated by *Triodia basedowii* with sparse *A. decaisneana* and *Acacia pruinocarpa* above shrubs including *G. eriostachya*, *Aluta maisonneuvei* and *A. dictyophleba.*
5	Mallee woodland consisting of *Eucalyptus gamophylla*, *E. mannensis*, *E. oxymitra* and *E. socialis* with an understorey of *Triodia* spp.
6	Dune complex dominated by *Acacia ammobia* and interdune fields dominated by *A. aneura* with an understorey of *Triodia* spp.
7	Expansive sand plain dominated by extensive *T. basedowii* with a sparse overstorey of *A. decaisneana*.
8	On a drainage line running from the northern edge of the Kata Tjuṯa domes, this site contains riparian communities of *Melaleuca glomerulata* and *Eucalyptus camaldulensis*, woodlands and shrublands including *A. aneura*, *A. tetragonophylla*, *H. divaricata*, *Eremophila longifolia* and *Stemodia viscosa.* There are incursions of *C. ciliaris*.

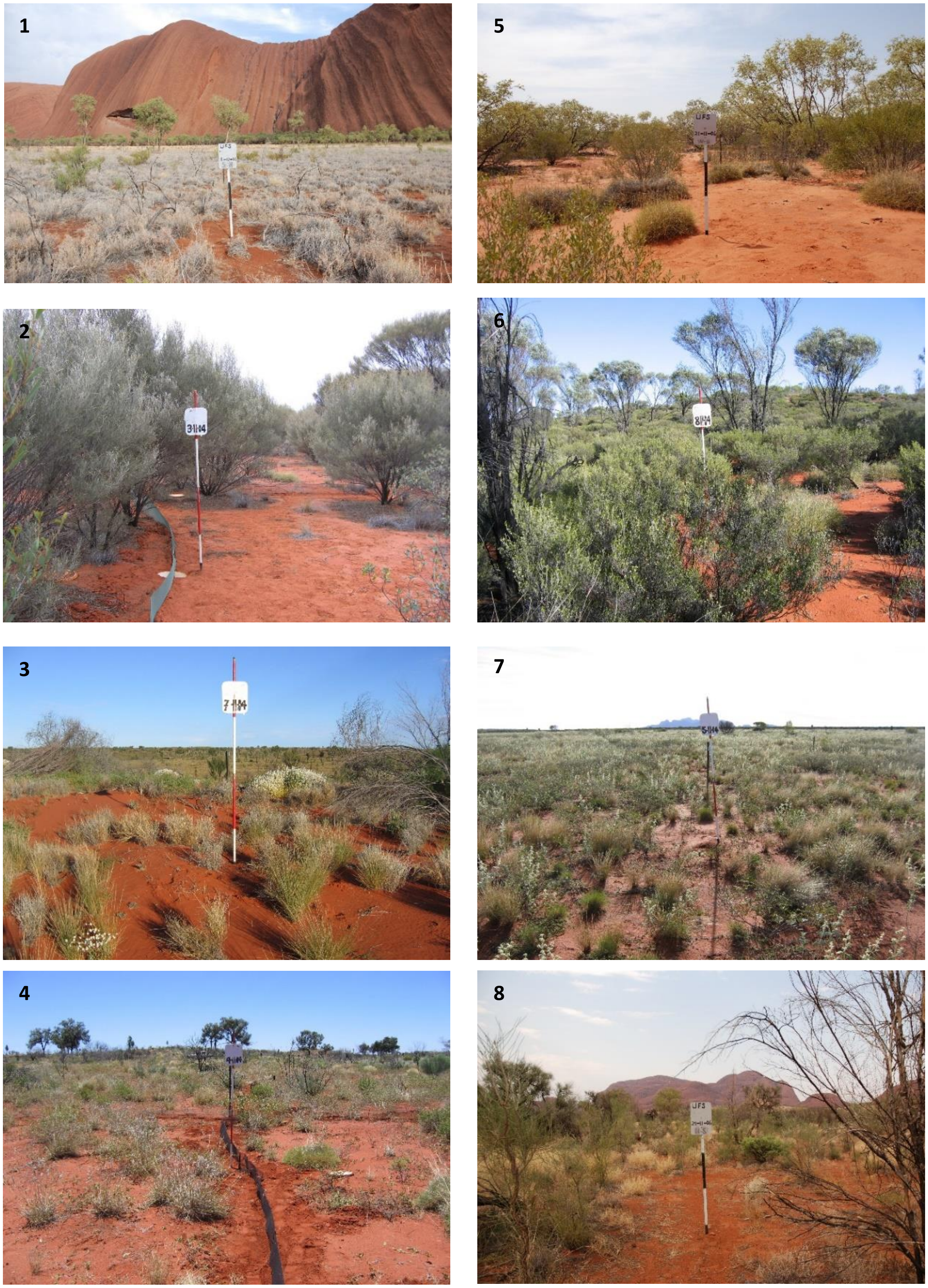


Figure 3.1. Eight fauna sampling sites at Uluru Kata Tjuta National Park. Numbers in top left corner are site numbers (corresponding to the site numbers in Table 3.1. See Appendix 2 for the location of the sites within Uluru-Kata Tjuta National Park.

Elliott traps were baited with oats, peanut butter and water in the late afternoon and checked in the early morning. Pitfall traps were checked 2–3 times daily depending on ambient temperatures. All traps remained available for three days at each site on each survey.

Prior to 2000, data are available for species identity only; from 2000 onward, animals were weighed and inspected for sex and reproductive condition; all animals were released at the point of capture.

Bird surveys were carried out along permanently marked 2.5 km-long transects. One such transect was established in each site. The transects were rectangular in shape, with sides of 1 km and 250 m apart. Surveys took place immediately after sunrise and immediately before sunset for three days each survey, with each survey lasting 70 – 120 minutes depending on bird activity (Reid *et al.* 1993). All birds seen and heard were recorded.

Data analysis

To examine whether, and how, faunal communities change across vegetation types at UKTNP (H1), combined totals for each faunal group (captures for mammals and reptiles, observations for birds) were first calculated for each site to detect broadscale similarities or differences in faunal diversity and abundance, without reference to individual years. The data were then analysed using each site as a block, with survey years as (pseudo)replicates. To further scrutinise the influence of vegetation type in determining faunal structures, the analysis was then repeated separately for the reptile, bird and mammal groups (H2). Finally, to study the influence of changing conditions on the fauna communities at the individual site level, the analyses were completed for each site separately using each survey as a replicate to examine the temporal changes in faunal community composition over time (H3). For this analysis, as Site 8 was included in the survey regime only from 1995, all data from 1994 was omitted. Within each site, distinct faunal communities were identified by the number of significant R-values in pairwise comparisons (see below).

Analyses were conducted in PRIMER (Version 7). The data were transformed to adjust for the effect of dominant species by square root or fourth root transformations. Following the transformations, Bray-Curtis similarity coefficients were calculated between each pair combination of sites, and hierarchical agglomerative clustering used to separate the samples into groups based on their similarity. Non-metric multi-dimensional scaling (nMDS) was then undertaken to produce ordination plots showing similarity (or dissimilarity) of these clusters as pairwise distances. Plots with stress values < 0.20 are considered to be reliable (Clarke and Gorley 2006). An analysis of similarity (ANOSIM) was then conducted to test for statistically significant differences between species similarity coefficients among the sites and for H3 between surveys within a site. The test statistic, 'R', is calculated by permutation tests, and ranges between 0 (no difference) and 1 (no similarity); statistical significance is taken to be $P \leq 0.05$. Individual sites are coded below by their number: S1, S2 and so on. And finally, to examine which species contribute to the change within a site through time a similarity percentages breakdown (SIMPER) analysis was undertaken. The SIMPER analysis calculates the contribution of each species (%) to the dissimilarity between each group, in this case between survey years. It is calculated from the Bray-Curtis similarity matrix.

Results

Hypothesis 1 and 2

In total, 172 species were recorded at UKTNP during the 16 years of the study: 10 species of mammal, 65 reptiles and 97 birds (Appendix 1). The most captured mammal was *Pseudomys hermannsburgensis* (1336 captures), while the least frequent was *Sminthopsis hirtipes* (8 captures). For reptiles, the most frequently trapped species was *Lerista bipes* (334 captures) and the least, *Brachyurophis fasciolatus*, *Tiliqua occipitalis*, *Varanus tristis* and *Gowidon longirostris (*Cogger 2018), all captured on a single occasion only. For birds, *Melopsittacus undulatus* was recorded 6454 times and *Lichmera indistincta* was recorded just once.

The *T. basedowii*-dominated dunefield site (S4) was the most species-rich, with 110 species detected (Table 3.2), followed by the *Eucalyptus*-dominated site (S5) with 106 species. The total abundance of all species was greatest at Kata Tjuṯa (S8) with 6005 total records followed by the site at Uluṟu (S1), with 5824 total records.

Table 3.2. Species diversity and total number of records of vertebrates at eight fauna survey sites, Uluṟu–Kata Tjuṯa National Park.

Habitat/site number*	All species		Mammals		Reptiles		Birds	
	Species #	Total # recorded	Species #	Total # recorded	Species #	Total # recorded	Species #	Total # recorded
Uluṟu (S1)	88	5824	8	768	21	189	59	4867
***A. aneura* (S2)**	81	3684	6	119	26	159	49	3406
***T. pungens* (S3)**	100	5609	7	302	43	568	50	4739
***T. basedowii* (S4)**	110	4318	9	416	47	471	54	3431
***Eucalyptus* spp. (S5)**	106	5297	7	174	43	447	56	4676
***A. ammobia* (S6)**	100	4814	8	187	37	353	55	4274
Sand plain (S7)	85	5149	9	544	33	433	43	4172
Kata Tjuṯa (S8)	95	6005	5	210	27	250	63	5545

*See Table 3.1 for full description, and Appendix 1 for full species lists.

The initial analysis combined counts for each survey into a total for each site, across all the surveyed taxa, to compare similarity in community structure at this broad scale. The ordination plot (Fig. 3.2) shows that the eight sites form five relatively distinct faunal groups. Sites 1 and 8 (Uluṟu and Kata Tjuṯa) cluster as a group as do sites 3 and 4 (the two *Triodia* dunefield sites) and sites 5 and 6 (*Eucalyptus*- and *A. ammobia*-dominated woodlands, respectively, Fig. 3.2). However, overall differences between the groups are significant (R = 0.92, p = 0.002), as are all sets of pairwise group comparisons (R = 1.0 in all cases).

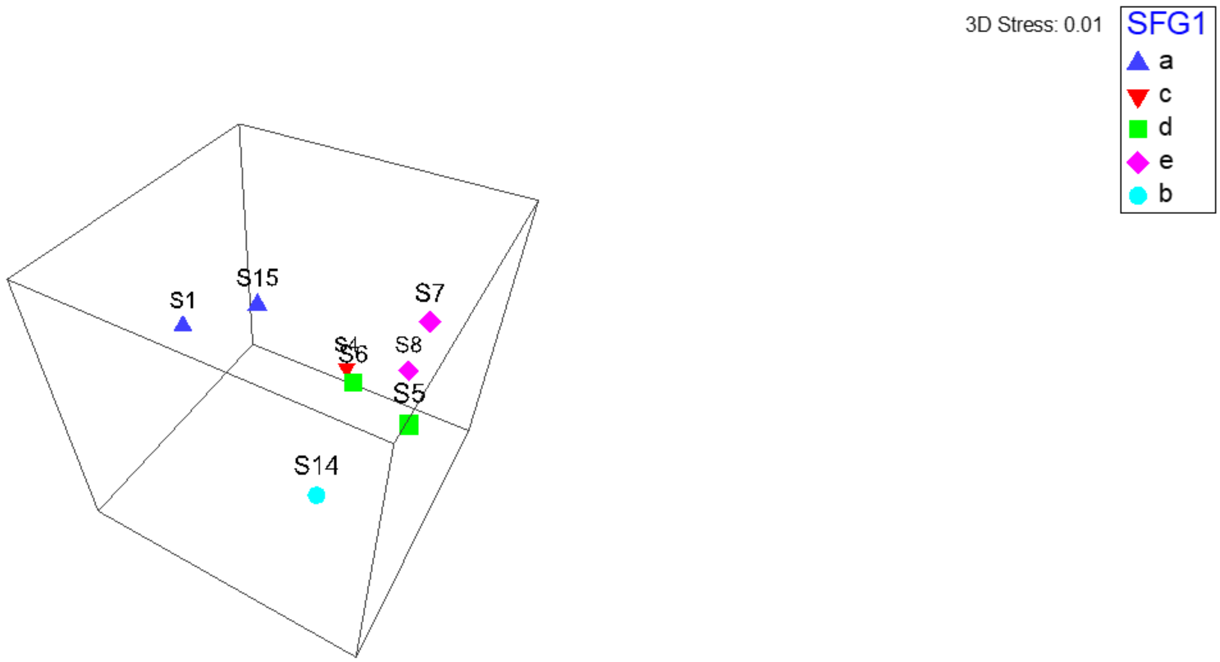


Figure 3.2: Non-metric multidimensional scaling plot of similarity between eight fauna survey sites (S1 – S8) at Uluṟu Kata Tjuṯa National Park (distance in space between two sites indicates how relatively similar the sites are). Symbols indicate sites that cluster.

There were highly significant differences between sites when each survey was used as a site replicate (R = 0.87, p = 0.001, Fig. 3.3a). The pairwise comparisons between each site are shown in Table 3.3. The two spinifex dunefield grassland sites (Sites 3 and 4) were the most similar (R = 0.351, Table 3.3) followed by Site 4 (hard spinifex dunefield) and Site 5 (*Eucalyptus* woodland, R = 0.464) and Site 2 (mulga woodland) and Site 6 (*A. ammobia* woodland, R = 0.528, Table 3.3).

To further clarify and examine the cause of differences in faunal community composition among the major vegetation types at UKTNP, the analyses were completed separately for reptiles, mammals and birds (Fig. 3.3 b, c, d). The mammal communities at the sites were comparatively similar (average R = 0.313), except that Site 8 appeared as an outlier (Fig. 3.4c). Greater variation is apparent in the reptile (Fig. 3.4b) and bird (Fig. 3.4d) communities between the sites, with average global R-values of 0.691 and 0.779, respectively.

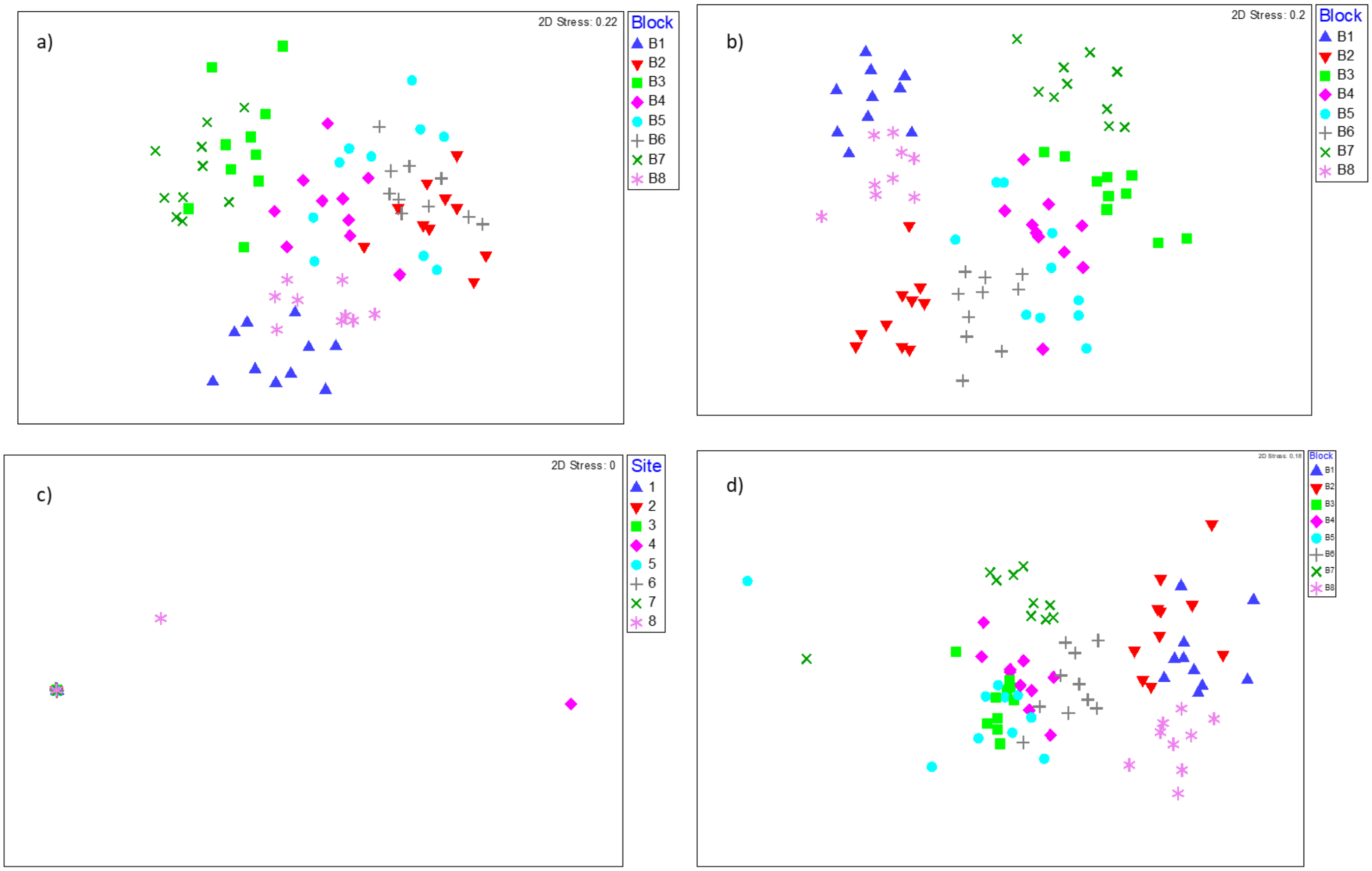


Figure 3.3. Non-metric multidimensional scaling plots of similarity between eight fauna survey sites (S1 – S8) at Uluṟu Kata Tjuṯa National Park, with surveys from different years (1994–2010) used as site replicates (distance in space between sites indicates how similar the sites are). Ordination plots are shown for all groups combined (a), reptiles (b), mammals (c) and birds (d). Note most of the mammal sites have clumped together giving the impression of only 3 points. The same number of sites has been included in the analysis for mammals.

The similarity (or dissimilarity) between pairs of sites was not consistent for the reptile and bird faunal groups. The most similar reptile communities occurred between the *Triodia*-dominated dunefield sites (S3 and S4, Table 3.3), soft spinifex and *Eucalyptus* woodland (S3 and S5, Table 3.3) and hard spinifex and *Eucalyptus* woodland (S4 and S5, Table 3.3). In comparison, the most similar avian communities were found between mulga and *A. ammobia* woodlands (S2 and S6, Table 3.3).

Table 3.3. Pairwise similarity comparisons (R-values) between eight survey sites (S1 – S8) at Uluṟu Kata Tjuṯa National Park, with surveys from different years (1994–2010) used as site replicates, shown for all fauna groups and separately for reptiles, birds and mammals. R values in bold indicates a significant p value (<0.05).

Site Pair	All fauna groups	Reptiles	Birds	Mammals
S1 and S2	**0.988**	**0.57**	**0.989**	**0.632**
S1 and S3	**0.997**	**0.997**	**0.902**	**0.617**
S1 and S4	**0.981**	**0.988**	**0.919**	**0.656**
S1 and S5	**0.992**	**0.829**	**0.962**	**0.622**
S1 and S6	**0.995**	**0.935**	**0.986**	**0.49**
S1 and S7	**0.997**	**0.878**	**0.994**	**0.42**
S1 and S8	**0.832**	**0.58**	**0.746**	**0.429**
S2 and S3	**0.998**	**0.988**	**0.923**	**0.463**
S2 and S4	**0.878**	**0.937**	**0.491**	**0.484**
S2 and S5	**0.945**	**0.818**	**0.78**	**0.344**
S2 and S6	**0.528**	**0.699**	**0.258**	**0.242**
S2 and S7	**0.992**	**0.846**	**0.982**	**0.608**
S2 and S8	**0.92**	**0.622**	**0.882**	0.35
S3 and S4	**0.351**	**0.137**	**0.397**	0.077
S3 and S5	**0.724**	**0.113**	**0.775**	0.043
S3 and S6	**0.924**	**0.686**	**0.866**	0.018
S3 and S7	**0.777**	**0.742**	**0.303**	**0.278**
S3 and S8	**0.983**	**0.974**	**0.823**	**0.368**
S4 and S5	**0.464**	**0.225**	**0.506**	0.004
S4 and S6	**0.609**	**0.434**	**0.496**	0.022
S4 and S7	**0.819**	**0.616**	**0.74**	**0.023**
S4 and S8	**0.899**	**0.94**	**0.686**	**0.425**
S5 and S6	**0.654**	**0.508**	**0.552**	0.001
S5 and S7	**0.978**	**0.604**	**0.969**	**0.287**
S5 and S8	**0.939**	**0.795**	**0.862**	**0.282**
S6 and S7	**0.991**	**0.73**	**0.987**	**0.252**
S6 and S8	**0.985**	**0.925**	**0.953**	**0.185**
S7 and S8	**0.996**	**0.866**	**0.976**	**0.334**

Hypothesis 3: Temporal changes in faunal community composition at individual sites

Intra-site variation in faunal communities (mammals, reptiles and birds grouped together) across the different survey years was large. Only two sites (Uluṟu, S1 and sand plain, S7) had faunal communities that did not change significantly with time. Faunal communities at all other sites clustered into two or more groupings when compared across the 16 years of the study, with surveys at the mixed *Eucalyptus* site (S5) clustering into six distinct faunal communities out of nine possible surveys (Fig. 3.4).

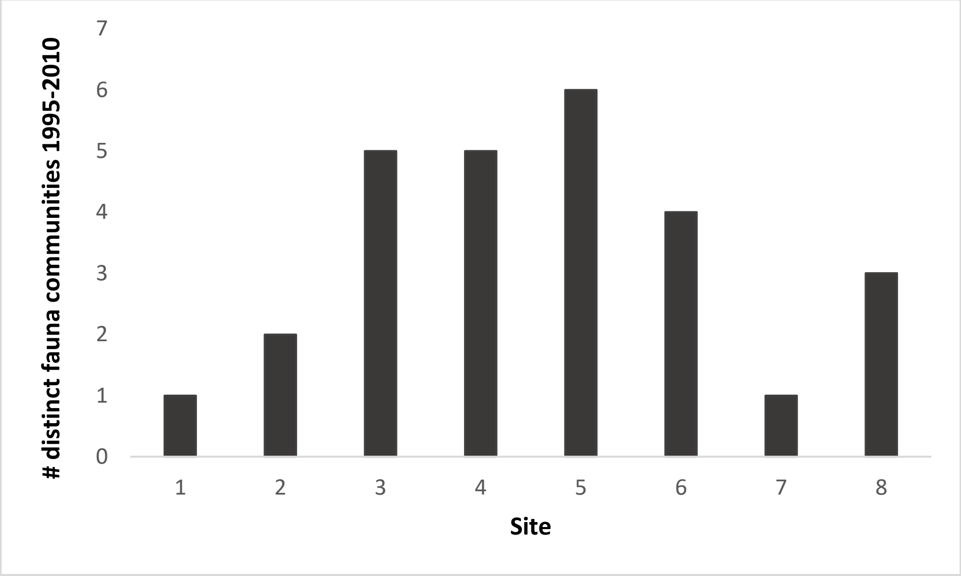


Figure 3.4. Changes in species composition over time, showing the number of distinct faunal communities identified over the nine surveys (1995–2010) within each of eight sites (1–8) at Uluṟu Kata Tjuṯa National Park, based on the number of statistically significant pairwise ANOSIM comparisons between survey times

Discussion

Although this study was conducted over a longer timeframe than most, it shows that even within the same sites, faunal assemblages across time at UKTNP can be variable and unpredictable in size and composition. In the discussion below, are considered some of the sources of variation in the faunal communities at UKTNP over space and time. These considerations are brief, as the broad findings in this chapter are used to help inform more detailed explorations of the dynamics and structure of selected components of the faunal communities in later chapters.

H1. Animal assemblages will differ between vegetation communities at UKTNP

Mulga woodland and the vast sand plain expanse at Site 7 had largely distinct faunal communities. The remaining sites showed patterns that, at this broadest level, corresponded to the dominant plant community or landscape locations of the sites with the two sites adjacent to the monoliths of Uluṟu and Kata Tjuṯa generally similar, as where the two spinifex dominated dunefield sites and two woodland sites (S2 and S5).

H2. Vegetation type is a key determinant of the species of birds, mammals and reptiles that occur in a given site at UKTNP

Variation in the faunal communities became clearer when the mammal, bird and reptile groups were examined separately.

Mulga woodland (S2) and the sand plain in the north of the park (S7) continued to remain largely distinct from all the other sites when looking at the vertebrate groups individually, albeit less so for mammals than for birds or reptiles. However, the remaining sites showed less consistency. The mammal and reptile communities at Site 1, with alluvial and other mesic habitats at the base of Uluṟu, were distinct, with the mammal group here being quite unique. This site was, for example, the only one where *Pseudantechinus macdonnellensis* was captured. The site closest to the base of Uluṟu (S1) was the drainage lines of Kata Tjuṯa (S8), with some similarity for reptiles, but less so for birds and mammals. Birds showed little similarity between the two sites despite the influence at both sites of the large monoliths and the increase in water flows funneling off the rocks and through these areas. The mammal fauna of the drainage lines at Kata Tjuṯa were very distinct, characterized by the dominance of *Pseudomys hermannsbergensis* and *Mus musculus* and the very reduced abundance of marsupials (only four *Sminthopsis youngsonii* captured over the whole survey period) and a complete lack of *Notomys alexis*.

The two dunefield grassland sites – S3, soft spinifex, and S4, hard spinifex – had very similar mammal and reptile communities but showed unexpected, albeit small, variation for birds. As the primary difference in the habitats lies in the character of the spinifex leaf (hard spinifex is an extremely spiky rigid grass compared to its softer counterpart), it may be that the leaf structure of spinifex plays a pivotal role in the choices that birds make about where to live and browse. It is likely that many granivorous/insectivorous birds in spinifex grasslands forage for seeds or invertebrates by hovering at the top of the hummocks, or choosing nesting sites within hummocks, tasks perhaps made easier amongst soft spinifex than hard and driving a preference for soft spinifex over the spiky hard spinifex (e.g. Tischler *et al.* 2013). In contrast, the species of spinifex grass does not appear to be a factor affecting habitat selection by reptiles and mammals, with little dissimilarity in species composition between the sites. Many species of reptile found in spinifex are thin-bodied and svelte, and active at the base of the grass hummocks, perhaps avoiding the worst of the spikes or using them to escape larger predators. Pianka (1969), for example, described skinks of the genus *Ctenotus* as 'swimming through the spinifex', which may help to explain the overlap between reptile communities in the two grassland sites. Alternatively, and aligning more with other studies, it may be that other habitat components such as percentage cover of all vegetation (Pianka and Pianka 1976, Downey and Dickman 1993, Daly *et al.* 2008), termite abundance (Pianka and Pianka 1976, Morton and James 1988) and presence or absence of predator activity (Molyneux 2017) dictate the choices made by species in these groups rather than the spinifex type. Mammals were also very similar in the *Triodia* grassland sites. The mammals in these landscapes are small and mostly quadrupedal which may help in squeezing under the sharp leaf spikes in the *T. basedowii* landscapes, thus allowing them to live in either habitat. The relationship between small mammal behaviour and hard spinifex habitats is explored further in Chapter Seven.

The similarity in reptile assemblages between the spinfex dunefield sites (S3 and S4) and the *Eucalyptus* woodland (S5) may reflect the presence of a spinifex understorey in the eucalypt habitat. However, there is also a spinifex understorey in the *A. ammobia* woodland (S6), and reptiles here were dissimilar to the reptiles at both the hard and soft spinifex sites. Moreover, the dissimilarity between the reptile fauna at the eucalypt site compared to the *A. ammobia* site points towards other factors unrelated to the spinifex understorey in driving reptile assemblages in these areas.

While the two *Acacia*-dominated woodlands had similar bird and mammal assemblages, the reptile community was distinct. The reptile species composition in mulga was also quite different from that in either of the spinifex-dominated grasslands and the eucalypt woodland. This variation amongst reptile communities may reflect the way that different reptile species forage or move through their habitat. Pianka (1969) found that many skinks (particularly *Ctenotus* spp.) are shy and wary and readily exploit the dense protective cover provided by spinifex, whereas larger dragon lizards are relatively clumsy and slow when moving in or around spinifex; their longer limbs give them greater mobility in open habitats such as open woodlands. Pianka and Pianka (1976) also demonstrated in geckoes, at least, that several species are associated strongly with *Acacia aneura*, using the base, trunks and thin terminal branches for foraging or shelter to finely subdivide the mulga-tree resource.

Bird communities showed the largest variation between sites. This may reflect, in part, the long temporal span of the study as many species of birds at UKTNP are non-residents, migrating to the region to exploit short-lived resource pulses. However, even among the woodlands (S2, S5 and S6), where resident populations may have been expected to occur, there were clear differences in bird communities. Studies elsewhere in arid Australia have demonstrated that bird assemblages are linked to vegetation components such as grassland and woodland (Pavey and Nano 2009, cf Tischler *et al.* 2013) rather than being influenced by climatic variables. The association with vegetation structure lies in the differential use that different bird species make with respect to their food resources and foraging modes, shelter requirements and relationships with predators, competitors and other biotic components (Cody 1974). The distinction in bird communities at UKTNP between habitat types adds support to this explanation.

H3. Animal assemblages remain consistent within a vegetation community over time

I found unexpectedly varied results when investigating the influence of time on vertebrate community composition at each site. There was some support for the hypothesis that assemblages would remain consistent within a vegetation type as the fauna makeup of S1, Uluṟu and S7, the vast spinifex sandplain site did not change over time. However, these were the only sites where the fauna assemblage remained consistent through time regardless of the climatic differences that occurred across the 16 years, which included drought and heavy rainfall, as well as events such as wildfire with, I assume, associated boom and bust resource pulses, shifts in cover, levels of predation threat and other factors.

At the other sites, little evidence was found of stability in animal community composition with different faunal communities detected at the individual sites over time particularly due to changes in bird species abundance. Site S5, the eucalypt woodland site, was the most diverse, with six distinct faunal assemblages identified from the nine survey years, with fluctuations in the population sizes of *Lichenostomus plumulus* and *Manorina flavigula* the main contributor. The spinifex-dominated dunefield sites (S3 and S4) each yielded five distinct assemblages over the period of study. Fluctuations in the populations of *Lichenostomus virescens* and *Artamus cinereus (*S3) and *Melopsittacus undulates* and *Epthianura tricolor* (S4) primarily contributing to the difference. The temporal fluxes in weather were presumably a stronger determinant of assemblage composition than vegetation type, perhaps because fluctuations in resources, predators or other factors in these vegetation types are relatively extreme. In *Triodia*-dominated sites in the Simpson Desert, for example, Dickman *et al.* (2010, 2011) documented large fluctuations in both seed resources and levels of population activity of native and introduced vertebrate predators between periods of drought and heavy rainfall; Tischler *et al.* (2013) recorded similar fluctuations in eucalypt communities in the same region. In contrast, sites that are climatically buffered from such fluctuations could be expected to retain a similar suite of species over time. In this study, the assemblage stability of Site 1 could be due to the proximity of the Uluṟu monolith. In other parts of arid Australia, large rock outcrops and rocky ranges provide both stability of food resources (e.g. Gilfillan 2001) and protection from climatic exigencies, and thus support stable populations of a wide range of animal species (McDonald *et al.* 2015).

The vast hard spinifex-dominated sandplain (Site 7) at UKTNP remains an anomaly worthy of further investigation: this is an open site that could have been expected to show similar patterns of temporal change in faunal assemblages to sites 3 and 4. It is also where most of the still-extant threatened species are found, such as the communally burrowing great desert skink (*Liopholis kintorei)*. The faunal community here was consistent across time and apparently resistant to the drivers of temporal change displayed in the other habitat types. However, the fauna community is also very distinctive, showing large dissimilarity between it and almost all other survey sites (the exception is S3-soft spinifex, interesting as most *Triodia* on the sand plain is the hard species *T. basedowii*).

At the broad scale of analysis presented in this chapter, there appears to be little consistency in faunal assemblages across time, even within the same sites at UKTNP, with differences in species composition, numbers and distributions between sites and survey years. These findings suggest that it may be variation in top down and bottom up environmental influences that structure the fauna community at these sites in UKTNP rather than intrinsic characteristics of the vegetation community itself.

While the species contributing to these differences have not been examined in detail here to maintain breadth of analysis over the large number of species,, the findings highlight that factors other than the vegetation community alone influence vertebrate faunal groups at most of the studied sites at UKTNP.

In Chapter Four, using the same sites and data, I begin to explore the effect of two of the most important bottom up drivers of change in desert landscapes—rainfall and fire—using mammals as a focal group.

Chapter Four - Synchronous boom-bust cycles in central Australian rodents and marsupials in response to rainfall and fire

Introduction

Improved conditions in most arid regions are brought about by heavy rains that stimulate pulses of productivity (Whitford 2002), although floods from rains that have fallen elsewhere can have similar effects (Letnic and Dickman 2010). These pulses produce food for primary consumers and shelter in the form of increased vegetation cover, and are the most reliable predictors of rodent irruptions in arid regions (e.g., Newsome and Corbett 1975); links between rainfall and rodent booms have been traced over periods exceeding 100 years (Plomley 1972; Greenville *et al.* 2012). Ensuing bust phases result from declines in productivity as conditions dry but can be hastened and prolonged by events such as wildfire (Letnic *et al.* 2005). Wildfires remove vegetation cover and food resources and create open habitats that increase the hunting efficiency of predators on small mammals (McGregor *et al.* 2015). Although boom and bust dynamics have been described for many species of desert-dwelling mammals (e.g., Whitford 2002; Fox 2011; Ojeda *et al.* 2011), they appear to be most pronounced in rodents that occupy regions with unpredictable rainfall regimes (e.g., Australia, Dickman *et al.* 1999a, 2010; Namibia, Griffin 1990). Rodents in these regions often exhibit opportunistic breeding in response to rainfall events (Breed and Ford 2007). They also show greater flexibility in diet and social behaviour than do their counterparts in deserts where rainfall is low but seasonably reliable (Murray *et al.* 1999; Lima *et al.* 2008; Fox 2011; Shenbrot 2014), perhaps increasing the efficiency with which temporary resource pulses can be exploited (Letnic and Dickman 2010).

Mammals in arid environments often show pronounced fluctuations in population size, oscillating from being almost absent to being ubiquitous and present at very high density. The low, or ‘bust’, phases of populations usually occur during prolonged periods when the environmental carrying capacity is low (Yang *et al.* 2010) and resources are depressed (Letnic *et al.* 2005). Large or mobile mammals may respond to such conditions by dispersing to areas where resources can be accessed more readily (e.g., Fennessy 2009), but terrestrial small mammals are usually constrained in mobility and must deal with resource shortages in situ (Degen 1997; Fox 2011). Some species can make directed movements of several kilometres to access fresh resources (Dickman *et al.* 1995; Letnic 2002) or retreat to refuge habitats (Milstead *et al.* 2007; Pavey *et al.* 2014, 2017). Others persist by exploiting cached food resources (Kelt 2011), foraging selectively in the highest-quality food patches (Bleicher and Dickman 2016), or reducing their needs for energy and water via physiological mechanisms such as nest-sharing or torpor (Morton 1978; Geiser 2004). When conditions improve, desert mammals often respond via elevated reproduction, survival, and immigration to achieve, within a few months, populations that may be 2-3 orders of magnitude greater than those present during the bust phase (D'Souza *et al.* 2013; Greenville *et al.* 2013). Population peaks, or 'booms', are often ephemeral, and may last less than a year if conditions deteriorate rapidly (Dickman *et al.* 2010).

Despite the apparent ubiquity of the rainfall-rodent association in arid environments and our mechanistic understanding of how it works, neither rodents nor other small mammals always increase after rainfall. Long-term field programs are increasingly uncovering circumstances where study species show inconsistent responses to rainfall events, and even negative effects of rainfall on population size. In Chile, for example, Meserve *et al.* (2011) showed that caviomorph rodents sustain larger populations than sigmodontine rodents if there are moderate rainfall events between years of high rainfall, whereas the latter rodents dominate if rainfall pulses are widely separated. The difference may be explained by differences in life history traits between the 2 groups of rodents, with fast-breeding sigmodontines better able to exploit ephemeral resource pulses and slower-breeding, longer-lived caviomorphs better able to maintain their populations if conditions during bust periods allow persistence (Previtali *et al.* 2009, 2010). In the Negev Desert, negative relationships between rainfall and rodents in dry river bed habitats may arise due to flash floods in some years (Shenbrot *et al.* 2010), while in the Chihuahuan Desert inconsistent relationships between rainfall and rodent responses over a 28-year period appear to have arisen due to interactions between rainfall and shrub density and other factors (Thibault *et al.* 2010).

Insectivorous small mammals might be expected to show smaller populations and delayed responses to rainfall pulses because of their dependence on secondary productivity (invertebrates). Some species, such as *Onychomys* spp. (Thibault *et al.* 2010) and *Notiosorex crawfordi* (Chung-MacCoubrey *et al.* 2009), do indeed behave as expected, but others show no evident demographic response to rainfall (Meserve *et al.* 2011; Greenville *et al.* 2016) and may even decline after heavy precipitation events (Woolley 1984). These observations suggest that rainfall often triggers irruptions of desert mammals, but also that the relationship is complex, and support the call of Lindenmayer *et al.* (2012) for more long-term studies to help understand the processes that drive animal populations.

Fire also can affect the composition of communities in fire-prone landscapes. In spinifex dominated habitats in central Australia, post-fire recovery involves a predictable succession of plant species, beginning with forbs and grasses, followed by the dominance of spinifex again 5-10 years later after sufficient heavy rains have fallen (Latz 1995; Allen and Southgate 2002; Southgate and Carthew 2008; Nguyen *et al.* 2015). Leonard (1976) found a 50-90% reduction in litter invertebrates following prescribed burns in forests and Pianka and Goodyear found that fire reduced the abundance of desert invertebrates. Fire can affect small mammals by direct mortality or indirectly by removing food and shelter and exposing individuals to increased risk of predation (Sutherland and Dickman 1999; Letnic *et al.* 2013).

In this paper, we investigate temporal changes in populations of rodents and dasyurid marsupials over a period of 16 years at sites in central Australia. The dominant species of rodents—spinifex hopping-mouse (*Notomys alexis*, average weight 32.1 g, range 26.3-38.7 g), sandy inland mouse (*Pseudomys hermannsburgensis*, average weight 13.2 g, range 9.3 -17.8 g), desert mouse (*Pseudomys desertor*, average weight 25.1 g, range 14.5-31.5 g), and house mouse (*Mus musculus*, average weight 12.6 g, range 9-17.5 g)—often respond positively to rainfall elsewhere in Australian desert habitats (e.g., Masters 1993; Pavey *et al.* 2008; Letnic *et al.* 2011a), but the responses vary in magnitude and timing (Southgate and Masters 1996), and are sometimes muted even after heavy rainfall events (Dickman *et al.* 1999a). These species are broadly omnivorous, although seeds and green plant material form >50% of their diets (Murray and Dickman 1994b; Murray *et al.* 1999). The dominant dasyurid species at the study sites, including the brush-tailed mulgara (*Dasycercus blythi*, ~100 g), wongai ningaui (*Ningaui ridei*, average weight 8.2 g, range 5-10 g), and lesser hairy-footed dunnart (*Sminthopsis youngsoni*, average weight 10.4 g, range 6-12.4 g) sometimes increase after rain, but results again are not consistent across studies (Masters 1993; Dickman *et al.* 2001; Masters and Dickman 2012; Greenville *et al.* 2016). Invertebrates comprise the bulk of the diet of the dasyurids, although *D. blythi* also hunts small vertebrates (Fisher and Dickman 1993; Masters 1998). All these small mammals generally decline after wildfire (Letnic *et al.* 2004; Pastro *et al.* 2011), although muted responses are sometimes reported (Southgate and Masters 1996; Bennison *et al.* 2013). Introduced predators such as the European red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) may hasten post-fire declines, especially of rodents, which are selectively depredated in open habitats compared to dasyurids (Spencer *et al.* 2014).

We expected that populations of these small mammals generally would respond positively to rainfall and negatively to wildfire, and that variation in the strength and timing of responses would arise due to differences in life history traits and diets of the study species. We used long term data (1994-2010) to test the following 3 broad hypotheses:

> H1: Dasyurid marsupial populations will exhibit less variability and lower capture rates than sympatric rodents.
>
> H2: Mammals generally will respond positively to rainfall, with rodents responding more quickly and strongly and declining more rapidly during drought than marsupials.
>
> H3: Rodents and dasyurids will decline following wildfire, with rodents showing greater preference for post-fire regeneration than marsupials.

For the 3rd hypothesis we assumed that the omnivorous diets of Australian desert rodents (Murray *et al.* 1999) would allow them to exploit the new plant growth available after a fire more quickly than dasyurids, which need to wait for invertebrates to recolonize post-fire. We assumed that during drought, the ability of marsupials to store energy resources in their tails and enter periods of torpor (Geiser 2004) would allow them to persist longer than rodents, which need a more consistent supply of food.

Methods

Study sites

The study was carried out at Uluṟu - Kata Tjuṯa National Park (UKTNP) in the southwest of the Northern Territory, 320 km southwest of Alice Springs, central Australia. The park covers 1,325 km^2 and is managed jointly by Parks Australia and Aṉangu Traditional Owners (Director of National Parks 2010). The dominant landscape features include Uluṟu, a red sandstone rock formation 9.4 km in circumference and 340 m high, and Kata Tjuṯa, a complex of 36 basalt and granite conglomerate domes that cover 35 km^2 and rise to 500 m above the surrounding desert. Sand dunes and plains surround these rocks (Director of National Parks 2010). The climate of the park is semi-arid, with annual rainfall averaging 280 mm and temperatures ranging from < 0°C on winter nights to > 40°C in summer (Bureau of Meteorology 2010). Rainfall is extremely variable (< 150 mm to > 800 mm per year), with heaviest rainfalls during summer.

The study sites were originally selected by the Commonwealth Scientific and Industrial Research Organisation's Division of Wildlife and Ecology between 1987 and 1990 for ecological surveys of the vertebrate fauna of UKTNP (Reid *et al.* 1993). Site selections were based on having 1 site in each of the park's six major land classes: alluvial fans at Uluṟu, alluvial fans at Kata Tjuṯa, sedimentary foothills at Kata Tjuṯa, mulga shrubland, soft spinifex, and hard shard spinifex. An additional two sites in the soft spinifex land class included the distinctive vegetation types of mallee (*Eucalyptus gamophylla*, *E. mannensis*, *E. socialis*, and *E. oxymitra*), and *Acacia ammobia* open woodlands. The closest distance between sites was 5 km. Mammal surveys (see details below) were continued at the same sites for this study and were considered spatially independent with respect to the movements of small mammals, but not temporally independent. Surveys were completed by members of the Muṯitjulu community, staff from UKTNP, and Steve McAlpin, a consultant ecologist.

Rainfall and fire

Rainfall records were compiled from daily rain gauge data collected near the UKTNP headquarters building from 1968 to the present. Fire histories were obtained for each site and each survey from satellite image-based fire mapping undertaken by the park. Widespread fires occurred frequently (e.g., 2002, 2004, and 2006), the most extreme of which occurred in 2002, affecting > 70% of UKTNP and 6 of the 8 study sites (Table 4.1).

Table 4.1. Survey sites affected by fire between 1994 and 2010. Red hatching indicates that the site had been partially or completely burnt within the previous five years.

Year	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
1994	▨		▨	▨	▨		▨	
1995	▨		▨	▨	▨		▨	
1997	▨		▨	▨			▨	
1999	▨						▨	
2000								
2002	▨		▨	▨		▨	▨	▨
2004	▨		▨	▨		▨	▨	▨
2006	▨		▨	▨		▨	▨	▨
2008	▨							
2010	▨		▨		▨		▨	

Field surveys

Site surveys were conducted in 1994, 1995, 1997, 1999, 2000, 2002, 2004, 2006, 2008, and 2010. With the exception of 1 survey in March 1995, all surveys were carried out in spring (October or November) to maximize the chance of recording mammal breeding activity, to coincide with reptile activity as part of broader survey objectives (not reported), and to minimize animal heat stress associated with trapping during summer.

Trapping effort at each site consisted of 250 aluminum ‘Elliott’ type-A traps (33 × 10 × 10 cm, Elliott Scientific Equipment, Upwey, Victoria, Australia) and 36 pitfall traps (20 l plastic buckets). Elliott traps were arranged in 10 rows of 25 traps, with each trap separated by 20 m. Pitfall traps were arranged in 4 arrays in a cross formation, with a central pitfall bucket surrounded by 4 ‘arms’ each containing 2 buckets spaced 5 m apart (i.e., 9 buckets per trap array). Pitfall trap lines were placed to sample the environmental or topographical variation within a site. A drift fence of wire mesh, 30 cm high, ran between each bucket to maximize the chance of animals encountering a trap. Elliott traps were baited with a mixture of oats, peanut butter, and water in the late afternoon and checked in the early morning. Pitfall traps were checked 2-3 times daily depending on ambient temperatures. All traps remained open for 3 days at each site on every survey. Prior to 2000, data were available for species identity only; from 2000 onward, animals were weighed, and inspected for sex and reproductive condition. All animals were released at the point of capture. Captured animals were marked using a permanent marker pen to ensure identification of recaptures on subsequent mornings; this involved placing a small mark on the inside of ears. All the methods employed conform to the American Society of Mammalogists' guidelines for animal research (Sikes *et al.* 2016). This work was conducted under approval from the Director of Parks Australia.

Tests of the 3 broad hypotheses

Changes in the total number of individuals captured (*C*; hereafter, 'captures' refers to numbers of individuals, i.e., excluding recaptures) over time formed the basis of tests of the 3 hypotheses (H1-H3 above). Capture success was determined for rodents and dasyurid marsupials (excluding *Pseudantechinus macdonnellensis*, which was not targeted by pitfall traps, and separately for the larger *D. blythi*, which is rarely caught in pitfall traps and has a restricted distribution across the park) by dividing the total number of individuals captured (*C*) by total trap nights for each survey occasion. Variability in the total number of individuals captured across years for the mammal groups and individual species was determined using the coefficient of variation (CV_C) expressed as a percentage of the mean. These analyses were used to test our first hypothesis (H1) that dasyurid marsupial populations would exhibit less variability and lower capture rates than rodents.

Hypothesis 2 relates to the speed and magnitude of mammal responses to rainfall. We first explored these relationships using parametric (Pearson) and non-parametric (Spearman) correlation analyses of small dasyurid and rodent captures and cumulative rainfall in the preceding 3, 6, and 12 months leading up to each survey (CR_3, CR_6, and CR_{12}). We used both aggregated pitfall and Elliott trap captures and pitfall-only captures between 1997 and 2010 as trappability of different mammal groups varied overall and in response to seasonal conditions (Supplementary Data SD1 *). Therefore, where data were available, we repeated some analyses with pitfall trap data alone to ensure consistency of results given the variation in efficiency and equivalency between the trapping methods. Differences in the temporal responses of dasyurid marsupials and rodents to rainfall were then assessed using estimates of the finite rate of increase (λ) across consecutive surveys (*t* and *t* + 1). Since our best estimates of population size were total numbers of individuals captured (*C*) within each survey, we simply estimated the finite rate of increase as $\lambda = (C_{t+1}/ C_t)$. Lambda (λ) values of > 1 and < 1 indicate increasing and decreasing populations, respectively.

Our 2nd hypothesis (H2) was that the dasyurid marsupials would respond more slowly (i.e., show delayed responses) and less strongly (i.e., smaller increases in captures across consecutive surveys) to rainfall than rodents. Cross-survey comparisons with different preceding rainfall (CR_3, CR_6, and CR_{12}) profiles yielded 5 general tests of this hypothesis (full details in Table 3.1). These tested for: 1) no change in marsupial or rodent captures across surveys (H2a), 2) an increase in rodents but not marsupials (H2b), 3) a decrease in rodents but not marsupials (H2c), 4) a larger increase in rodents than marsupials (H2d), and 5) a larger decrease in rodents than marsupials (H2e). Three cross-survey comparisons were available for H2c and H2d. All comparisons were made using all trap captures and pitfall-only captures (where available; Table 3. 1).

Finally, to explore the effect of prescribed burns and the large wildfire of 2002 that affected 6 of the 8 sites on the mammal groups (H3), we first determined the number of captures of dasyurids (excluding *D. blythi* and *P. macdonnellensis*) and rodents at each site within each survey year. Sites were then categorised as “burned” (sites containing at least some burned area within the past 5 years) and “unburned” (no burned areas within the past 5 years), and total captures of both mammal groups were determined across all burned and unburned sites within each survey year. Finally, total captures were determined for both the burned and unburned categories across all survey years. We first tested for a preference for burned versus unburned habitat within rodent and marsupial groups separately during each survey year using the chi-squared (χ^2) goodness of fit test assuming equal expected counts in burned and unburned plots. This tested for evidence of a preference for burned or unburned habitat

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* Supplementary data in Bennison *et al.* 2018.

within each mammal group. We then tested for differences in preference between the 2 mammal groups (rodents versus marsupials) using the chi-squared (χ^2) goodness of fit test with burn history and mammal group as blocked variables, again separately for each survey year.

Results

Capture rates and variability in dasyurids and rodents (H1)

From 1994 to 2010 the survey amassed 68,640 trap nights (60,000 Elliott and 8,640 pitfall; 1 trap night = 1 trap open for 1 night). This yielded 2,988 individual small mammals captured (2,676 rodents, 267 small dasyurid marsupials, and 45 *D. blythi*), with an overall trapping success of 4.4%. Total trapping success was highest for rodents (3.9%), followed by small dasyurids (0.4%) and *D. blythi* (0.07%). Ten mammal species were recorded: 4 rodents (*M. musculus*, *Pseudomys hermannsburgensis*, *P. desertor*, *N. alexis*) and 6 marsupials (*Pseudantechinus macdonnellensis*, *S. ooldea*, *S. youngsoni*, *S. hirtipes*, *D. blythi*, *N. ridei*).

Rodents dominated the mammal assemblage, with *P. hermannsburgensis* being the most commonly captured species (1,336 total pitfall and Elliott trap captures across 10 surveys), followed by the introduced *M. musculus* (803 captures) and the native *N. alexis* (381 captures; 44% of which occurred in 1 year). Small dasyurids were caught far less frequently than rodents, with *S. hirtipes* and *P. macdonnellensis* being least often encountered (7 and 12 captures, respectively). Even *S. youngsoni*, the most abundant marsupial (with 104 captures), was caught less frequently than *P. desertor*, the least common rodent (143 captures).

Capture rates varied widely across the mammal groups and species throughout the 16-year study period (Fig. 4.1 a-d). Overall, the fewest captures occurred in 2002 and 2008 (57 and 118 captures, respectively), and the most captures occurred in 1999 and 2000 (721 and 690, respectively; Fig. 4.1 a-b). Differences in total annual capture rates mainly reflected variation in captures of *P. hermannsburgensis*, *M. musculus*, and *N. alexis* (totals of 649 and 612 individuals captured in 1999 and 2000 versus 50 in 2002; Fig. 4.1c). This pattern deviated from that of marsupials (Fig. 3.1d), which had lower capture rates overall and a less pronounced peak in

1999-2000. Captures of marsupials still varied widely across years (from 5 individuals in 2002 to 67 in 2010) and fluctuated in a broadly synchronous way with rodents (Fig. 4.1b), especially for pitfall-only data (Fig. 4.1e). Some species also showed order of magnitude or greater population increases across surveys (e.g., *N. ridei* in 2008-2010 and *N. alexis* in 1997-1999; Fig. 4.1c-d) that did not occur in other species. *Dasycercus blythi* was caught in the 4 surveys up to 2000 but not thereafter (Fig. 4.1a).

Rodents exhibited greater overall variability in capture rates across surveys than marsupials (CV_C = 81% versus 64%), a pattern that was stronger if only pitfall data are considered (CV_C = 91% versus 64%; Fig. 4.1e). However, there were large interspecific differences within mammal groups, with annual captures of some dasyurid species being more variable than those of some rodents. For example, the most variable species were the dasyurids *N. ridei* (CV_C = 119%) and *D. blythi* (CV_C = 135%), and the rodent *N. alexis* (CV_C = 135%). Species with lower interannual variability in capture rates included both dasyurids (*S. youngsoni*, CV_C = 65%; *S. ooldea*, CV_C = 90%) and rodents (*P. hermannsburgensis*, CV_C = 77%; *P. desertor*, CV_C = 80%; and *M. musculus*, CV_C = 105%). Due to the higher overall capture rate of rodents versus dasyurids, the range of total rodent captures across years (52 to 670) was greater than that of dasyurids (5 to 71).

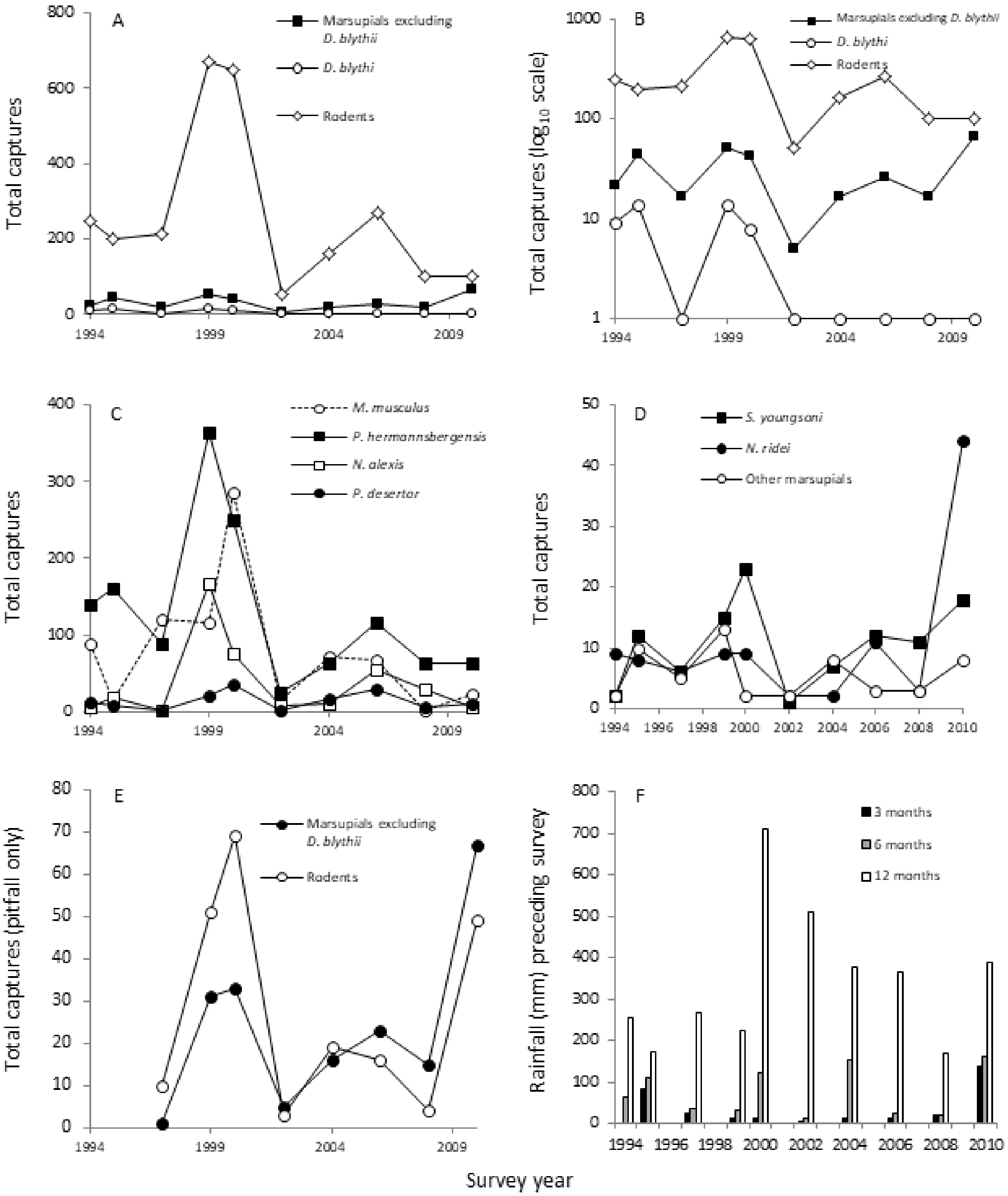


Figure 4.1. Captures of small mammals during the 1994-2010 study period. a) Total number of individuals captured of marsupials (small dasyurid marsupials and *Dasycercus blythi* shown separately) and rodents in each survey year; b) Total number of individuals captured of the same species and species groups on $\log_{10}$ scale; c) Total number of individuals captured of rodent species; d) Total number of individuals captured of marsupial species; e) Captures of rodents and marsupials in pitfall traps; f) Rainfall in 3-, 6-, and 12-month periods prior to each survey.

Response of dasyurids and rodents to rainfall (H2)

Total rainfall varied widely throughout the 16-year study period (Fig. 4.1f), with cumulative 12-month preceding rainfall (CR_{12}) ranging from 168 mm (2008) to 709 mm (2000). Rainfall in the 3- and 6- months preceding each survey (CR_3 and CR_6) was even more variable (CR_3 = 0 – 136 mm and CR_6 = 11 – 168 mm, respectively) and often uncorrelated with CR_{12}.

There were no obvious patterns between the preceding 12-month rainfall and mammal captures. For example, 690 mammals (34 small dasyurids, 8 *D. blythi*, and 648 rodents) were captured in the wettest survey year (2000; CR_{12} = 709 mm), fewer than those captured in 1999 (37, 14, and 670, for a total of 721), which was a relatively dry year (CR_{12} = 224 mm). In the very dry year 2008 (CR_{12} = 168 mm), 118 mammals were captured (17 dasyurids, 0 *D. blythi*, and 101 rodents), like the number captured in 2010 (169 total), which was much wetter (CR_{12} = 390 mm). Correlation analysis uncovered no significant relationships between CR_{12} and total captures of either marsupials (excluding *D. blythi*) ($P > 0.10$ for r and ρ; Fig. 4.2f) or rodents ($P > 0.10$; Fig. 4.2e).

In contrast, there were significant or marginally significant positive relationships between total captures of marsupials and cumulative rainfall in the previous 6 months ($P < 0.1$; Fig. 4.2 d) and 3 months ($P < 0.1$ and $P < 0.01$; Fig. 4.2b). Data from pitfall traps only also showed that capture rates of marsupials generally increased with CR_6 and CR_3 (Fig. 4.3 a,b) but not CR_{12} ($\rho = 0.33$, $P > 0.10$).

There were no relationships between total captures of rodents and CR_6 or CR_3 ($P > 0.1$; Fig. 4.2c,a), although a weak positive relationship existed between rodents captured in pitfall traps and CR_6 ($\rho = 0.69$, $P < 0.05$; Fig. 4.3c), and the highest capture rate for rodents occurred following the wettest preceding 12-month period (Fig. 4.3d).

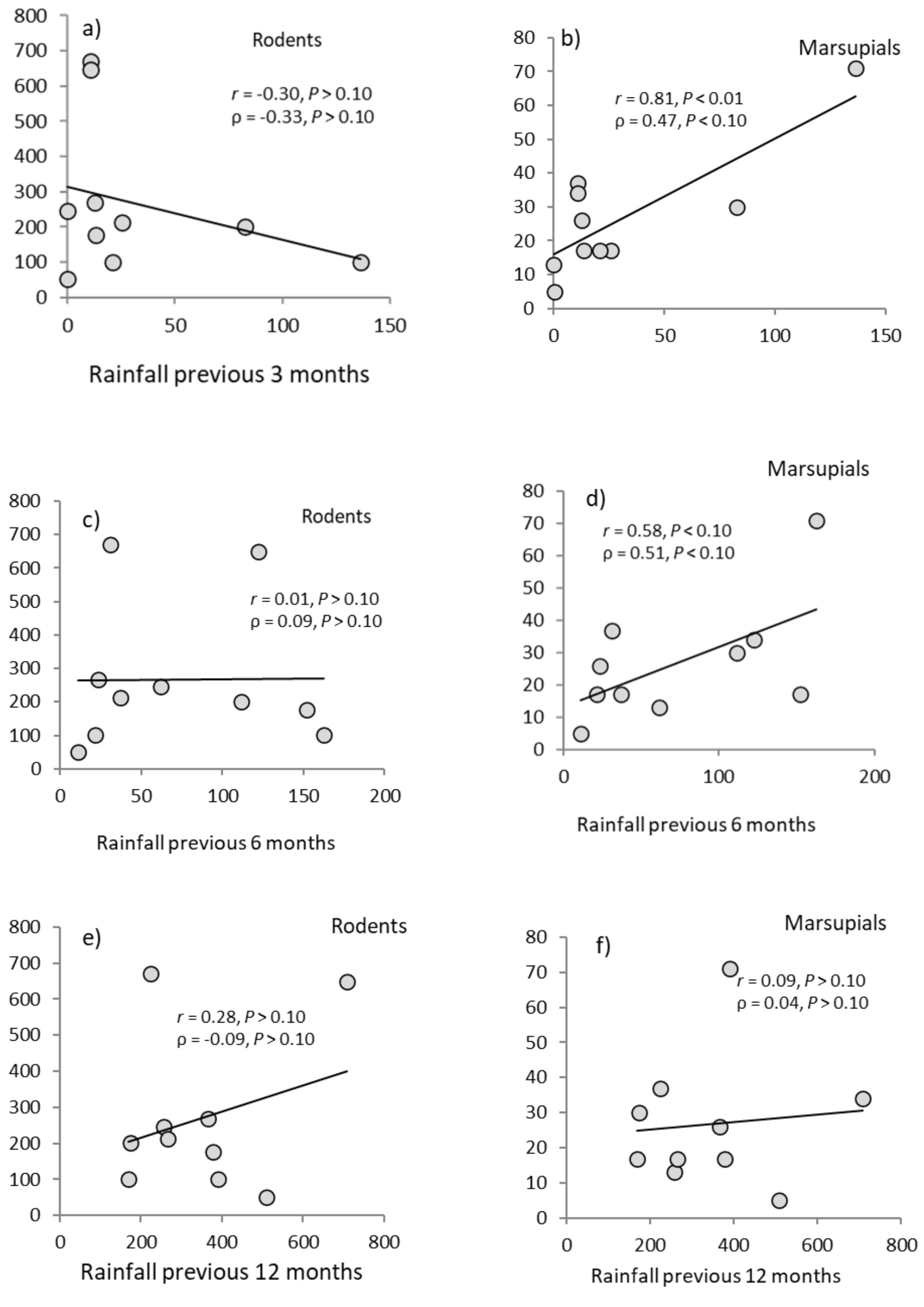


Figure 4.2 Relationships between total captures (in pitfall and Elliott traps) of marsupials and rodents with rainfall in the 3, 6, and 12 months preceding each survey over the 1994-2010 study period. a), c), and e) Rodents and rainfall in previous 3, 6, and 12 months respectively; b), d), and f) Marsupials and rainfall in previous 3, 6, and 12 months, respectively. Values for pearson correlation (r) and spearman correlation (ρ) are shown as well as corresponding p values.

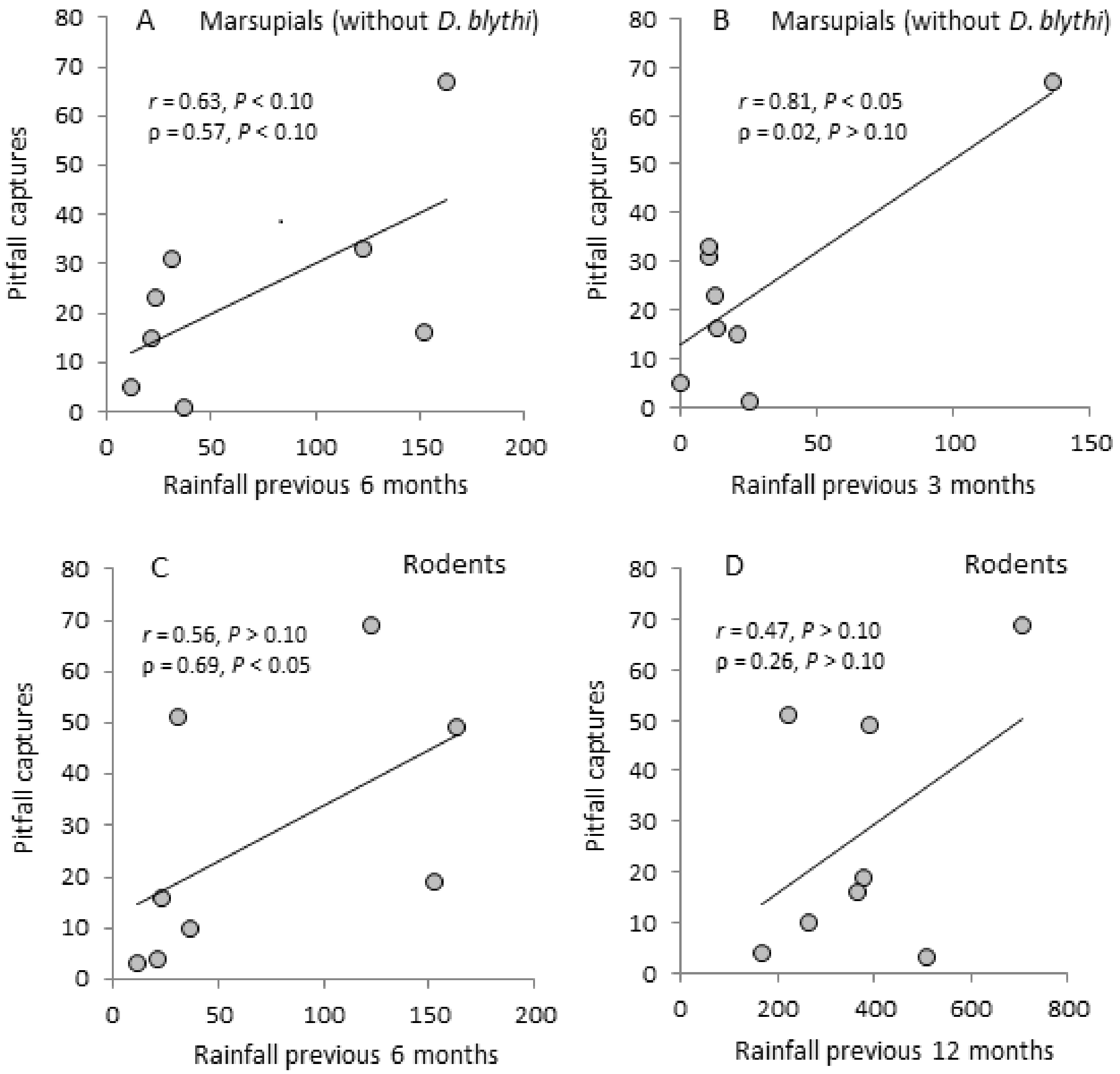


Figure 4.3. Relationships between pitfall trap captures of dasyurid marsupials and rodents with rainfall in the 3, 6, and 12 months preceding each survey over the 1994-2010 study period. a) Marsupials, 6 months; b) Marsupials, 3 months; c) Rodents, 6 months; d) Rodents, 12 months. Values for pearson correlation (r) and spearman correlation (ρ) are shown as well as corresponding p values.

Table 4.2 shows the finite rate of population growth (λ) in captures of mammal groups between consecutive surveys. First, we hypothesized (H2a) that capture rates of both rodents and marsupials would be similar in 1997 and 1999 due to similar preceding rainfall conditions in both years. However, total captures of both groups more than doubled in 1999 relative to 1997 (λ_{ROD} = 3.16 and λ_{MAR} = 2.18; Table 4.2). There was no evidence that rodents or marsupials responded to rainfall within 3 months (H2b), since between 1994 and 1995 marsupials increased (λ_{MAR} = 2.31) while rodents decreased (λ_{ROD} = 0.82). However, we lacked specific pitfall trap data for these years. There was also no consistent evidence that rodents or marsupials declined during short-term 3- to 6-month-long drought (H3c), with capture rates increasing or declining in either or both groups depending on the survey comparison (Table 4.2).

There was strong independent evidence, based on pitfall trap data only, however, that captures of rodents increased more than captures of marsupials following at least 6 months of favourable rainfall (H2d). Indeed, in all 3 relevant cross-survey comparisons (1999-2000, 2002-2004, and 2008-2010) λ_{ROD} exceeded that of λ_{MAR}, with the greatest difference occurring in the very wet year 2010 (12.25 versus 4.47; Table 4.2). There was also evidence that rodents declined more severely than marsupials under long term (12-month) drought conditions (H2e), based both on aggregate captures (λ_{ROD} = 0.38, λ_{MAR} = 0.65; Table 4.2) and on pitfall-only captures (λ_{ROD} = 0.25, λ_{MAR} = 0.65; Table 4.2). Collectively, these data suggest that rodents tended to respond more strongly to longer-term (6-12 month) but not short-term (3-month) rainfall patterns than marsupials.

Table 4.2. Cross survey comparisons of responses of rodent and dasyurid marsupial groups to antecedent rainfall in southwest Northern Territory, Australia. CR comp is the period of cumulative rainfall of interest prior to each survey (3, 6, or 12 months). δCR is the difference (mm) in cumulative rainfall between survey 2 (t + 1) and survey 1 (t) for each CR comp (nd = no data).

		Survey *t*	**Survey *t* + 1**	**CR comp**		**All traps**		**Pitfall traps**	
Hypothesis	Criteria				δCR (mm)	λ_{ROD}	λ_{MAR}	λ_{ROD}	λ_{MAR}
H2a	$\lambda_{ROD} = \lambda_{MA} = 1$	1997	1999	3,6,12	-15, -6, -42	3.16	2.18	5.1	31
H2b	$\lambda_{ROD} > \lambda_{MA} = 1$	1994	1995	3	+ 83	0.82	2.31	nd	nd
H2c	$\lambda_{ROD} < \lambda_{MA} = 1$	1995	1997	3	-57	1.05	0.57	nd	nd
		2000	2002	6	-111	0.08	0.15	0.04	0.15
		2004	2006	6	-129	1.52	1.53	0.84	1.44
H2d	$\lambda_{ROD} > \lambda_{MA} > 1$	1999	2000	6,12	+91, +485	0.97	0.92	1.35	1.07
		2002	2004	6	+141	3.38	3.4	6.33	3.2
		2008	2010	3,6,12	+115, +141, +221	1.00	4.18	12.25	4.47
H2e	$\lambda_{ROD} < \lambda_{MA} < 1$	2006	2008	12	-197	0.38	0.65	0.25	0.65

Rodent and dasyurid responses to wildfire (H3)

The number of study sites affected by fire in the previous 5 years varied widely across surveys, ranging from 6 (out of 8 sites) in 2002, 2004, and 2006, to none in 2000. At least one-half of all sites had been burned in 7 out of 10 surveys, with only 1999, 2000, and 2008 containing 2 or fewer burned sites. The extensive wildfires of 2002 reduced the capture rate of both mammal groups: in 2000, 648 rodents and 34 marsupials were captured during the survey, this reduced to 34 rodents and 5 marsupials following the fires in 2002.

More marsupials and rodents were captured on burned sites in all years except 1999, 2000, and 2008. However, this does not account for differing numbers of burned versus unburned sites across years. Assuming equal mean capture rates in unburned and burned plots, total captures of rodents were higher than expected in burned plots across all years ($\chi^2_1 = 95.6$; $P < 0.001$) and within all individual years ($P < 0.05$ for all) except 2002 ($\chi^2_1 = 1.64$; $P > 0.05$). Very high relative capture rates (RCR = mean capture rate in burned plots/mean capture rate in unburned plots) were observed in burned plots in 1994 (RCR = 7.6), 1995 (3.6), 1997 (5.4), 2004 (6.5), and 2006 (5.3). Rodents appeared to strongly prefer burned areas about 2 years after the widespread severe fires of 2002 (RCR = 6.5 in 2004), but this preference then declined through 2006, 2008, and 2010 (RCR = 5.3, 2.1, and 1.8, respectively).

Marsupials showed a significant preference for burned plots in 1994, 1995, and 2010 ($P < 0.05$ for all), but in all other years showed no significant preference. However, all captures ($n = 5$) in 2002 occurred in burned plots, and the RCR exceeded 1 in 1997 and 2004. As with rodents, the strongest preference for burned plots was observed soon after fire, especially in 1994 (RCR = 6.6), and to a lesser extent in 2010 (RCR = 2.5) and 2004 (RCR = 1.6). Unlike rodents, fewer marsupials were recorded in burned plots in 1999, 2006, and 2008 (RCR < 1), although these differences were not significant ($P > 0.05$). Consistent with these results, rodents and marsupials showed no difference in preference for burned versus unburned habitats in all years except in 1999 ($\chi^2_1 = 3.9$; $P < 0.05$), 2006 ($\chi^2_1 = 30.3$; $P < 0.001$), and marginally so in 2008 ($\chi^2_1 = 3.2$; $P < 0.07$), when rodents strongly preferred burned plots and marsupials showed no preference.

Discussion

The environmental fluxes associated with rainfall, drought, and fire in central Australian deserts are usually assumed to be responsible for the mammal 'boom' and 'bust' events that occur in these landscapes. However, these relationships have been little quantified, albeit with some notable exceptions (e.g., Southgate and Masters 1996; Pavey *et al.* 2008; Greenville *et al.* 2013, 2016). Over the 16 years of the present study, we tested specific hypotheses about the effects of varying rainfall and fire on desert-dwelling mammals in Australia. Unexpectedly, our initial predictions were supported only in part. Our study varied considerably from others conducted in arid Australia, most notably because the interval between samples was long (usually 2 years) and because we sampled a larger area than most previous studies. Because of these differences in our sampling design, it is possible that the immediate responses of small mammals to fire and rainfall were missed, that ephemeral irruptions could have occurred and subsided without being detected, or that responses differed in strength across the different land systems that we surveyed. We keep these possibilities in mind when discussing the results in terms of our broad hypotheses below.

Capture rates and variability in dasyurids and rodents

Rodents were caught more frequently than dasyurid marsupials, which supported our initial hypothesis, but our supposition that dasyurid populations would exhibit less variability than rodents was not well supported. In the same general study area, Masters (1993) observed a much greater increase in numbers of rodents (*P. hermannsburgensis*, *M. musculus*) than dasyurids (*D. blythi*, *N. ridei*, and *S. youngsoni*) following rain, and proposed that the observed stability of dasyurid populations arose from their tendency for reproduction to be locked into seasonal, temperature-driven changes in food availability. In contrast, our study showed broadly synchronous temporal and directional changes in capture rates and a typical boom and bust cycle in both rodents and marsupials, albeit of greater size for rodents.

Generally, this synchronicity may be partly explained by dietary overlap between groups, particularly following rain. Although rodents are omnivorous, some studies have shown a preference by rodents for invertebrates over seed and other food sources (Murray and

Dickman 1994b; Murray *et al.* 1999). Simultaneous exploitation of invertebrate resources (e.g., an abundance of termites following rain) by rodents and dasyurids may explain this pattern. The typically greater absolute fluctuation in rodent numbers may reflect their additional capacity to utilize seed resources. For dasyurids, the ability of most to store energy as fat in their tails, reduce energy demands via torpor during resource scarcity (Geiser and Körtner 2010), and selectively exploit high quality food patches during drought (Bleicher and Dickman 2016), may compensate for their reduced fecundity compared to rodents, resulting in similar overall demography.

The general situation is complicated, however, by differences within both mammal groups. For example, *P. hermannsburgensis*, *N. ridei*, and *D. blythi* underwent massive population fluctuations not seen in other species within their respective groups. Similarly, Letnic (2002) found that population growth of the rodent *N. alexis* was muted compared to that of other sympatric rodents in the Simpson Desert following rain. Within species, Dickman *et al.* (1999a) found that *P. hermannsburgensis* irrupted in the absence of rain at one study site and responded more slowly than expected to rainfall at another. These results suggest that many factors, perhaps including different habitat requirements, relationships with predators, competition, or breeding patterns may generate asynchronous population dynamics among some desert mammals (Greenville *et al.* 2016).

Responses of dasyurids and rodents to rainfall

Capture rates of mammals did not always fluctuate predictably with rainfall. Both rodents and dasyurids appeared to respond positively to accumulated rainfall over the prior 6 months, but only dasyurids responded over the 3-month timeframe. There was no evidence of a rapid boom in *M. musculus* numbers 2 months after rain, as described by Dickman *et al.* (1999a). Rodent numbers tended to decrease more quickly than those of dasyurids during long (12-month), but not short (3-6-month) droughts. However, factors other than just rainfall clearly influenced population size. In some surveys, capture rates increased following drought (e.g., 1999), and in others they failed to increase after rain (e.g., 2010).

Three additional factors may have influenced our results. In the Simpson Desert, Dickman *et al.* (1999a) reported peak populations of *N. alexis* and *P. hermannsburgensis* between June and August, with numbers declining precipitously by summer. As noted above, most of our surveys were carried out in late spring and 2 years apart, increasing the chance that actual population peaks and troughs were missed. Secondly, population increases during dry periods may reflect the high diversity of habitat and topography of our study sites (Bennison *et al.* 2013), that could influence food availability. Most previous studies have taken place in relatively uniform spinifex grassland (Masters 1993; Southgate and Masters 1996; Dickman *et al.* 1999a; Greenville *et al.* 2016) where mammalian dynamics could be expected to be more tightly attuned to the rainfall regime. The drainage lines, waterholes, and varied grassland and wooded habitats of our sites likely provided different levels of food resources at different times for the study species, potentially allowing increases in populations even during periods of low rainfall (Free *et al.* 2013, 2015). Finally, our results may be due to the timing of the surveys which generally coincided with the main dasyurid breeding season (Aslin 1995; McKenzie and Cole 1995).

Rodent and dasyurid responses to fire (H3)

Consistent with our hypothesis, fire appeared to immediately reduce capture rates of both rodents and dasyurids, with both groups declining drastically following the extensive wildfire in 2002 which occurred just prior to the survey. However, following this initial decline rodents and dasyurids rapidly increased in abundance, and by 2 years post-wildfire (e.g., 2004) both groups showed a strong preference for burned habitat. In rodent populations, but not dasyurids, this pattern of preference was sustained for at least 4-6 years after fire, and over the entire study period, which contained both wildfire and prescribed fire, rodents were consistently more numerous in plots that had burned within the past 5 years ("burned" plots). This tendency was weaker, but still present, in marsupials, which showed a preference for burned plots in 4 of the 10 census years, and no preference in other years.

The preference of both rodents and dasyurids for habitat that had burned within the past 5 years, and as soon as 2 years following major wildfire (e.g., 2002), suggests that prescribed burns and occasional severe wildfires in the landscapes of central Australia are not necessarily detrimental to mammal communities, and may be favourable as part of a landscape fire mosaic. This result accords with similar studies conducted in the Chihuahuan desert of North America (Monasmith 1997) but not with work reported elsewhere in arid Australia (Letnic *et al.* 2005; Pastro *et al.* 2011). The latter studies suggest instead that fires create open habitats that increase the hunting success of introduced predators such as European red foxes and feral cats. It is not clear whether introduced predators have similar effects at Uluṟu. Feral cats are subject to intermittent removal by National Park staff, and foxes are sometimes present. Possibly uncontrolled populations of the dingo (*Canis dingo familiaris*) at Uluṟu suppress populations of foxes and feral cats, as they do elsewhere in arid Australia (Letnic *et al.* 2011b), especially in the wake of fires (Bird *et al.* 2018). Although this possibility remains to be tested, dingoes are less likely than cats and foxes to heavily depredate dasyurids and small rodents (Spencer *et al.* 2014) and may allow these small mammals to exploit burned sites.

The omnivorous diet of Australian desert rodents (Murray *et al.* 1999) may facilitate the exploitation of the new plant growth and seed resources that are often available in recently burned areas. Captures of rodents surged in plots burned during the extensive 2002 wildfires, and then stayed higher than in unburned plots for at least 6 more years. This pattern of post-fire persistence was less pronounced in dasyurids, especially 2 years post-burn, perhaps due to the longer period that may be needed for the recovery of insect populations (Leonard 1976) in these habitats.

In summary, this 16-year study of small mammals at UKTNP showed that, contrary to expectation, both rodent and dasyurid marsupial populations fluctuated in a broadly synchronous manner over time. While the larger sizes of the rodent populations resulted in larger absolute changes in population size, boom and bust cycles, driven at least in part by rainfall, were characteristic also of dasyurids. Furthermore, both rodents and dasyurids recovered well from drought and wildfire and tended to prefer habitats burned 2-6 years previously. Our findings contrast with much previous research (e.g., Letnic *et al.* 2005; Pastro *et al.* 2011; Greenville *et al.* 2016). These differences may reflect, in part, differences in sampling regimes that have been used across studies but could also reflect differences in other factors such as levels of predator activity. This later possibility invites further research.

Chapter Five - Historical habitat use and spatial distribution of native vertebrates in three major habitats at Uluru-Kata Tjuta National Park

Introduction

While there is a mosaic of vegetation in Australian deserts, three communities are particularly dominant. Hummock grasslands, primarily containing grasses of the genus Triodia, dominate the arid interior of Australia covering close to 25% of Australia's land mass (Australian Bureau of Statistics 2020). Triodia grasses occur across a range of soil types and different topography (Moore 2005). The next most abundant arid zone vegetation community is low woodlands dominated by trees and shrubs in the genus Acacia and characterized particularly by *Acacia aneura* (mulga). Mulga woodlands stretch from the inland of Western Australia, across the arid interior to south- western Queensland and western New South Wales, dominating up to 20% of Australia's land mass (Australian Bureau of Statistics 2020). Mulga trees can grow to 14 meters and canopy cover is usually between 10 and 30%; an understory of herbaceous, chenopod or saltbush shrubs and grasses is usually present (Department of the Environment and Energy 2019a). Mulga trees are dormant during periods of drought, but they respond quickly to rainfall (Moore 2005) and are fire sensitive (Moore 2005). The third dominant vegetation community in Australian deserts after hummock grasslands and low woodlands is open woodlands dominated by trees in the genus Eucalyptus (Department of the Environment 2015) particularly multi-stemmed species of Eucalypt known as mallee eucalypts (Department of the Environment and Energy 2019b). Mallee woodlands are found throughout semi-arid areas of Australia. The trees grow 3-10 m high (Moore 2005) with a canopy cover of approximately 20% and an understory of hummock grasses, chenopods and other shrubs (Department of the Environment and Energy 2019b).

All three dominant vegetation types of the arid zone can be found in Uluṟu-Kata Tjuṯa National Park (UKTNP). At UKTNP hummock grasslands are divided into two broad groups: soft spinifex (*Triodia pungens*) and hard spinifex (*T. basedowii*) grasslands. Hard spinifex grasslands dominate but are interspersed with patches of soft spinifex. UKTNP also contains large stands of *Acacia aneura* scattered throughout interdune swales and on the firmer soils around Uluṟu and Kata Tjuṯa (Reid *et al.* 1993). Mallee woodlands are also present in the park, occurring in four large patches to the south and west of Uluṟu and are a mix of four *Eucalyptus* species: *Eucalyptus gamophylla*, *Eucalyptus mannensis*, *Eucalyptus socialis* and *Eucalyptus oxymitra* (Reid *et al.* 1993; Moore 2005).

Chapter Three analysed fauna data from a range of vegetation types at UKTNP, however many of these are particularly unique to the park. The sites close to the Uluṟu and Kata Tjuṯa monoliths are likely influenced by these neighbouring massive rock formations. The site situated in the sand plain is the only spinifex grassland in the park absent of sand dunes and the site containing open woodlands dominated by *Acacia ammobia* is also stand alone. It is for this reason that further historical analysis, contemporary experimentation and data collection and discussion within this thesis now focuses solely on the spinifex, mulga and mallee dominated areas of UKTNP, as these communities are the largest and most representative flora communities for the rest of arid Australia.

Previous chapters in this thesis have discussed the role of top down and bottom up drivers of change in deserts with a focus on rainfall and fire. However, as discussed in Chapter Three, the structure and composition of plant communities may drive the structure of the animal communities living within them regardless of the influence of top down or bottom up drivers of environmental change. Habitat selection by mammals and reptiles, based on preferences for the particular vegetation type, plant community or niche preference may evolve over generations (Krebs 2001) and has been demonstrated in arid zone rodents (Price 1978, Thompson 1982) and reptiles (Wilson 2012). For example, similar bird communities were found in similar plant communities in the Mojave Desert (Fleishman *et al*. 2003) and in the small mammal communities of deserts in New Mexico (Hallett 1982). Decreasing habitat complexity was linked to reduced athropod diversity in the semi-arid Chaco forest in Argentina (Gardner *et al.* 1995) and in the deserts of India, some small mammal species show preferences for particular habitat features while others do not (Idris 2009).

However, a particular vegetation community structure does not always accompany a particular suite of fauna. In the study sites in Chapter Three, fauna community composition varied across the survey years at some sites. This situation has been found in other arid zone studies, for example, habitat type did not account for the abundance or species richness of avian fauna in a study in the Tanami desert in Australia, rather the influence of changing seasonal conditions structured the community (Paltridge and Southgate 2001).

This chapter aims to explore the nature of the relationship between the three key vegetation types and reptile and mammal communities in UKTNP. This chapter uses the same long-term data set as that used in Chapters Four and Five, but narrows its scope to look more closely at the fauna of the dominant habitats of mulga and Eucalypt woodland and spinifex grassland, by examining species richness, composition and temporal consistency between and among these vegetation communities.

As in Chapter Four, but focusing here on the reptile and mammal communities of the mulga and mallee woodlands and spinifex grasslands at UKTNP, this chapter investigates the following hypotheses:

H1. The structure of reptile and mammal communities at UKTNP differs across sites representing different plant communities.

H2: Plant communities at sites across UKTNP dictate the composition of genera, families and functional groups of reptiles and mammals.

H3. Reptile and mammal assemblages are consistent across time at each site.

Methods

Study sites

Surveys were conducted at ~1 × 1 km sites in 1994, 1995, 1997, 1999, 2000, 2002, 2004, 2006, 2008 and 2010. Except for one survey, conducted in March 1995, all surveys were carried out in spring (October and/or November).

This chapter examines the animal communities of three of the eight original fauna survey sites established at UKTNP (see Chapter Two for full details). The study sites in this chapter are Site 2 (mulga-dominated woodland), Site 4 (hard spinifex grassland) and Site 5 (eucalypt-dominated woodland). Chapter Two provides detailed descriptions of these sites.

Data collection

Pitfall and Elliott traps were set in one hard spinifex, one mallee woodland and one mulga woodland survey site, as noted above, every two years between 1994 and 2010 to trap reptiles and mammals. Chapter Two again provides a detailed description of the study sites and data collection methods.

Data analysis

To examine differences in faunal communities across the three habitats at UKTNP (H1), the combined totals of reptile and mammal captures were calculated, and the data analysed using each site as a block, with survey years as replicates to detect broadscale similarities or differences in diversity and abundance. The analyses were then repeated separately for the reptile and mammal groups (H1). For the mammal analysis, Site 4 in the 2002 survey year was an extreme outlier, overpowering the analysis and making it difficult to look at the similarity of other sites due to its extreme difference (no mammals were caught), and so it was removed from the analysis of mammals as a group.

To further scrutinise the influence of vegetation type in determining faunal structure, the data were then analysed separately for genera, family and functional groups (H2). Mammals were divided into rodents and marsupials and these groups were analysed separately. Reptiles were divided into their family groups: skinks, agamids, varanids, pygopodids, geckoes, elapids and blind snakes. The skink group was then further sectioned by separating the large and species-rich genus *Ctenotus* from all other skinks.

Reptiles were then analysed based on their dietary and foraging preferences in the following categories: nocturnal generalists (active at night and eating a range of foods), nocturnal specialists (active at night but largely only eating one food type, usually termites), diurnal generalists (active during the day and eating a range of foods) and diurnal specialists (active during the day but largely eating one food type, H2, see Appendix 3).

Finally, to study the influence of changing environmental conditions on the faunal communities at the individual site level, analysis was carried out for each site separately using each survey as a replicate, to examine temporal changes in faunal community composition over time (H3). Within each site, distinct faunal communities were identified by the number of significant R values in pairwise analysis of similarity (ANOSIM) comparisons.

Analyses were conducted in PRIMER (Version 7). The data were transformed to adjust for the effect of dominant species by square root or fourth root transformations. Following the transformations, Bray-Curtis similarity coefficients were calculated between each pair combination of sites, and hierarchical agglomerative clustering used to separate the samples into groups based on their similarity. Non-metric multi-dimensional scaling was then implemented to produce ordination plots showing similarity (or dissimilarity) of these clusters as pairwise distances. Plots with stress values < 0.20 are considered valid representations (Clarke and Warwick 2001). An analysis of similarity was run to test for statistically significant differences between species' or groups' similarity coefficients among the sites. The test statistic, ‘R’, is calculated by permutation, and ranges between 0 (no difference) and 1 (no similarity). Finally, to examine the contribution of individual species to any dissimilarity between groups, analysis of similarity percentages for each pairwise site comparison was run using the SIMPER procedure of PRIMER. Species that are abundant within groups are those that contribute the most to the similarity within groups.

Results

Species diversity and abundance

A total of 10 species of mammal and 65 species of reptile occupied the three study habitats over the 16 years of surveys. Skinks, rodents and geckoes dominated the faunal communities (Fig. 5.1). Spinifex grassland was the most species-rich and fauna-abundant site of the three (Fig. 5.1), except for the elapid and dragon groups where species richness was similar between the mallee and spinifex sites, but abundance was greater in the mallee woodland. The mulga woodland site was characterised by relatively few species and returned considerably smaller numbers of captures than either of the other two sites (Fig. 5.1).

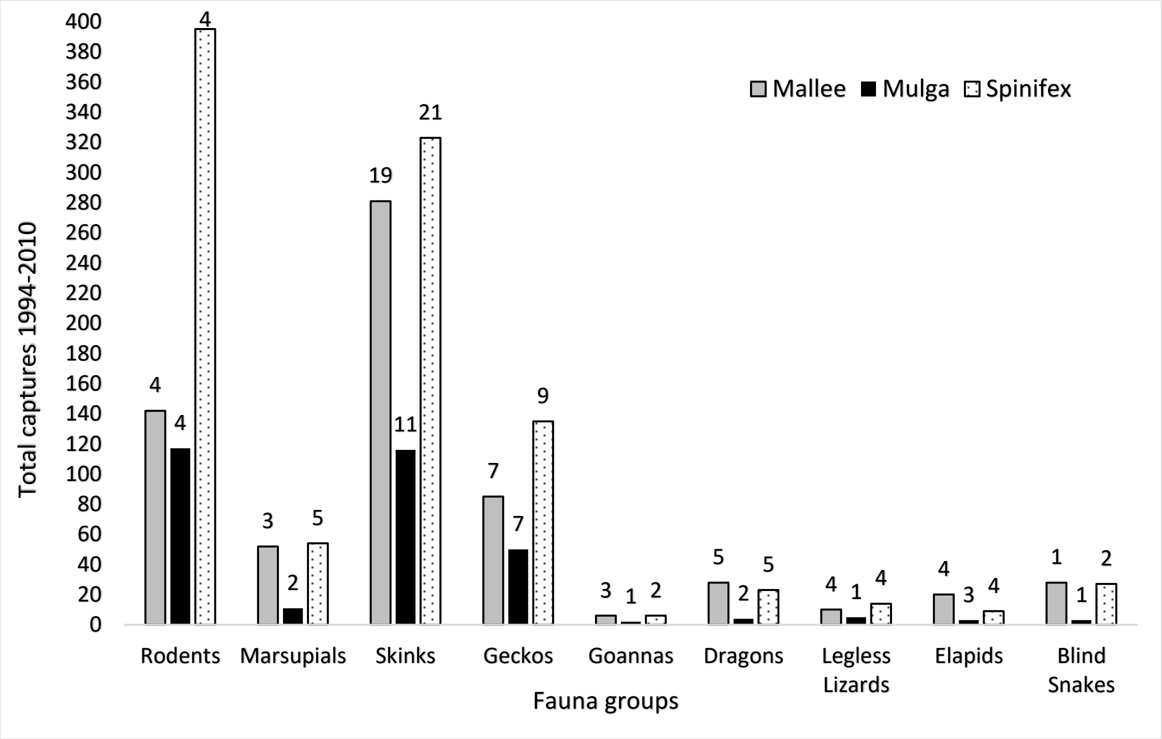


Figure 5.1. Abundance of different fauna groups in mallee and mulga woodland and spinifex grassland survey sites at Uluṟu-Kata Tjuṯa National Park pooled from 10 surveys between 1994 and 2010. The numbers on the y axis represent the total number of captures within each of the different fauna groups. The numbers above the bars represent the number of each species in each fauna group and habitat.

H1:The structure of reptile and mammal communities at UKTNP differs across sites representing different plant communities.

The initial analysis combined mammals and reptiles to compare the similarity of these faunal communities between the sites. At this broad scale there was significant dissimilarity in fauna between the sites (Fig. 5.2a, R = 0.658, $p < 0.001$), with this difference due largely to the uniqueness of fauna in the mulga woodland site. The reptiles and mammals of mulga differed significantly from those in both spinifex grassland (R = 0.939, $p < 0.001$) and mallee woodland (R

= 0.849, p < 0.001) sites. The mallee woodland and spinifex grassland faunal communities were more similar to each other in composition (Fig. 5.2a, R = 0.194, p = 0.007).

H2: Plant communities at sites across UKTNP dictate the composition of genera, families and functional groups of reptiles and mammals.

The mammals of the spinifex grassland and mallee woodland sites showed overlap in ordination space (R = 0.264 p < 0.001, Fig. 5.2b). However, the mammal communities in mulga woodland and spinifex grassland sites differed more markedly (R = 0.48, p < 0.001. Fig. 5.2b), the difference resulting largely from marsupials whose populations showed little similarity between the mulga woodland and spinifex grassland (Table 5.1). This difference was largely the result of partitioning of the *Sminthopsis* genus in the two habitats: *S. youngsoni* was abundant in the spinifex grassland site, whereas *S. ooldea* dominated the marsupial fauna in the mulga woodland site. This difference amounted to 65% of the cumulative average difference between the two sites.

Table 5.1. Global R values and site by site comparison R values of different mammal and reptile groups in three plant communities at UKTNP. An asterisk indicates global R values that were significant (p <0.05).

Fauna Group	Global similarity coefficient	Pairwise site comparisons		
		Mulga/Mallee	Mulga/Spinifex	Mallee/Spinifex
Rodents	0.044	0.081	0.123	0.075
Marsupials	0.359*	0.441	0.578	0.017
Blind Snakes	0.136*	0.272	0.19	0.049
Elapids	0.073	0.189	0.08	0.041
Dragons	0.149*	0.361	0.049	0.037
Geckos	0.169*	0.23	0.211	0.06
Legless lizards	0.135	0.236	0.027	0.169
Goannas	0.057	0.055	0.136	0.004
Skinks	0.703*	0.868	0.99	0.245
Skinks - *Ctenotus*	0.213	0.034	0.243	0.457
Other skinks	0.472*	0.64	0.655	0.126

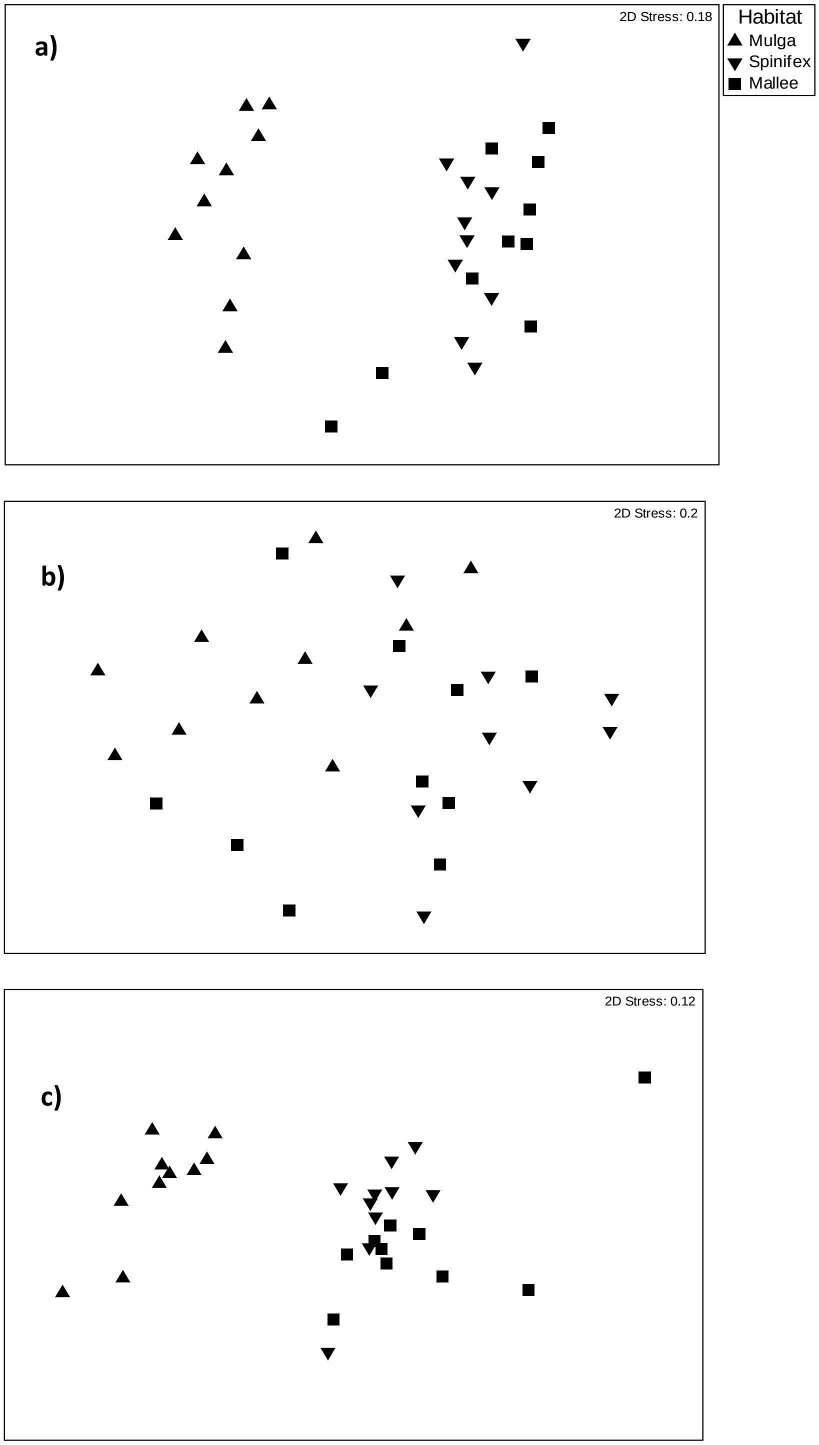


Figure 5.2. Ordination plots of the level of similarity between the combined mammal and reptile communities of mallee and mulga woodlands and spinifex grassland fauna survey sites at Uluṟu-Kata Tjuṯa National Park (distance in space between two sites indicates how similar the sites are). The mammal and reptile groups are plotted together (a) and then separately (b mammals and c reptiles).

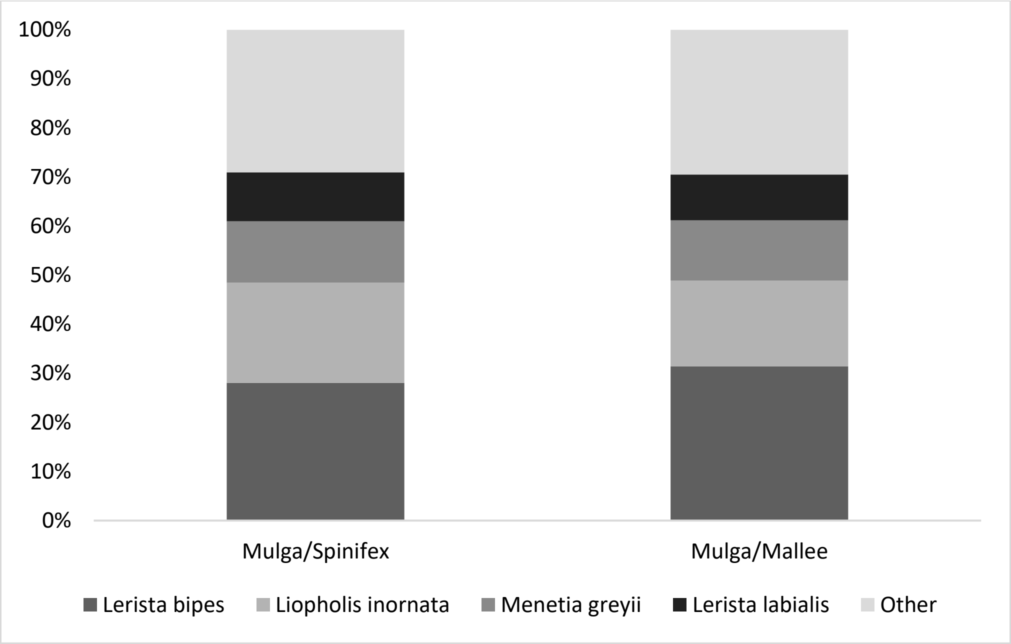


Figure 5.3. SIMPER-revealed contributions of individual skink species to differences in reptile faunal composition between mulga, mallee and spinifex survey sites at UKTNP.

Reptile communities in the mulga woodland site were notably different from those in the other two sites (Table 5.1, Fig. 5.2c), with the variation caused largely by differences in skinks from genera other than *Ctenotus* (Table 5.1). SIMPER analysis showed that these differences were primarily associated with the variation in abundance of two species, together contributing 50% of the cumulative difference (Fig. 5.3). *Lerista bipes* was absent in the mulga woodland site but plentiful in the spinifex site and *Liopholis inornata* was relatively abundant in the mulga site compared to the spinifex and mallee woodland sites (Fig. 5.3).

There were also significant differences in the diurnal generalist reptile group between the plant communities (Table 5.2). *Ctenotus quattuordecimlineatus* and *Ctenotus brooksi* dominated in the spinifex grassland and mallee woodland sites (together comprising 23.2% and 25.1% of the cumulative percentage difference between these two sites, respectively, and mulga woodland), whereas *Ctenotus leonhardii* and *Liopholis inornata* were common in the mulga woodland site (20.5% of the total cumulative difference between the mulga and spinifex sites and 19.96% between the two woodland sites). The smaller dissimilarity between the mallee woodland and spinifex grassland sites, in contrast, is explained largely by the difference in abundance of *Menetia greyii* and *Ctenotus leae* - the former species was more abundant in spinifex and the latter in mallee woodland (contributing 8.6% and 8.4% of the cumulative difference between the two plant communities).

There was less difference in the nocturnal generalist reptile group between the sites, largely because of the similarity between the spinifex and mallee sites (Table 5.2). Diurnal specialist reptile communities were also very similar in mallee woodland and spinifex grassland sites (Table 5.2). There was some difference in the mulga woodland site compared to the spinifex grassland site, due to the presence of *Ctenotus pantherinus* and *Ctenophorus isolepis* in spinifex grassland (84.4% of the cumulative difference). Differences in the abundance of *Ctenophorus isolepis* was responsible for most of the difference in diurnal reptile specialists between the mulga and mallee woodland sites (71.5% of the difference). Nocturnal specialist reptile communities did not differ between sites (Table 5.2).

Table 5.2. Global R values and site by site comparison R values for categories of reptiles based on trophic groups in three plant communities at UKTNP. An asterisk indicates global R values that were significant (p <0.05).

Reptile Group	Global similarity coefficient	Pairwise site comparisons		
		Mulga/Mallee	**Mulga/Spinifex**	**Mallee/Spinifex**
Diurnal Generalists	0.786*	0.986	0.982	0.338
Diurnal Specialists	0.414*	0.636	0.511	0.138
Nocturnal Generalists	0.323*	0.534	0.469	0.007
Nocturnal Specialists	0.114	0.176	0.136	0.039

H3: Comparison of temporal changes in faunal community composition at sites

The faunal community at Site 2, the mulga woodland, was stable across the survey and showed no temporal variation (Fig. 5.4a). At Site 4, the spinifex grassland site, the faunal communities (mammals and reptiles grouped together) were broadly similar across time (R=0.83, p=0.1) with the exception of the survey in 2002 (Fig. 5.4b). This difference was brought about largely by the

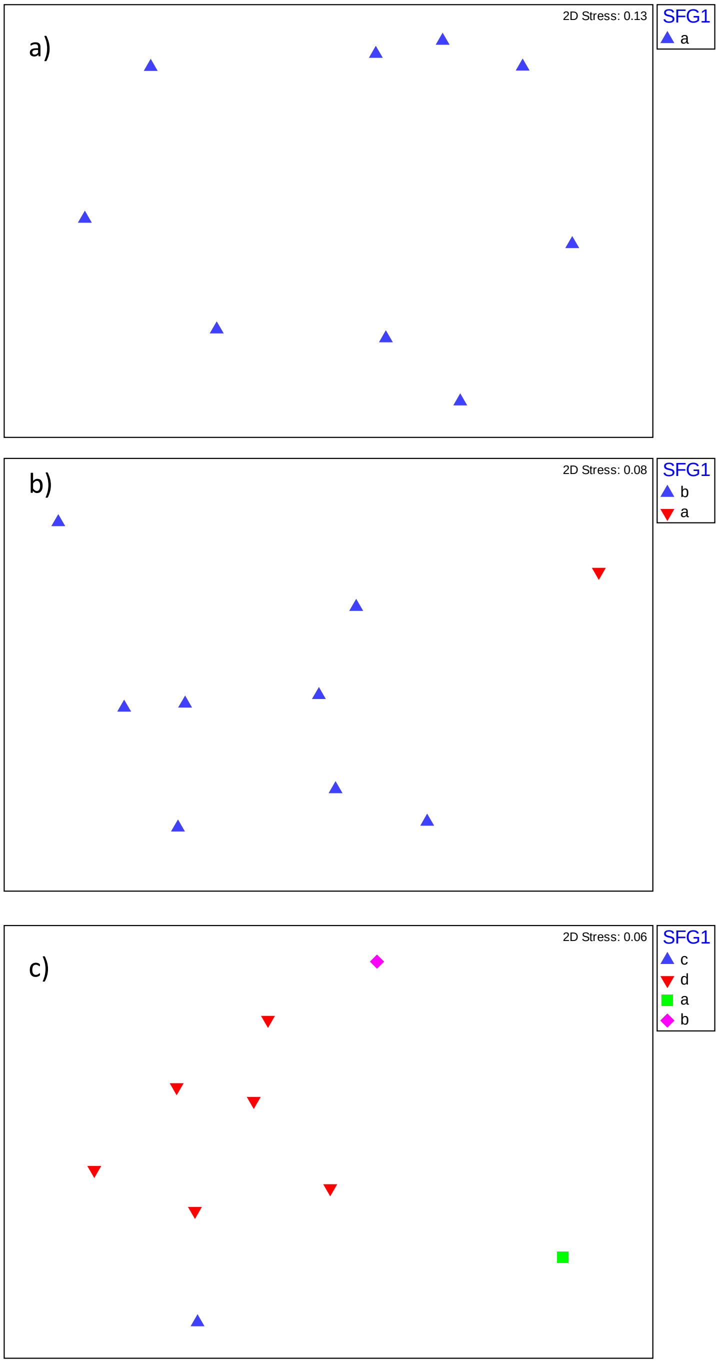


Figure 5.4. Ordination plot of the level of similarity in faunal composition (reptiles and mammals together) in the mulga woodland (a), spinifex grassland grassland (b), and eucalypt woodland (c) sites across survey years at Uluṟu-Kata Tjuṯa National Park (distance in space between two survey times indicates how similar the fauna community at each survey are). The different colour symbols represent distinct groups of fauna.

disappearance of *Pseudomys hermannsburgensis* and *Notomys alexis* from the survey in 2002, as well as an increase in the abundance of Ctenotus helenae and Ctenophorus nuchalis in 2002, in comparison with the other survey years (these changes contributed to 30% of the cumulative total dissimilarity).

Temporal intra-site variation was more marked at Site 5, the Eucalypt woodland site (R=0.87, p=0.012, Fig. 5.4c). Faunal communities at this site clustered into four distinct groups across the 16 years of the study, group a (2000), group b (2010), group c (1995) and group d (all other years, Fig. 5.4c). The difference in 2000 arose primarily from the reduced abundance of *Lerista bipes* and increase in abundance of *Pseudomys hermannsburgensis* and *Notomy alexis* (23.5% of total cumulative difference). In 2010, reduced abundance of *L. bipes* as well as of *Nephrurus laevissimus* and an increase in abundance of *Ningaui ridei*, *P. hermannsburgensis* and *Ctenotus helenae* contributed to 27.7% of the total difference between the sites. The disimilarity in 1995 largely reflected (23.8%) the reduced abundance of *L. bipes, Sminthopsis youngsoni, Liopholis inornata* and *Lucasium stenodactylum* and an increase in abundance of *Ctenophorus nuchalis*.

Discussion

This chapter furthers the investigation of the structure and spatial and temporal dynamics of faunal communities at UKTNP by narrowing the focus to investigate the area's three main habitats: mulga and mallee woodland and spinifex grassland, and two fauna groups, mammals and reptiles. This point of focus will be retained for the next three chapters.

H1: The structure of reptile and mammal communities at UKTNP differs across sites representing different plant communities.

I found some support for the hypothesis that fauna exploit particular plant communities at study sites in UKTNP. Reptile and mammal communities in the mallee woodland and spinifex grassland sites were broadly similar across the 16 years of this study, but fauna at the mulga woodland remained consistently different even when birds were removed from the analysis (see Chapter Two). Mulga woodlands may provide critical resources for some desert fauna that are less abundant or non-existent in the other desert habitats. In many woodlands, dead and dying trees can be a critical resource for lizards (Wilson 2012). Cody 1994 found that the nesting, resting and hiding sites that are provided by dead and dying trees in mulga woodlands were important for resident birds species and similar associations are likely to exist with mulga and reptiles and mammals. The loose bark and rings of litter that often circle the bases of trees may provide a soft substrate for feeding, movement and buffering from intense weather condition (Wilson and Swan 2012). Mulga trees may also offer resting sites off the ground which may be important for temperature regulation in the middle of the day (Melville and Schulte 2001). The more closed and dense nature of mulga compared to mallee woodland perhaps increases the amount and availability of these resources, providing a partial explanation for why mulga contains different suites of fauna to the other two habitats. Species such as *Ctenotus leonhardii* and *Liopholis inornata*, as well as *Sminthopsis ooldea* (Bennison *et al.* 2013) appear to prefer these conditions.

Despite potentially offering resources that are critical for some species, the mulga woodland site had fewer vertebrate species and far fewer captures than either the mallee woodland or spinifex grassland sites. Some desert mammals have been shown to be negatively affected by the presence of clay which is commonly found in mulga areas (Gibson and McKenzie 2009). Both of these latter sites offered soft, sandy substrates in which to burrow as well as greater or lesser coverage of *Triodia* spp. Spinifex provides some protection from larger vertebrate predators such as birds of prey and invasive mammalian predators, and also provides a staple source of food for termites, these factors together may elevate the abundance and diversity of termite-specialist lizards (Morton and James 1988; Pianka 1989). For example, several species of *Ctenotus* include termites as a greater or lesser part of their diets (e.g., *C. brooksi*, *C. quattuordecimlineatus*, *Ctenotus pantherinus;* Wilson and Swan 2012), and all these species were more abundant in the spinifex grassland site. However, perhaps most importantly, mallee woodland—and especially spinifex grassland—respond to large rainfall events by producing large but ephemeral pulses of seed, fruit, green plant and invertebrate resources (e.g., Letnic and Dickman 2010). These pulses in turn trigger irruptions in many consumer species, including some reptiles and rodents (Letnic and Dickman 2010). The 'boom' and 'bust' cycles that typify these habitats may be muted in mulga. Dickman *et al*. 2010 found that in a similar species, *Acacia cambagei*, invertebrate numbers, seed abundance and the availability of shelter resources such as low shrubs and woody debris did not change between periods of nondrought and drought. The existence of a similar situation in mulga woodlands may account both for the relatively few captures of vertebrates in the mulga site compared with the sites in the other two plant communities over the course of the study, as well as the observed stability in community composition over time in the mulga woodland site but not in the spinifex grassland or mallee woodland sites. In addition, and as explored further below, fire is a further driver of vertebrate community change that is more likely to occur in spinifex grassland and mallee woodland than in mulga woodland (Greenville *et al.* 2009).

H2: Plant communities at sites across UKTNP dictate the composition of genera, families and functional groups of reptiles and mammals.

The different faunal community in the mulga woodland site was predominantly due to the clear partitioning of reptiles in the Family Scincidae, between those that live in mulga and those that occur in both spinifex grassland and mallee woodland. The lack of *Lerista bipes* and presence of *Liopholis inornata* in the mulga woodland site made a large contribution to this difference. There are few obvious biological or life history differences between these two species that would clearly explain their habitat preferences. Both species have a general invertebrate diet (Wilson and Swan 2012). *L. bipes* is a reduced-limbed, egg-laying, fossorial skink that swims through the sand (Wilson and Swan 2003). It is possible that this species prefers softer soils for movement, much as does the ecologically and morphologically very similar *L. labialis* (Greenville and Dickman 2009). The present study reflects similar findings from other fauna surveys showing that *L. bipes* is an abundant inhabitant of spinifex grasslands in central Australia (Cowan 2004; Dittmer and Bidwell 2018; Masters 1996; Molyneux *et al.* 2018) and is readily caught in a variety of pitfall trap designs (Morton *et al.* 1988; Hobbs *et al.* 1994). *Liopholis inornata* is a larger skink, living in multi-entranced burrows and bearing live young (Wilson and Swan 2012). As noted, it may be that the firmer soils in mulga woodland are inaccessible to the fossorial and relatively small *L. bipes*, while providing *L. inornata* with robust and durable burrows that require little maintenance. However, while the local distribution of *L. bipes* appears unaffected by fire (Masters 1996), *L. inornata* chooses recently burnt areas and its occurrence declines linearly with increasing time since fire (Nimmo *et al.* 2013). Given that fire is ubiquitous and frequent in occurrence in central Australia, it seems unlikely that *L. inornata* would be found only in mulga woodlands if this species preferred burnt areas; indeed, mulga seldom burns, and *L. inornata* can be relatively abundant in some habitats that have remained long unburnt for long periods (Downey and Dickman 1993).

Choices made by individual species to occupy one habitat over another may be easier to explain for specialist feeders, by the nature of their speciality. For example, *Ctenophorus isolepis* specializes largely on eating ants and prefers to stay in more densely vegetated areas with lower temperatures when feeding during the day. Its association with spinifex habitats, therefore, where ants are plentiful, and shade is supplied by the hummock grass (Daly *et al.* 2007, Daly *et al.* 2008; Pianka and Goodyear 2012), makes intuitive sense, however as ants were not recorded in this study it is difficult to test this theory for these sites in UKTNP. In contrast, the diurnal generalists, *Ctenotus brooksi* and *Ctenotus leonhardii* prefer open areas (Craig *et al.* 2006 and Read 1995, respectively), and therefore the tendency of *C. brooksi* to use the more open habitats provided by the spinifex and mallee sites also makes sense. However, *C. leonhardii*, despite showing a preference for open areas, particularly open areas with saltbush shrub (Read 1995), has been trapped at the same rate in the mulga woodland site regardless of the percentage of ground cover (Schlesinger 2007), demonstrating that the selection of habitats by this species can be complex.

H3: Comparison of temporal changes in faunal community composition at sites

The reptile and mammal species composition of the site in mulga woodlands remained consistent over the time of this study. This constancy occurred despite the fluctuations in rainfall across the study period outlined in Chapter Four, and the dynamic nature of semi-arid ecosystems discussed in Chapter Two. While the mulga woodland site had two distinct faunal communities across 16 years when birds were included (Chapter Two), the removal of birds from the dataset in this chapter showed no significant variation in mammals and reptiles present in the mulga woodland site from the ten surveys.

By contrast, the reptile and mammal fauna of the spinifex grassland site remained less consistent over time, with a distinct compositional shift in 2002, a year when UKTNP (including this site) experienced large wildfires that in turn followed heavy antecedent rains (see Chapter Four). In the 2002 survey, the abundance of *Ctenophorus nuchalis* likely reflected the preference of this species for newly burnt areas (Letnic *et al.* 2004; Daly *et al.* 2007; Pianka and Goodyear 2012). Similarly, as was shown in Chapter Four, rodent abundance reduced dramatically in spinifex grassland following fire, and may explain the disappearance of *N. alexis* and *P. hermannsburgensis* in 2002.

Chapter Three demonstrated the variability of the *Eucalyptus* woodland site when the faunal community also included birds. This variability seemed most easily interpreted as due to the immigration and emigration of non-resident birds following the boom and bust cycles of semi-arid desert systems. However, the analysis in this chapter shows that the less mobile reptile and mammal assemblages at this site nevertheless also change over time. Fire appears to drive change in reptile communities in mallee woodland, with species composition transitioning with age since fire, starting with a higher abundance of nocturnal fossorial species and moving to a community that is more dominated by species that live in leaf litter (Smith *et al.* 2013), or transitioning from a community containing more nocturnal species to one where diurnal species dominate (Smith and Bull 2013); these changes may explain why the nocturnal and fossorial *L. bipes* was such an important species contributing to compositional change in this plant community which had experienced a fire within the last five years in three of the 10 surveys. The different mammal communities occurring across time at this site may also be shaped by species preferences for particular microhabitat components of mallee, or by such drivers as changing floristic diversity and recent rainfall that triggers short term resource pulses (Kelly *et al.* 2013).

The next chapters begin to weave into this analysis the influence of the various top down and bottom up drivers discussed in Chapter Two that may be acting at UKTNP to shape fauna communities in addition to, or instead of, the nature of the plant community. Using the same three study sites set in the representative plant communities of the arid zone, mulga and mallee woodland and spinifex grassland that occur within UKTNP, but introducing greater spatial replication, these analyses begin with a close examination of the abundance and interaction between the three main mammalian predators (Chapter Six) and their influence on faunal behaviour (Chapter Seven), followed finally by an examination of the influence of macro and microhabitat components (Chapter Eight).

Chapter Six - Spatial and temporal relationships between a top predator and mesopredators in an arid environment

Introduction

The removal of an apex or top predator from an ecosystem can have landscape-scale consequences that range from changes in carbon sequestration (Estes *et al.* 2011, Ripple *et al.* 2014) to hyper-herbivory (Ripple and Larson 2000, Beschta 2003, Ripple and Beschta 2004, Letnic *et al.* 2012, Lyons *et al.* 2018), with consequent changes in vegetation communities. The loss of a top predator can also lead to an increase in the abundance and distribution of smaller, lower order 'mesopredators' that had hitherto been suppressed by their apex counterpart, and a consequential increase in pressure on vulnerable prey species at lower levels in the food web. This latter outcome is an example of mesopredator release (Soule *et al.* 1988, Estes 1996), a phenomenon that has been demonstrated in a very diverse range of terrestrial and aquatic ecosystems around the world (Schaller 1970, Rudzinski *et al.* 1982, Mills and Biggs 1993, Palomares *et al.* 1994, Strong *et al.* 1996, Mills and Gorman 1997, Courchamp *et al.* 1999, Henke and Bryant 1999, Palomares and Caro 1999, Crooks and Soule 1999, Fedriani *et al.* 2000, Soule *et al.* 2005). Despite such examples, however, the apparent ubiquity of mesopredator release is debated. It has been challenged on the grounds that much evidence is based on weak inference (e.g. Gehrt and Clark 2003, Hayward and Marlow 2014). There is, in addition, increasing recognition that the effects of top predators on mesopredators can vary over time (Piovia-Scott *et al.* 2017) and space (Newsome *et al.* 2017), with the specific identity of the interactants (Donadio and Buskirk 2006), and with context, especially in human-dominated landscapes (Haswell *et al.* 2017).

Similar debate attends the concept of mesopredator release in terrestrial Australian systems, particularly with respect to the effect of the dingo (*Canis dingo / familiaris*) in suppressing two species of introduced mesopredator, the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*). Indeed, this debate is of particular importance in the Australian context. The two introduced mesopredators have driven many species of small native mammals to low abundance or to extinction (Woinarski *et al.* 2015). Consequently, there is much interest in understanding whether foxes and cats are ‘released’ and increase predation pressure on small prey species in areas where dingo control is undertaken (Newsome *et al.* 2015).

Some Australian studies have provided evidence of intraguild predation, that is, of dingoes killing and eating foxes and cats (Marsack and Campbell 1990, Newsome *et al.* 1983, Thomson 1992, Eldridge *et al.* 2002, Paltridge 2002), while others suggest that dingoes exert pressure on foxes and cats primarily by competing with them for shared resources (Eldridge *et al.* 2002, Corbett 1995, O’Neill 2002, Glen *et al.* 2007). Cats and foxes may reduce the risk of encountering a dingo by using closed or heavily vegetated areas away from tracks or open areas that dingoes frequent, or by being active at different times to the top predator (Eldridge *et al.* 2002, Edwards *et al.* 2002, Algar and Burrows 2004, Wang and Fisher 2012, Schroeder *et al.* 2015). Without exploring the mechanisms of interaction, several studies have also reported an inverse relationship between dingo and fox abundance (Letnic *et al.* 2012, Jarman *et al.* 1987, Lundie-Jenkins *et al.* 1993, Smith and Quin 1996, Newsome *et al.* 1997, Kinnear *et al.* 1988, Newsome *et al.* 2001, Brawata and Neeman 2011, Letnic *et al.* 2011b, Greenville *et al.* 2014, Moseby *et al.* 2018) and the abundances of dingoes and cats (Jarman *et al.* 1987, Lundie-Jenkins 1993, Brawata and Neeman 2011, Greenville *et al.* 2014, Pettigrew 1993, Gibson *et al.* 1994, Christensen and Burrows 1995, Dickman 1996a, b, Brook *et al.* 2012).

However, conflicting or ambiguous results have also been published, suggesting that dingoes may not always exert suppressive effects on the two mesopredator species (Algar and Burrows 2004, Schroeder *et al.* 2015, Newsome *et al.* 2001, Catling and Burt 1995, Fleming 1996, Paltridge *et al.* 1997, Mitchell and Banks 2005, Allen *et al.* 2015). Some studies note that the relationship between foxes, cats and dingoes can vary with habitat, season, level of resource availability and other local situations (Glen *et al.* 2007, Wang and Fisher 2012, Greenville *et al.* 2014, Brook *et al.* 2012, Claridge and Hunt 2008, Allen *et al.* 2011, Kennedy *et al.* 2012). In particular, dingoes are subject to lethal control over vast areas of Australia, and this may reduce their abundance to levels below which any effects they have on foxes and cats are muted or difficult to discern (e.g. Newsome *et al.* 2017).

Although the causes of decline of native mammals in Australia are likely to be multifactorial, predation by foxes and cats is considered a key driver (Woinarski *et al.* 2015, Johnson 2006) and the primary reason for the failure of many reintroduction programs (Clayton *et al.* 2014). There is ongoing discussion about the possible contribution of dingoes to protecting native species from cats and foxes, as Australia searches for ways to reduce the nation's unacceptably high extinction rates of native fauna. Some studies report a protective effect of dingoes on native fauna (Lundie-Jenkins *et al.* 1993, Short and Smith 1994, Short 1998, Fleming *et al.* 2001, Meek and Shields 2001, Short *et al.* 2002, Johnson and Wallach 2016) and recommend the cessation of dingo control or reintroduction of dingoes where they are locally extinct (Dickman *et al.* 2009, Letnic *et al.* 2009, Newsome *et al.* 2015). However, other studies report no protective effect of dingoes on prey (Allen *et al.* 2014) or note that dingoes may themselves have negative effects on native fauna (Allen and Fleming 2012), and advocate caution in making changes to dingo management.

Dingoes are not controlled in all areas and may be allowed to persist locally where cattle are run or where 'predator-friendly' farming is an objective (Johnson and Wallach 2016, Wallach *et al.* 2017). However, such areas are usually small (< 5000 km^2) and not large enough to preclude the effects of dingo control on neighbouring properties (Allen *et al.* 2014). Uluṟu-Kata Tjuṯa National Park (UKTNP) is one of the few regional areas in Australia where there have been few if any dingo control programs (Allen *et al.* 2011). As the nearest pastoral station to the national park is over one hundred kilometres away and dingo control is not common, and historically has not been common, we consider the park’s population unlikely to have been significantly modified by historical or current dingo control programs. Additionally, UKTNP is Aboriginal land, and contemporary land management practices reflect the continued occupancy, ongoing customs and traditional land use patterns of Aṉangu, the local Aboriginal people. As the dingo is an important ancestor in the region’s creation stories and valued as a companion by Aboriginal communities, it has been protected, rather than controlled, in and around the park (Director of National Parks 2010). Further, Newsome *et al.* (Newsome *et al.* 2013), studying dingo genetics in Aboriginal communities further north in central Australia, found that ‘camp’ (resident) dogs were genetically distinct from pure dingoes just outside these communities, indicating minimal interbreeding. These factors suggest that the population of dingoes at UKTNP—being remote and presumed genetically distinct from the hybrid dingo/dogs within the park at the local Mut̲itjulu Community—provides a firm basis for study of the effects of stable dingo packs on foxes, cats and native fauna communities.

The park contains resident populations of foxes and cats. These predators have driven declines in the distribution and abundance of several native vertebrate species including the rufous hare wallaby (*Lagorchestes hirsutus*) and great desert skink (*Liopholis kintorei*) (Clayton *et al.* 2014, Johnson *et al.* 1996, Dennison *et al.* 2015, Hardman *et al.* 2016) that occur, or once occurred, throughout the park. A common method of fox and cat control, particularly in areas where dingoes have been extirpated, is the use of toxic baits; however, this is avoided at UKTNP because it also kills dingoes. This limits options for fox and cat control and restricts management to less effective and smaller scale methods such as trapping and shooting. During this study, cat and fox trapping was primarily limited to the areas immediately surrounding the Uluṟu monolith and the park's office infrastructure including the UKTNP cultural centre. All study sites avoided these areas.

The broad aim of this study is to clarify the relationships between dingoes, foxes and cats in UKTNP. Using occupancy modelling and uncovering patterns in temporal activity distribution, we seek to understand what factors influence the spatial distribution of foxes and cats, including the presence of dingoes. We use passive camera trapping in the three main habitats in the park: structurally complex mulga (*Acacia aneura*) and mallee (*Eucalyptus* spp.) woodland and open spinifex (*Triodia* spp.) grassland and based on past research, as outlined above, we predict that dingoes will influence the spatial distribution and choices of the mesopredators.

Methods

Study area and species

The study was undertaken at Uluṟu-Kata Tjut̲a National Park in central Australia. Vegetation in the area is a mosaic of spinifex grassland and dune-dominated systems interspersed with patches of primarily mallee and mulga woodland. The park has unsealed tracks and roads. The

Katiti-Petermann Indigenous Protected Area surrounds the park, extending these landscape types to a regional landscape scale. Mammalian predators at UKTNP include the dingo, feral cat, red fox and the much smaller, native brush-tailed mulgara (*Dasycercus blythi*, ~75 g). Taxonomic references are from Jackson and Groves 2015.

Camera trap sampling

Movements of cats, foxes and dingoes through thirty study sites were monitored from summer (December-February) 2012 through autumn (March- May) and into winter (June-August) 2013. Sites were established in spinifex grassland (10 sites), mallee woodland (8 sites) and mulga woodland 12 sites) throughout UKTNP (Appendix 2). Existing vegetation mapping (Director of National Parks 2010) was used to identify patches of the three different habitat types. Sites were located randomly within each habitat type provided there was no recent history of fire within 5 km. Half the cameras were placed alongside tracks (as all three carnivore species are known to use tracks) and the other half were placed away from tracks.

Each site contained a Reconyx HC600 Rapidfire infra-red camera (Reconyx, Holmen, Wisconsin, USA). Track and non-track sites were at least 1.5 km apart to maintain a degree of independence. Cameras were placed on tree trunks, 1 m vertically from the ground, and angled slightly downwards. If the camera was on a vehicle track it was sighted along a track rather than across it. Vegetation that may have resulted in false triggers was either trimmed or removed. No bait was used to attract animals into the field of view. Cameras were set to take three photos for each trigger with no delay. Cameras were installed and left to run at all sites, with regular visits to check battery life and download camera SD cards.

For each photograph we recorded the predator species, date, and time. An individual encounter was classed as one regardless of how many individuals were present at the same time and location (i.e., in the same photo). An encounter was considered individual if photos were separated by at least 30 minutes to establish a degree of independence of each record. Dingoes, foxes and cats were readily distinguishable in all images that we obtained, although we could not identify individuals within each species with confidence.

Temporal relationships

Differences in temporal activity patterns between the three carnivore species were examined by categorising each 24-hour period into eight-time categories (Table 6.1). Each individual photo encounter was then assigned to a category based on the time the photo was taken from its time stamp.

Table 6.1. Time categories used for analyses of predator temporal activity, Uluṟu-Kata Tjuṯa National Park, central Australia.

Time Category	Time period encompassed by category
1	sunset to 2 hours after sunset
2	2 hours after sunset to midnight
3	Midnight to 2 hours before sunrise
4	2 hours before sunrise to sunrise
5	Sunrise to2 hours after sunrise
6	2 hours after sunrise to noon
7	Noon to 2 hours before sunset
8	2 hours before sunset to sunset

Occupancy analysis

We undertook an occupancy analysis to examine how a range of site and survey variables related to cat and fox detectability and occupancy in the national park. Single species, single season occupancy models were used as we assumed that occupancy of cats and foxes, at a population scale, did not change during each season or camera deployment period and therefore the assumptions of the model could be met (MacKenzie *et al.* 2006). Seasons were calendar seasons i.e., summer (December-February), autumn (March-May) and winter (June-August). Within each season, a survey was defined as the first 25 days of camera data for each month.

A ‘site’ in the occupancy analysis context was defined as a single camera station. Models were constructed in PRESENCE 4.0 (Hines 2006). The probability of occupancy and detection were modelled as a function of five site covariates: habitat (mulga, mallee or spinifex), distance to the nearest town and thus potential source of human-derived food (Yulara resort or Mut̲itjulu community – whichever was closest), distance to the nearest rock (Kata Tjut̲a or Ulur̲u – whichever was closest, as a proxy for water availability), the presence of a vehicle track (where 1 was a camera station on a track and 0 was a camera station in a remote location), and dingo presence (the number of surveys when dingoes were present at the site, with 0 = no dingoes, 1 = dingoes present in one survey period, 2 = dingoes present in two of the three surveys and 3 = dingoes present in all three survey periods). Occupancy of foxes and cats was also modelled as a function of one survey covariate, dingo activity, where 0 = no dingoes during the survey, 1 = dingoes present on 0-25% of survey nights, 2 = dingoes present on 26-50% of survey nights, 3 = dingoes present on 51-75% of survey nights, and 4 = dingoes present on 76-100% of survey nights. Covariates were modelled as individuals and additive, and models ranked using Akaike’s Information Criterion (AIC). Models with small AIC value differences (delta AIC ≤2) from the top-ranked model were considered reasonable descriptors of the data. Akaike weights (w_i) were also calculated, representing the probability that model *i* is the best for the data (between 0 and 1), given the entire set of candidate models (Burnham and Anderson 2002).

Results

Camera traps

On average, each camera was active for 260 nights (range 166-274) for a total of 7814 trap nights. Across the nine months of the camera survey, 74 encounters of cats, 117 of foxes and 745 of dingoes were obtained. In addition, four encounters of Australian bustards (*Ardeotis australis*) were recorded, as were 249 encounters of camels (*Camelus dromedarius*), 64 of kangaroos (*Osphranter* spp.), four of sand goannas (*Varanus gouldii*) and one of an emu (*Dromaius novaehollandiae*).

The two canid species were generally encountered along tracks (Table 6.2) whereas cats were encountered fairly evenly between track and remote sites (Table 6.2). Cats and dingoes were most commonly encountered in spinifex sites compared with foxes who were most commonly encountered in the woodland sites (Table 6.2).

Table 6.2. Frequency of encounters and percentage of encounters based on tracks for three carnivorous predators, dingoes, foxes and cats at Uluṟu-Kata Tjuṯa National Park, central Australia.

Species	% of encounters occurring on tracks	Encounters in spinifex sites /100 traps night	Encounters in mallee sites/100 traps night	Encounters in mulga/100 trap nights
Dingo	98.5	15.3	2.2	9.2
Cat	55	1.1	0.7	1
Fox	85	1.2	1.6	1.6

Temporal relationships

All three predators showed the same peak in temporal activity patterns, with the time between midnight and two hours prior to sunrise being the most active (Fig. 6.1). There were 18 occasions when a single camera recorded two different species during the same 24-hour period. Only one of these occurrences involved the species being photographed during the same time category (category 3- midnight to 2 hours before sunrise), with a dingo photographed at 0.14 h and a cat at 3.28 h.

Occupancy analyses

The camera trap data were used to fit single season occupancy models to explore the relationship between a range of covariates and the probability of site occupancy and detection for feral cats (Table 6.3) and foxes (Table 6.4) in summer, autumn and winter. Dingoes were the most important predictor for the probability of detecting feral cats within the national park, with 50% of the highest-ranking models and those within 2 AIC points of the top-ranking model in winter, 100% in autumn and 25% in summer associating a decreasing detection probability with increasing levels of one of the two dingo covariates.

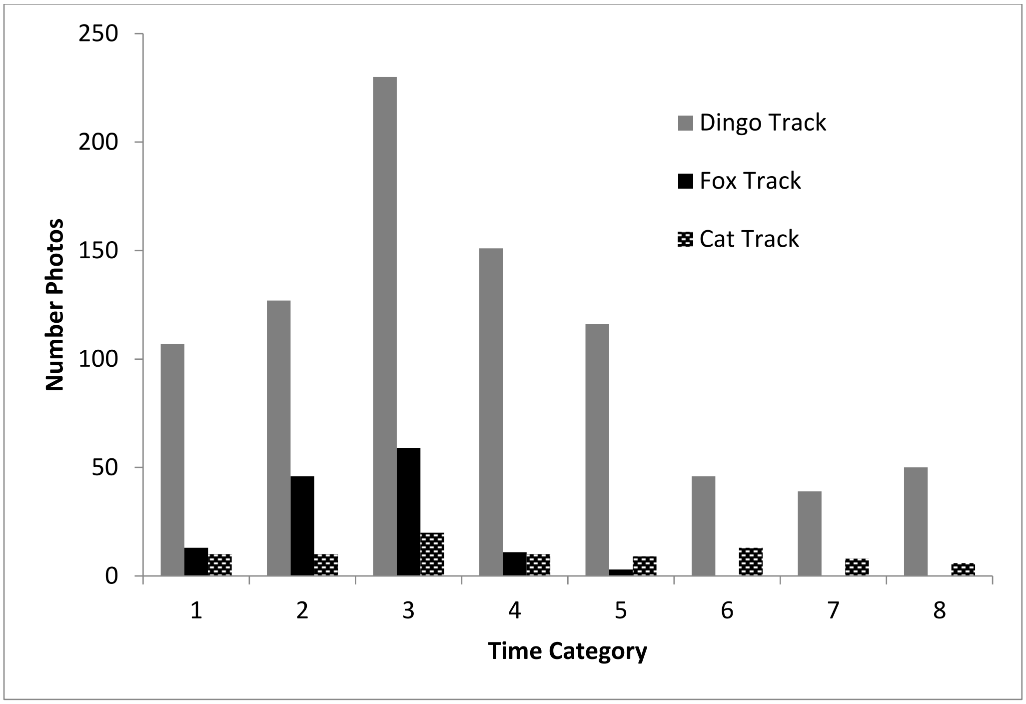


Figure 6.1. Temporal patterns of activity of dingoes, foxes and cats on tracks at Uluṟu-Kata Tjuṯa National Park, central Australia, as shown by numbers of animals photographed (1-sunset and the next 2 hours, 2- 2 hours post-sunset to midnight, 3- midnight to 2 hours pre-sunrise, 4- 2 hours pre-sunrise to sunrise, 5- sunrise and the next 2 hours, 6- 2 hours post-sunrise to noon, 7- noon to 2 hours pre-sunset, 8- 2 hours pre-sunset to sunset).

Other covariates, including habitat type and the presence of tracks, did not feature as consistent explanatory variables. The situation differed with regards to predicting the probability of occupancy of cats in the park, with dingoes responsible for only 37.5% and 20% of the variation in summer and winter occupancy, respectively; dingoes were not a predictor at all in autumn. None of the measured covariates consistently predicted the probability of cat occupancy at a site (Table 6.3).

Table 6.3. The highest ranking single-season occupancy models and those within two AIC points of the top-ranking model for feral cats at UKTNP. The terms in parentheses represent the sources of variation in model parameters: ‘dingo presence’ denotes the number of dingoes seen on cameras for the duration of the survey; ‘distance rock’ denotes distance to Kata Tjuṯa or Uluṟu (as a proxy for water availability); ‘distance town’ denotes distance to Yulara resort or Muṯitjulu community – whichever was closest (as a likely food source); ‘track’ denotes the presence of a track; ‘dingo activity’ denotes the percentage of survey nights a dingo was present at the site. ‘.’ indicates a parameter set equal across survey times. Delta AIC is the difference in AIC values between each model and the model with the lowest AIC. AIC wt is the model weight. *Number of parameters in the model. **Twice the negative log-likelihood. ‘psi’ is the probability of site occupancy and ‘p’ the probability of detection.

Model - Cats Winter	**AIC**	**delta AIC**	**AIC wt**	**Model likelihood**	**No. par ***	**- 2 x LogLik ****
psi (.) p(.)	82.66	0.00	0.0571	1.0000	2	78.66
psi(dingo presence) p(time)	82.66	0.00	0.0571	1.000	2	78.66
psi(distance rock+track) p(dingo presence)	83.06	0.40	0.0467	0.8187	4	75.06
psi(track) p(dingo presence)	83.80	1014	0.323	0.5655	4	75.80
psi(.) p(dingo presence)	83.95	1.29	0.0299	0.5247	3	77.95
psi(track) p(.)	84.07	1.41	0.0282	0.4941	3	78.07
psi(.) p(dingo activity)	84.24	1.58	0.0259	0.45383	3	78.24
psi(.) p(distance town)	84.29	1.63	0.0253	0.4426	3	78.29
psi(distance rock + dingo presence) p (dingo activity)	84.29	1.63	0.0253	0.4426	5	74.29
psi(habitat) p(.)	84.48	1.82	0.0230	0.4025	4	76.48
Model - Cats Autumn	**AIC**	**delta AIC**	**AIC wt**	**Model likelihood**	**No. par ***	**- 2 x LogLik ****
psi(.) p(distance rock + dingo presence)	19.34	0.00	0.0011	0.0034	4	11.34
psi(.) p(dingo presence)	19.53	0.19	0.0010	0.0031	3	13.53
psi(dingo presence) p(dingo presence)	20.23	0.89	0.0007	0.0022	4	12.23
psi(.) p(habitat + dingo presence)	20.55	1.21	0.0006	0.0019	5	10.55
Model - Cats Summer	**AIC**	**delta AIC**	**AIC wt**	**Model likelihood**	**No. par ***	**- 2 x LogLik ****
psi(distance town) p(distance town)	55.65	0.00	0.1277	1.0000	4	47.65
psi(.) p(distance town)	56.09	0.44	0.1025	0.8025	3	50.09
psi(.) p(.)	56.22	0.57	0.0960	0.7520	2	52.22
psi(distance rock) p(distance rock)	56.22	0.57	0.0960	0.7520	2	52.22
psi(dingo activity) p(.)	56.64	0.99	0.0778	0.6096	3	50.64
psi(.) p(dingo activity)	56.64	0.99	0.0778	0.6096	3	50.64
psi(dingo activity) p(dingo activity)	57.32	1.67	0.0554	0.4339	4	49.32
psi(dingo presence) p(.)	57.54	1.89	0.0496	0.3887	3	51.54

The probability of detecting a fox at a site, or of a fox occupying a site in the national park, was less consistently influenced by dingoes, except during autumn when dingo activity and/or presence featured in 50% of the highest-ranking models for probability of occupancy and detection (Table 6.4).

Table 6.4. The highest ranking single-season occupancy models and those within two AIC points of the top-ranking model for foxes at UKTNP. The terms in parentheses represent the sources of variation in model parameters: 'dingo presence' denotes the number of dingoes seen on cameras for the duration of the survey, 'distance rock' denotes distance to Kata Tjuṯa or Uluṟu (as a proxy for water availability), 'distance town' denotes distance to Yulara resort or Muṯitjulu community –whichever was closest (as a likely food source), 'track' denotes the presence of a track, 'dingo activity' denotes the percentage of survey nights a dingo was present at the site. '.' indicates a parameter set equal across survey times. Delta AIC is the difference in AIC values between each model and the model with the lowest AIC. AIC wt is the model weight. *Number of parameters in the model. **Twice the negative log-likelihood. 'psi' is the probability of site occupancy and 'p' the probability of detection.

Model - Foxes Winter	**AIC**	**delta AIC**	**AIC wt**	**Model likelihood**	**No. par ***	**- 2 x LogLik ****
psi(.) p(habitat + track)	64.26	0.00	0.2764	1.000	5	54.26
psi(.) p(track)	64.55	0.29	0.2391	0.8650	3	58.55
Model - Foxes Autumn	**AIC**	**delta AIC**	**AIC wt**	**Model likelihood**	**No. par ***	**- 2 x LogLik ****
psi(dingo presence) p(.)	79.95	0.00	0.0559	1.000	3	73.95
psi(.) p(dingo presence)	80.18	0.23	0.0525	0.89143	3	74.18
psi(distance rock + dingo presence) p(.)	80.32	0.37	0.0490	0.8311	4	72.32
psi(dingo presence) p(distance town)	80.70	0.75	0.0405	0.6873	4	72.70
psi(distance town) p(dingo presence)	80.89	0.94	0.0384	0.6250	4	72.89
psi(.) p(.)	81.41	1.46	0.0296	0.4819	2	77.41
psi(.) p(distance town + dingo presence)	81.69	1.74	0.0257	0.4190	4	73.69
psi(dingo presence) p(dingo presence)	81.75	1.80	0.0250	0.4066	4	73.75
psi(dingo presence) p(dingo activity)	81.80	1.85	0.0244	0.3965	4	73.80
psi(dingo presence + distance town) p(.)	81.87	1.92	0.0235	0.3829	4	73.87
Model - Foxes Summer	**AIC**	**delta AIC**	**AIC wt**	**Model likelihood**	**No. par ***	**- 2 x LogLik ****
psi(distance town) p(track)	75.65	0.00	0.1900	1.0000	4	67.65
psi(distance town) p(dingo activity)	77.67	2.02	0.0692	0.3642	4	69.67

Discussion

The methods used in previous studies to investigate relationships between dingoes, foxes and cats have been critiqued for their limited sampling across different habitats and seasons, and for the use of potentially biased estimators of activity such as sand pad-based indices (Allen *et al.* 2011). The present study was designed to try to overcome these issues by using unbaited and remotely set cameras to collect data, and by sampling across multiple seasons and habitat types.

For cats, dingoes were the most important and consistent predictor of detectability throughout the year, but particularly during the autumn. Fox detectability similarly was predicted by dingoes, but only in autumn. Other factors affected the detectability of foxes in other seasons. Those factors predicting occupancy of sites for both mesopredators, regardless of season, appeared to be less obviously associated with dingoes and remain unclear. These factors do not relate to any of the covariates included in the occupancy models in this study. Even though the predators were encountered more frequently in particular habitat types (spinifex for dingoes and cat and the woodlands for foxes) habitat type did not feature as a predictor in any of the top-ranking models. This may reflect the real situation – that habitat type has no influence on predator activity – or may relate to the inherently high parameterisation of the habitat models and therefore their lower likelihood of being included in the top ranks as the AIC is partially calculated on the number of parameters in each model.

An important consideration and limitation of this present study was the lack of inclusion of direct measures of prey availability as a covariate. It is plausible that resource availability affects the choices made by foxes and cats about when and where to be active. Allen *et al.* 2015 suggest that bottom up processes (i.e., prey availability) may be strong enough to temper the top down influence that dingoes exert over cats, however Greenville *et al.* 2014 found a more consistent negative relationship between dingoes and cats regardless of prey availability. Variation in resource availability is an important and potentially interacting environmental variable not examined in the current models.

This present study, with dingoes appearing to be consistently associated with the detectability of cats but more variably associated with foxes' mirrors the situation found by Greenville *et al.* (2014) were a consistently negative relationship between photos of dingoes and cats existed regardless of the prevailing environmental conditions (i.e. boom and bust phases of arid environments). The relationship between dingoes and foxes however was only negative when prey was restricted (bust phases). The probability that interference competition between the two canid predators is more acute when prey is scarce could also be a factor explaining the variability of results in the present study. I consider this unlikely however, as prevailing conditions in the lead up and during this study at UKTNP had been dry. Therefore, it is assumed that prey would not have been plentiful. Similarly, as dingoes, foxes and cats share some dietary overlap (Spencer *et al*. 2014), it would have been expected that dingoes would influence the detectability of both species more during winter when reptile prey is scarce, however this was not found to be the case. It is possible that the increase in dingo activity expected during the Autumn mating season may have been influencing fox detectability in this season compared to others.

Even with all three predators most active in the same time period there was only a single instance of them occupying the same camera site, suggesting that there is deliberate spatial avoidance in the movement patterns of these species in peak time periods. As discussed in Chapter Two, one mechanism by which an apex predator can exert pressure on mesopredators is by inducing avoidance behaviour (a mesopredator adjusts its behaviour and distribution to avoid encountering an apex predator). This study suggests that cats and foxes do not avoid being active when dingoes are active, rather any avoidance is spatial. All three species were most active during the same time, but with very limited spatial overlap between the species at any site. The avoidance of high-use dingo areas by the mesopredators has been demonstrated in similar studies (Algar and Burrows 2004, Schroeder *et al.* 2015, Brawata and Neeman 2011, Brook *et al.* 2012), however Greenville *et al*. 2014 found that dingo activity occurred consistently later than the activity of the smaller predators and speculated this may be influenced by the crepuscular patterns of a favoured food source, the red kangaroo (Spencer *et al*. 2014a).

There are several reasons why the temporal activity patterns of dingoes in the current study may have differed from the observed pattern in Greenville *et al*. 2014. Firstly, this study occurred in a consistently dry period possibly reducing the breeding rates of red kangaroos and dispersing the remaining numbers more widely across the national park. Secondly the local indigenous community are enthusiastic hunters of red kangaroos, potentially reducing their availability to dingoes even further. Therefore, it may be that at UKTNP the prey overlap is greater between the three carnivores than seen elsewhere, in turn inducing the overlap in peak activity periods and the spatial (rather than temporal) avoidance observed between the species.

Regardless of the mechanism, the lack of spatial overlap between the three predators at the peak activity time of midnight to two hours prior to sunrise, is evidence to support the hypothesis that dingoes affect the spatial, rather than temporal, distribution of foxes and cats in the park. Our findings lend support to the presence of this form of mesopredator suppression occurring at UKTNP.

While the canids were primarily active on tracks, cats did not seem to travel on tracks more or less often than in remote areas. Areas where trees are present may favour cats by providing easily accessible tree limbs that enhance hunting and allow escape from dingoes (Edwards *et al*. 2002). Mallee woodland has a relatively open ground stratum for easy hunting and enough grass to support a range of ground-dwelling prey. Other studies have reported that cats are more active in 'uncomplicated' landscapes like mallee woodland and less active in habitats that are difficult to move through, such as mountain slopes, rocky hills and dense grass cover (McDonald *et al.* 2015, Hohnen *et al.* 2016, McDonald *et al.* 2016, McDonald *et al.* 2017).

It is difficult to determine if the apparent influence of dingoes on cats in all seasons and foxes in Autumn, reduces the abundance of the mesopredators or any impact they may have on prey communities. Whether dingo-induced shifts in the spatial activity of cats in summer, autumn and winter and foxes in autumn are sufficient to translate to protective effects on the prey communities that are depredated by the mesopredators remains an open question in the study region and is the focus of the next chapter.

Chapter Seven - The influence of dingoes on the foraging intensity of small mammals in Uluru-Kata Tjuta National Park

Introduction

Chapter Six investigated the spatial and temporal distribution, and the detectability, of red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) at Uluṟu-Kata Tjuṯa National Park (UKTNP), including if dingoes are significant influencers on these species. I found evidence suggesting that dingoes are likely to affect the spatial distribution and detectability of cats and to a lesser extent, foxes using occupancy analysis and examining temporal activity overlap between the three species. The relationships between dingoes, foxes and cats are important to understand, particularly with respect to the influence that their presence may have on native small mammals. As described in Chapter One, many species of small and medium-sized native mammals have declined in arid Australia over the last century or more, and predation by the red fox and feral cat have been implicated as primary causes of these declines (Johnson 2006; Woinarski *et al.* 2015), either by direct predation (Burrows *et al.* 2003) or by altering their behaviour to avoid predators (Geiser and Kortner 2010).

In this chapter, giving-up densities (GUDs) are used to examine whether interactions between the predators influence the foraging choices of native prey species. Specifically, I use GUDs to examine the effect of the regular and predictable dingo presence on the foraging choices of small mammals. GUDs are used to measure the 'trade off' that animals make between time spent foraging in resource-rich patches against the risk of predation that is inherent in continuing to forage in those patches. Animals are predicted to 'give up' and move from a site when the effort of finding and continuing to eat food there is no longer worth the risk of predation (Bowers *et al.* 1993; Jacob and Brown 2000). The giving-up density is the amount of food that remains in foraging patches after foraging bouts have concluded. It is a simple and readily quantified measure of the trade-off between the prey animals' need to find enough food and their need for safety (Brown 1988).

Dingoes in central Australia have been shown to be present on tracks commonly and tracks are often used to monitor the species (Edwards *et al.* 2000, Read and Eldridge 2002). Results in the previous chapter suggest that dingoes within UKTNP also follow this pattern of track use, but foxes and particularly cats using tracks to a lesser extent. The present study builds upon this finding and tests the assumption that the common use of tracks by dingoes, but less so by the mesopredators, affects the way that small mammals perceive predation risk and if they, in turn, change their foraging behaviour near tracks. Perception of reduced risk of predation by the smaller predators could arise simply if small mammals encounter few cues, such as odours, left by foxes and cats, or if they associate cues to dingo presence directly with limited mesopredator activity (Jones *et al.* 2016). Several studies in arid Australia show that small mammals are the primary prey of both foxes and cats, but less so of dingoes who prefer larger prey such as macropods, although dietary shifts in all three species can be expected depending on the relative abundance of large and small mammals and other prey under different environmental conditions (Cupples *et al.* 2011; Spencer *et al.* 2014a).

Nonetheless, factors other than a fear of predation might also influence the foraging choices of desert-dwelling mammal species. In using GUDs, where food is usually placed in trays or other discrete containers to create resource-rich patches, at least two factors are potentially important. Firstly, the attractiveness of the food resource used to lure animals to the feeding trays could influence the decision to stay for longer or shorter periods. Highly prized (energetically and nutritionally profitable) food would be expected to result in lower GUDs than less highly prized food. Secondly, the microhabitat surrounding feeding trays may affect the balance struck between foraging time and predation risk: several species in Australia's central deserts have been shown to avoid long periods of foraging in open areas between vegetation (Dickman *et al.* 2010), although species with high mobility and quick escape responses may spend longer in open and potentially risky habitats (Spencer *et al.* 2014b). In general, the proximity of a burrow or secure shelter may increase 'comfort' levels and result in longer foraging times than when foraging on open ground with no such shelter.

In this chapter, I aim to examine the foraging responses of small mammals near to and away from tracks, using tracks as a proxy for dingo activity. I also aim to quantify the influence of other considerations—microhabitat and bait type—on small mammals' GUDs in the presence of higher dingo activity (i.e. near tracks) and low dingo activity (i.e. remote from tracks). Specifically, I test the following hypotheses:

> H1. Small mammals in central Australia (UKTNP) will forage for longer and thus show lower GUDs near tracks than in remote sites.
>
> H2. Small mammals in central Australia (UKTNP) will forage for longer and thus show lower GUDs in the open near tracks than in the open in remote sites.
>
> H3. Food type will make less difference to foraging intensity (as shown by GUDs) near tracks than in remote sites.

For H1, the rationale for the prediction is that small mammals will perceive less predation risk from mesopredators (foxes and cats) in areas where dingoes are more active (near tracks) than where dingoes are scarce (away from tracks). This prediction is based on the occupancy modelling of the previous chapter where dingoes were found to affect the detectability of feral cats (and to a lesser extent) foxes and the patterns of temporal activity distribution which suggest that mesopredators may spatially avoid dingoes (even though their peak activity times coincide). For H2, the rationale is that small mammals will perceive less risk of predation and therefore have less need for cover where dingo activity is high than where it is low, again based on the results of analysis from the previous chapter. For H3, the rationale is that any reduced risk of predation near tracks will allow more foraging time and less need to select between, and prioritise, preferred foods. We assumed that of the two food types used, mealworms would be favoured over peanuts by the insectivores and omnivores that dominate small mammal assemblages in central Australia, including at UKTNP (Bennison *et al.* 2018). Small dasyurid marsupials are entirely insectivorous (Fisher and Dickman 1993), and most native rodents prefer insects over seeds or green plant material when offered equal access to each food type in cafeteria-type trials (Murray and Dickman 1994a, b).

Methods

Study sites

The study was undertaken in 2014 at a subset of the sites used in Chapter Six, located in spinifex grassland habitat within UKTNP. Each of these sites is open sandplain (there are no sand dunes in the immediate area) where the dominant vegetation is spinifex and associated shrub communities (refer chapter Six for a description of the sites and see sites 12-16 Appendix 2). Spinifex was chosen for the location of this study owing to the high levels of dingo activity that were found in this habitat (refer Chapter Five) and because it was expected to support a wide range of small mammals (Reid *et al.* 1993; Bennison *et al.* 2018). The same sites were used as described in Chapter Five, except for Site 16. This site was not used owing to the absence of any small mammals during trials.

Use of tracks by dingoes, foxes and cats at the time of the present GUD study was assumed to reflect the patterns of the same time period in the previous year (June to September 2013) when motion sensing cameras were installed at the spinifex sites. For logistical reasons, it was unfortunately not possible to install cameras on and away from tracks during the present GUD trials. However, I assumed that relative use of tracks by dingoes and the mesopredators were likely to be similar between years for three reasons: 1) There is no dingo control at UKTNP, and there was also no control of cats and foxes during the field studies for this PhD. Hence, there was no reason to expect that human disturbance may have affected either the numbers or behaviour of the predators. 2) Climatic and environmental conditions were similar between years; no fires were experienced, and rainfall and maximum and minimum temperatures continued to track either at or below seasonal average levels between 2013 and 2014. 3) My own casual observations showed many more dingo foot prints on the tracks during the present study. Taken together, these observations provide some support for the assumption that dingoes were using the tracks during the GUD trials, and that dingo track use would be greater than that of either foxes or feral cats as was observed the year before.

Foraging stations

Field work was conducted between July and September 2014. Each site was divided into two subsites. One subsite was immediately adjacent to a vehicle track known to be used by dingoes (refer Chapter Six) - hereafter referred to as 'track' subsite. The other subsite was parallel to, but at least 1.5 km away from the former and is hereafter referred to as the 'remote' subsite. These contrasting subsites were used to examine the effects of the presence of vehicular tracks—and, by extension, dingo activity—on the foraging behaviour of small mammals.

Twelve pairs of feeding stations were positioned 25 m apart in each subsite. Each feeding station consisted of a shallow plastic container (tray) measuring 10 cm × 15 cm × 5 cm deep. The trays were placed on the sand. To examine the effect of microhabitat on foraging, one tray in each pair was placed in the 'open'- at least 10 m from any vegetation large enough to provide shelter (Fig. 6.2). These are subsequently referred to as 'open' trays. The other tray in the pair was placed at least 10 m from the open tray and immediately adjacent to a large spinifex hummock (Fig.6.3). These are subsequently referred to as 'closed' trays.

To examine the effect of food type on GUDs, the paired trays alternated between containing peanuts or mealworms, resulting in six paired foraging stations per bait type per site.

Each individual tray held 200 grams of sand collected from the surrounding area. In the late afternoon, 10 discrete pieces of food (halved peanuts or mealworms, *Tenebrio molitor*) were mixed into the sand in the trays. The following morning, trays were checked, and the number of remaining food items recorded to give a GUD value by station for each night. This was repeated for three consecutive mornings at each site. Pilot trials indicated that 10 food items per tray were sufficient to induce exploration by small mammals, and were also seldom foraged to exhaustion, thus ensuring that GUDs would provide a reasonable measure of the risk versus reward trade-off.

Species identification

To identify the species foraging at each station, a motion sensing camera (Reconyx HC600) supported by an aluminium dropper was placed approximately 1 metre from the feeding tray at a height of 30 cm above the ground, with the focus of the camera on the tray.

After the third morning, memory cards were collected from the cameras, the photos examined, and species identified. Data were excluded from analyses if the species was not a small mammal. Different species of small mammal were more difficult to identify. The characteristically long ears and long tail with a small tuft of hairs on the tip of the tail made identifying spinifex hopping mice (*Notomys alexis*) straightforward (Figs 7.1 and 7.2). Relatively few visits were made to the feeding trays by other species (see Results), so analyses were focused on *N. alexis*.

Fig. 7.1. An 'open' feeding tray and spinifex hopping mouse (at right), showing characteristically long, tufted tail and long ears.

Fig. 7.2. A 'closed' feeding tray and a curious spinifex hopping mouse.

Analyses

Average GUDs for each foraging station were calculated by dividing the total GUD of each station by three (three nights), following Dickman *et al.* (2010). A multi-factor ANOVA was used to compare the effects of site, location (track versus remote), microhabitat (spinifex versus open) and food type (peanuts versus mealworms) on the GUD value.

All data were transformed (square root) prior to analysis of variance to reduce the effects of non-normality. Although this improved the data fit, it did not entirely remove the divergence from normality and a reduced significance level (0.03) was therefore used (McDonald 2017). Initial analysis showed that there were significant interactions between site and other factors. To complete tests of each of the specific hypotheses raised in the Introduction, further analyses were completed using a series of non-parametric Kruskal-Wallis *H*-tests to examine differences in ranked means on a site by site basis. As *H*-tests are not sensitive to non-normality in data compared to parametric procedures such as ANOVA, *P*-values ≤ 0.05 were taken to indicate statistically significant differences. All analyses were carried out in Genstat (18th Edition, VSN International Limited).

Results

Foraging stations

Small mammals were recorded foraging at 62.5 % (90 out of 144) of the feeding stations at the three sites.

Of the ninety feeding stations that were visited, 46 were near tracks and 44 were in the remote subsites. GUDs across the study area had an overall mean of 7.45 ± 2.95 SE for mealworms and 9.52 ± 0.86 SE for peanuts.

Species identification

Photos from the foraging stations showed that > 98% of visits were made by *Notomys alexis* (spinifex hopping mouse). All subsequent analyses were completed for this species alone, as results were too few for other species. Crows were very rarely observed feeding at the trays and on one occasion a sand goanna (*Varanus gouldii*) investigated the trays but was not observed removing food items.

Analyses

Results from the multi-factor ANOVA are shown in Table 7.1. There were significant variations in GUD values between sites, as well as interactions between site and other factors, and food type, microhabitat and location (Table 7.1). Because of the importance of site, tests of each of my three hypotheses are made on a per-site basis in comparisons below.

Table 7.1. Multi-factor ANOVA results on GUD values for the spinifex hopping mouse at UKTNP, averaged over three nights and compared between sites, locations, microhabitats and food types. Significant P-values are shown in bold (i.e. P < 0.03).

	Terms	**ss**	**ms**	***F***	***P***
All bait	Site	1.21	0.61	3.9	**0.023**
	Microhabitat (spinifex/open)	0.07	0.07	0.45	0.503
	Location (track/remote)	0.55	0.55	3.52	0.063
	Food (mealworms/peanuts)	5.66	5.66	36.36	**<0.001**
	Site × Microhabitat (spinifex/open)	0.53	0.26	1.7	0.187
	Site × Location (track/remote)	0.92	0.92	5.93	**0.016**
	Site × Food (mealworms/peanuts)	1.92	0.96	6.17	**0.003**
	Microhabitat (spinifex/open) × Location (track/remote)	0.18	0.18	1.15	0.285
	Microhabitat (spinifex/open) × Food (mealworms/peanuts)	0.03	0.03	0.2	0.657
	Location (track/remote) × Food (mealworms/peanuts)	0.92	0.92	5.93	**0.016**

Hypothesis 1- Small mammals in central Australia (UKTNP) will forage for longer and thus show lower GUDs near tracks than in remote sites

GUDs were lower on the remote stations compared to the stations near tracks at two out of the three sites (Site 12 and 15, Fig.7.1). This difference was significant at Site 12 ($H = 8.46$, $P < 0.01$) but not at Site 15 ($H = 2.292$, $P > 0.05$). At Site 14, GUDs on the remote station were significantly higher than on the track sites ($H = 19.1$, $P < 0.001$).

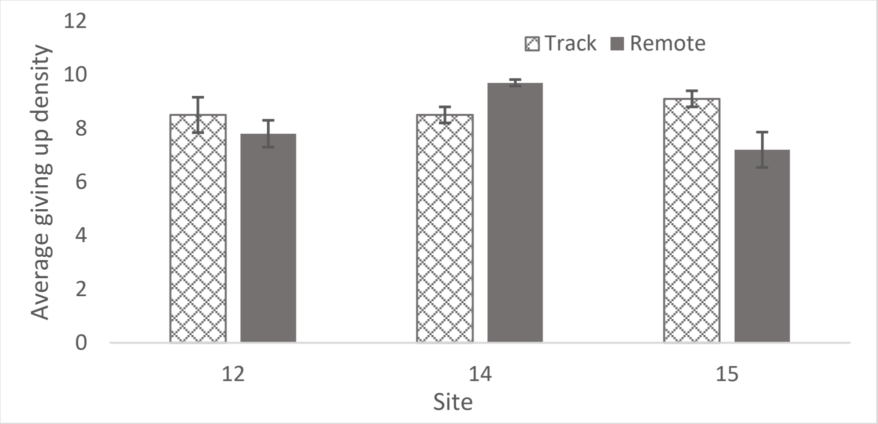


Figure 7.1. Means and SE of average GUD values for the spinifex hopping mouse at track-adjacent and remote subsites at Sites 12, 14 and 15 (spinifex sandplain habitat) at Uluṟu-Kata Tjuṯa National Park, central Australia.

Hypothesis 2 Small *mammals in central Australia (UKTNP) will forage for longer and thus show lower GUDs in the open near tracks than in the open in remote sites.*

GUDs were significantly lower on the open track stations compared to the open remote stations at Site 14 (*H* = 8.82, *P* < 0.01, Fig. 7.2), but showed a reverse pattern in the other two sites. This difference was significant at Site 12 (*H* = 6.66, *P* < 0.01) but not at Site 15 (*H* = 1.1, *P* > 0.05).

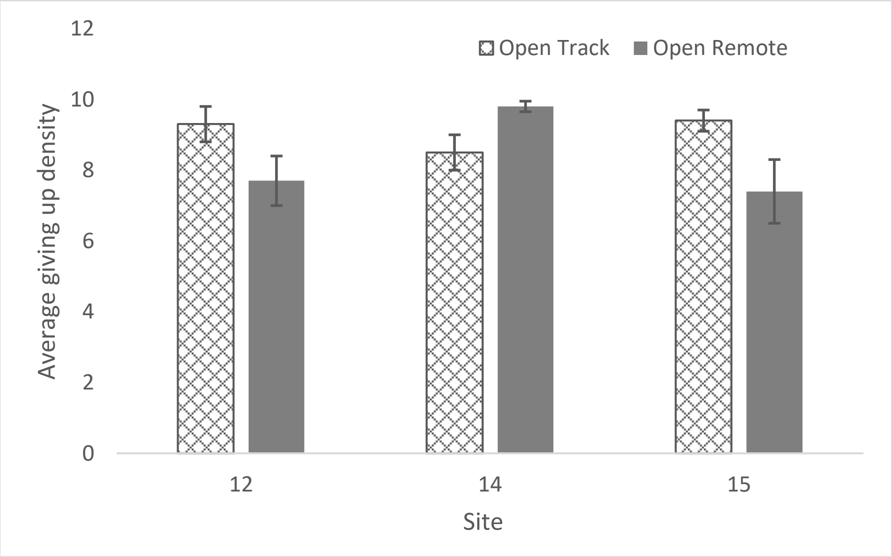


Figure 7.2. Means and SE of average GUD values for the spinifex hopping mouse at open track-adjacent and open remote subsites at Sites 12, 14 and 15 (spinifex sandplain habitat) at Uluṟu-Kata Tjuṯa National Park, central Australia

Hypothesis 3. Food type will make less difference to foraging intensity (as shown by GUDs) near tracks than in remote sites.

At Site 15 significantly more mealworms than peanuts were browsed in the remote sites, but not at the track sites (Table 7.2). This pattern was not repeated at the other two sites. At Site 14 peanuts and mealworms were browsed equally at both the track and remote sites, and at Site 12 mealworms were preferred at both the track and remotes sites (Table 7.2).

Table 7.2 Kruskal-Wallis results on GUD values for the spinifex hopping mouse, comparing location and food type, at Sites 12, 14 and 15 (spinifex sandplain habitat) at UKTNP for the three study sites and significant p values in bold (i.e. P < 0.05).

Site	Location	*H*-value	*P*-value
12	Mealworms vs peanuts-track	5.63	**<0.05**
	Mealworms vs peanuts- remote	9.3	**<0.01**
14	Mealworms vs peanuts-track	1.3	>0.05
	Mealworms vs peanuts- remote	1.7	>0.06
15	Mealworms vs peanuts-track	0.17	>0.05
	Mealworms vs peanuts- remote	11.9	**<0.01**

Discussion

Neither proximity to tracks, location or microhabitat appear to consistently influence the foraging intensity of small mammals at UKTNP, and the ambiguity of the results provide variable support for the three initial hypotheses.

While similar studies have demonstrated that the presence of dingoes in an area does lead to more risky foraging behaviour by prey and positive correlations between dingo activity and small mammal abundance (Gordon *et al*. 2015), and that control of dingoes leads to reduced foraging times for small mammals compared to areas where dingoes are not controlled (Lu 2011), we were unable to demonstrate a similar situation consistently at UKTNP. There was limited evidence to support H1, that small mammals perceive less predation risk close to tracks used by dingoes at UKTNP, with *N. alexis* showing a variable response to foraging near tracks. At Site 14, there was a preference for more intense foraging at near-track stations. Site 14, in the previous year, had the highest number of fox encounters and so foraging near where dingoes were more active may have offered some protection from fox predation. In contrast, at Site 15, where there was no fox encounters, animals foraged to lower GUDs at remote sites more than at near-track sites. At Site 12, where there was the least number of cat and dingo encounters of all sites, and lower numbers of fox encounters than at site 14, *N. alexis* foraged similarly at remote and near-track stations.

There was similarly poor support and more variability in results for H2 and H3. The hypothesis that there would be less need for foraging cover near tracks (H2) was supported at only one site, Site 14, where GUD values at track-based open feeding trays were significantly lower than open trays at the remote area. Evidence for the hypothesis that bait type would make less difference to foraging times near tracks than in remote sites (H3) was similarly lean. Only at Site 15 did *N. alexis* show a preference for foraging longer at mealworm trays compared to peanut trays in the remote subsite, but there was no such preference near the tracks.

The results overall provide very little support for the initial hypotheses and suggest that alternative or additional explanations need to be considered. In the first instance, dingoes may not be effective top predators at UKTNP and may not influence fox and cat populations enough to consistently modify the perceived risk of predation by *N. alexis*. This seems unlikely: the effects of dingoes on foxes, at least, are known to be stronger in areas where dingoes are not culled or otherwise controlled (Newsome *et al.* 2017), and UKTNP is a large regional area where dingo populations have been left intact for decades (Chapter Six). Another explanation may be that, at this larger scale, the presence of dingoes did not have significant effects on the activity of mesopredators at UKTNP because mesopredator populations may already be regionally relatively low due to the large and uncontrolled dingo population. And finally, it is possible that my initial assumption regarding the level of dingo activity was incorrect and dingo activity at my study sites was less in 2014 than it had been in 2013, despite casual observations that dingoes were still present in 2014. Nonetheless, dingo activity could not be quantified during the present study, so the assumption that the activity results from the previous year would accurately reflect the situation in the study year was not justified.

Alternatively, although found in the diet of dingoes in previous studies (Pavey *et al.* 2008, Spencer *et al.*

2014, Doherty *et al.* 2019) dingoes are less likely to choose small mammals such as *N. alexis* as prey (Corbett 1995; Paltridge 2002), especially during dry periods such as that experienced during the present study (Pavey *et al.* 2008, Spencer *et al.* 2017) or when larger macropods are available (Spencer *et al.* 2014a) , it could be that this prey species does not perceive a difference between carnivores in terms of predation risk. Carthey and Banks 2015, found that bush rats responded to dingo activity by reducing feeding time and increasing vigilance. The same result was not seen when the mesopredators were active. The authors in this paper hypothesized that prey species may still be naïve to the more recently introduced fox and cat but perceive dingoes as a threat. A similar situation may be occurring at UKTNP. Assuming that the prey species can detect and recognise carnivores, generically, as a threat, it could then be expected to avoid all carnivores rather than just the mesopredators. All three carnivore species have been shown to consume hopping mice (Pavey *et al.* 2008). This may explain why *N. alexis* foraged for longer in the remote stations at Site 15 where dingo activity on the track was high in comparison to the other sites, and why *N. alexis* avoided the tracks accordingly at that site (dingo encounters the previous year was two times and greater than four times higher at Site 15, than at Site 14 and Site 12, respectively). Alternatively, the long association between dingoes and small mammals in central Australia may have selected for behaviours in prey species that result in inherent wariness of dingoes. By contrast, and as suggested in similar studies (Carthey and Banks 2015), small mammals may be relatively naïve to the dangers of the recently introduced foxes and cats and may not 'know' to avoid them whilst foraging.

Thirdly, the lack of consistency between sites and general lack of support for the initial hypotheses may be because only *N. alexis* was detected at the feeding stations. Individual *N. alexis* are fast moving, agile and can quickly accelerate to high speeds. Once reaching a burrow they are safe: their burrows are vertical, deep and likely to be difficult to infiltrate (Watts and

Aslin 1981). These characteristics may make the species less wary of predation in general than other sympatric mammals. Rather than making pre-determined or strategic choices of foraging site to avoid predators, *N. alexis* may depend on these traits to escape danger. This might explain the lack of variation in foraging intensity between feeding sites. Indeed, in a sand dune environment in the Simpson Desert, Spencer *et al.* (2014b) also showed that *N. alexis* foraged primarily in the open and moved preferentially across open sand, suggesting that the species relies on escape rather than avoidance behaviour to manage predation risk. Alternatively, as these hopping mice use multiple burrows throughout the landscape (Dickman *et al.* 2010), perhaps their proximity to many refuge options allow them to reduce their risk of predation even when foraging in the open.

The significant site-based differences in the GUD results suggest that there may have been subtle differences between the spinifex sand plains sites that were not examined in this study, despite the sites being visually very similar. Heavy local rainfall events and small-scale fires in central Australia can produce patchy areas of high productivity interspersed with adjacent areas that missed out on an ephemeral rainfall event, or that suffered an intense fire or have been long unburnt and are senescing (Latz 1995). Accordingly, a further explanation for the variability in the results of this chapter could be that there were differences in the availability of food and other resources between sites. It may be that individuals at one site were under more resource pressure than another, resulting in different foraging behaviour reflective of resource availability rather than differences in perceived predation risk. These considerations are examined further in Chapter Eight.

Chapter Eight - The influence of microhabitat and resource variation in structuring fauna communities at Uluru-Kata Tjuta National Park.

Introduction

Previous chapters of this thesis have investigated various components of the Uluru-Kata Tjuta National Park (UKTNP) environment – habitat type, rainfall, fire, predators and their interactions, and the placement of tracks – and explored their effects on the composition and stability of the region's faunal communities. This chapter examines the influence that fine scale differences in microhabitat components and resources can have on terrestrial fauna.

For animals, fine scale microhabitat variation, or variation in an animal's immediate locality, can influence the local intensity of activity of individuals as well as the diversity and abundance of different species at a site (Gonnet and Ojeda 1998, Whitehouse *et al.* 2002). Changes in local availability of food, differences in vulnerability to predation, habitat quality, availability of refuges and burrows or nesting sites and other resources can all influence an individual's fitness and may have varied effects among animals with different life strategies. For example, sedentary fauna may need an abundance of mobile prey or a broad dietary niche to survive and reproduce, while the relative abundance and fitness of more mobile species may be determined by the availability of clumped or inactive prey types (Bergallo and Rocha 1994, Hodar *et al.* 2006). Omnivores may rely on seasonal differences in food availability that necessitate switching between herbivorous and insectivorous diets, depending on local conditions (Murray and Dickman 1994b). For insectivores, local variation in vegetation composition can affect the availability of soil invertebrates (Doblas-Miranda *et al.* 2009), and bare ground reduces the abundance of litter-dwelling invertebrates (Corbalan 2006); variation in vegetation composition can also influence the soil seed bank (Marone *et al.* 2004) and change the utility of a habitat for foragers by modifying the balance between searching for food and remaining safe while doing so (Downey and Dickman 1993, Dickman *et al.* 1999a, Haythornthwaite 2005). Species and, by extension, faunal assemblages, may therefore respond differently across time and space depending on local conditions and security of access to key resources.

We have seen throughout this study, from analysis of data from unreplicated survey sites placed in different habitat types, that the faunal communities within UKTNP often varied across time even in the same place. By re-surveying habitats, with replication, this chapter re-examines the conclusions of Chapters Three and Five and completes the study by examining the effect of microhabitat characteristics and resources on the structure of faunal communities in eucalypt and mulga woodlands and spinifex grasslands at UKTNP. I measured microhabitat and resource components at 24 sites across UKTNP, at the same time as surveying fauna, to test the following hypotheses:

H1: Mammal and reptile assemblages differ between the main habitat types.

H2: Differences in mammal and reptile assemblages are driven by variation in resources and microhabitat characteristics.

Because of the importance of vegetation in creating and structuring microhabitats for animals, vegetation sampling formed the basis of the field surveys undertaken to test these hypotheses. However, because the faunal communities being sampled comprised both small insectivores and omnivores, invertebrates and seeds from the soil seed bank were included to ensure that key food resources were sampled. Further, because of the potential for predator-presence to influence where the small vertebrates were likely to be foraging, the activity of large mammalian predators was also assessed.

Methods

Field Sampling

Survey sites

The 24 survey sites were a subset (remote and track based sites 2, 3, 4, 5, 7, 8, 9, 11,12, 14, 15, 16, Appendix 2) of the sites used in Chapter Six and (for spinifex grasslands) Chapter Seven. The

24 surveyed sites were chosen from the 30 used in earlier chapters based on the logistics associated with site access.

Fauna survey

Between December 2012 and March 2013, the small terrestrial vertebrate fauna was surveyed once at the 24 study sites (Table 8.1). The fauna surveys consisted of two lines of pitfall traps, located randomly within each site. Each line had five traps spaced 5 m apart, with a 30 m drift fence linking the traps. Trap lines weaved around vegetation where necessary to avoid undue disturbance and disruption to the site. Pitfall traps alternated between 20 L buckets and PVC pipes (60 cm deep, 16 cm wide), both dug into the ground so that the lip was flush with the surface. At each end of each drift fence were two funnel traps, making four funnel traps per pitfall line and eight per survey site. Trapping at each site also used 25 Elliott type-A traps (30 × 10 × 9 cm) placed in a grid pattern of five lines of five traps, with each line 25 m apart.

Traps were checked each morning for three consecutive mornings, then closed after the morning check (generally between 9.30 and 10am) and re-opened in the afternoon (generally between 3.30 and 4.00pm) which was considered a compromise between reducing the individuals exposure to the midday heat while still allowing diurnal species to feature in the survey. Although daytime trap closure would have reduced the capture of diurnal reptiles, this was an ethical requirement owing to the high daytime temperatures that were expected (and experienced) during the December - March study period.

Each individual vertebrate caught was identified to species, marked with a texta line in the ear (mammal) or on the ventral abdomen (reptile), weighed, sexed (where possible) and released.

Predator activity

At each site during the fauna survey period of December to March (as outlined in Chapter Six), a Reconyx 600 camera was positioned on the site to record predator activity. Cameras were attached to trees at approximately hip height (1 m) and were checked periodically to inspect SD cards and battery levels, and to replace cards and batteries if needed. An activity index for each of the three large mammalian predator species, the dingo (*Canis dingo/familiaris*), red fox

(*Vulpes vulpes*) and feral cat (*Felis catus*) for each site was calculated by dividing the total number of encounters of that species by the total number of functioning camera nights throughout the survey period (December 2012 to March 2013). An encounter was taken to be an individual predator if photos were separated by at least 30 minutes to establish a degree of independence for each record.

Table 8.1. Timing of 24 surveys undertaken at Uluṟu-Kata Tjuṯa National Park between December 2012 and March 2013. Early= the first 10 days in the month, Mid= the middle 10 days, Late= the rest of the month.

Site Number	Habitat	Survey timing
2 Remote and Track	Mulga woodland	Late February
3 Remote and Track	Mulga woodland	Mid-January
4 Remote and Track	Mulga woodland	Late March
5 Remote and Track	Mulga woodland	Mid-March
7 Remote and Track	Mallee woodland	Early March
8 Remote and track	Mallee woodland	Mid-February
9 Remote and Track	Mallee woodland	Mid-December
11 Remote and Track	Mallee woodland	Early March
13 Remote and Track	Spinifex grassland	Late January
14 Remote and Track	Spinifex grassland	Early December
15 Remote and Track	Spinifex grassland	Mid-December
16 Remote and Track	Spinifex grassland	Late December

Invertebrate collection

Invertebrates (excluding ants and termites) that fell into the bucket or PVC-pipe pitfall traps were collected each morning during the fauna survey. Specimens were dried and then identified into one of six categories: beetles and cockroaches, centipedes, spiders, scorpions, orthoptera and other. These coarse groupings of invertebrates were considered suitable for the purposes of this study as they formed key groups of prey that are eaten by dasyurid marsupials and many lizards (Pianka 2017, Fisher and Dickman 1993). Ants were excluded, due to logistical difficulties and because—apart from specialist myrmecophagous species such as the thorny devil *Moloch horridus,* central military dragons *(Ctenophorus isolepis)* and desert skink *Liopholis* *inornata*—ants form only a minor or incidental part of the diet of all the study species (Fisher and Dickman 1993, Murray and Dickman 1994b). Termites were excluded from the study due to a failure of the survey technique attempted (toilet rolls buried underground).

After collection, each invertebrate group was weighed, and the collective weight recorded in grams. The invertebrates sampled at sites 8 and 16 were damaged during transportation from the field and were unusable, and therefore omitted from further analyses.

Soil seed availability

At each site during the fauna survey, four soil samples were taken at random locations using a hollow square steel template measuring 20 × 20 × 5 cm deep. The template was pushed into the soil until the edges were flush with the ground surface, and all soil within the template was then carefully removed and placed in a zip-lock bag.

The soil in each bag was weighed and then sieved to remove the seeds and other organic debris. Using the 4 X magnifying lens of a binocular microscope, the samples were re-examined to remove all remaining seeds. The total weight of the seeds was recorded after drying. A measurement of seed weight/kg of soil was then calculated for each sample by dividing total seed dry weight by the weight of dry soil from the original sample. Once all four soil samples within each site were processed, the values were averaged to yield one value for each site.

Vegetation community composition

Vegetation community composition was assessed during the fauna survey, within a 50 m × 50 m quadrat placed randomly within each fauna survey site. At each site the abundance and coverage of trees (categories: > 15 m height, 5-15 m and < 5 m), shrubs (categories: 1.5-2.0 m height, 1.0-1.49 m, 0.5-0.99 m and < 0.5 m), grasses (categories: < 0.5 m height and ≥ 0.5 m height) and hummocks of spinifex grass were estimated using the following cover abundance scores: 1 = solitary plant, 2 = isolated plants, 3 = sparsely present and small coverage (< 5%), 4 = plentiful but of small coverage (< 5%), 5 = any number of individuals covering 5-25% of the area, 6 = any number of individuals covering 25-50% of the area, 7 = any number of individuals covering 50-75% of the area and 8 = any number of individuals covering > 75% of the area. Assessments were made by eye by one observer, the author.

Flora surveys

Two Elliott traps and two pitfall buckets within each site were selected randomly during the fauna survey, and all flora species within a 2 m radius identified. For each species, a percentage cover estimate, and the most common life stage were also recorded. The life stage categories were seeding, budding, flowering, fruiting/shedding, shed (seeds already dropped, leaving the husks on the plant), vegetative (alive but no signs of impending or recent reproduction), dead or dormant. Individuals that could not be identified were sampled and later identified by reference to herbarium specimens.

Data analyses

Capture data for each species was pooled across each habitat type and the capture mean and standard deviation for each species by habitat was calculated. Vertebrate species data were then organized to produce a site by taxon matrix. Spearman's rank correlations were computed between all pairs of microhabitat variables, and variables removed that were highly correlated with others (i.e., $r_s > 0.7$; Quinn and Keough, 2002). A final set of largely uncorrelated environmental variables was then produced. As noted above, sites 8 and 16 were removed from further analysis due to the lack of invertebrate data for these sites. The fauna communities of each habitat were compared to each other and to the environmental variables to examine the extent to which habitat type and variability in resources and microhabitat components explained variability in fauna composition, using each survey site as an independent replicate.

The fauna data were initially transformed to adjust for the effect of dominant species by square root transformations, zero adjusted where necessary (i.e., if many zeros produced too many undefined cells, Clarke *et al.* 2006), and Bray-Curtis similarity matrices were then calculated between each pair-combination of sites. To test for differences between the fauna communities of each habitat type, a permutational analysis of variance (PERMANOVA) was undertaken. If a significant difference was detected, a canonical analysis of principal coordinates (CAP, Anderson and Willis 2003) was then used to model the fauna communities and the influence of environmental variables in shaping their composition.

CAP analysis is a discriminant procedure using principal coordinates to find axes through a multivariate cloud of points that best discriminate among *a priori* groups (in this case the habitat types of mallee and mulga woodland and spinifex grassland, Pastro *et al.* 2013). Using a leave-one-out residual sum of squares cross validation method, CAP avoids over-parameterisation to ensure the model has maximum predictive ability (Anderson *et al.* 2008). CAP was also used to model the effect of resource and microhabitat variables and find the strongest correlations between the set of environmental variables most likely to be associated with fauna assemblage structure. For both analyses, the size of the first two canonical correlations (between 0 and 1) indicates the strength of the association between the multivariate data clouds and the group difference or effect of environmental variables (Anderson *et al.* 2008). Following analysis of the combined mammal and reptile dataset, to further scrutinise the influence of varying resource and microhabitat characteristics in determining faunal structures, the analysis was then repeated separately for the reptile and mammal groups.

If the CAP model identified distinguishable groups, Pearson correlations (*r*) were calculated to assess the strength of association between the individual species or variables with the model CAP axes. This is because any variables that show an increasing or decreasing relationships with the CAP axes (which are expressly drawn to separate groups as well as possible) are likely to be the ones that are responsible for the observed difference. Environmental and species variables with a correlation coefficient of 0.5 or greater were assumed to be contributing to the observed group differences and were superimposed on the plot as vectors to form a biplot. The length and direction of each vector indicates the strength and sign of the relationship between that variable and each of the CAP axes. All analyses were performed in the PERMANOVA + add on package for PRIMER V7.

Microhabitat variables

Microhabitat variables were pooled across each habitat type and the mean and standard deviation for each variable per habitat type was calculated. Prior to incorporation into the CAP analysis, spearman rank correlation coefficients between all pairs of variables showed that the shrub categories were highly correlated ($r_s > 0.7$), so all height classes were removed from the analysis except for the most abundant shrub category, shrubs 1.5-2.0 m in height. The removal of shrub sub-categories reduced the number of variables included in the subsequent analyses to: centipedes, spiders, beetles, scorpions, seeds, dingo activity, fox activity, cat activity, % bare ground, trees > 15 m high, trees 5-15 m, trees < 5 m, shrubs 1.5-2.0 m high, grass < 50 cm and hummock grasses (Table 8.4).

Results

Fauna survey

In total, 190 individual animals excluding recaptures (eight blind snakes, five elapids, 22 geckoes, five goannas, 120 skinks, five dragons, 19 marsupials and six rodents, Table 8.2) were captured in 3080 trap nights. Capture means and standard deviation for each species in each habitat is shown in Table 8.3. Most of these captures were in the mallee woodland (100, Table 8.2), followed by spinifex grassland (66, Table 8.2) and then mulga woodland (26, Table 8.2). Skinks were the most common species captured within the lizard group, comprising 79% of the total lizard captures. Of this total, more than a half of the captures were from two species, the panther skink *Ctenotus pantherinus* (23% of total skink captures) and north-western sand slider *Lerista bipes* (30% of total skink captures). The interior blind snake *Ramphotyphlops endoterus* was the most common snake encountered during the surveys (62% of all snakes), whilst the wongai ningaui *Ningaui ridei* was the most frequently captured marsupial (37% of all marsupial captures, Table 8.2) and the sandy inland mouse *Pseudomys hermannsburgensis* was the most commonly captured rodent (83% of all rodent captures).

Predator activity

Activity levels varied between habitats and species (Table 8.4). Dingo activity was highest in the spinifex grassland, while cat and fox activity was low and relatively consistent across the habitats (Table 8.4).

Resource availability-seeds and invertebrates

Average combined seed weight ranged between 0.74 and 1.34 grams/kilo of soil (Table 8.4). Beetles were the most abundant invertebrate by dry weight. Scorpions and centipedes were abundant in mallee woodlands while spider abundance was consistently low in all habitats (Table 8.4).

Table 8.2. Fauna species diversity and abundance at 24 sites in UKTNP in summer 2012/13. Sites 2-5 are mulga woodland, sites 7-11 are mallee woodland and sites 12-16 are spinifex grassland. T=track, R=remote; numbers in the table represent numbers of captures of each species per site.

Species	S2T	S2R	S3T	S3R	S4T	S4R	S5T	S5R	S7T	S7R	S8T	S8R	S9T	S9R	S11T	S11R	S12 T	S12 R	S14 T	S14 R	S15 T	S15 R	S16 T	S16 R
Ningaui ridei	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	1	1	0	0
Notomys alexis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pseudomys herm.	0	0	0	0	0	0	1	0	0	0	1	1	0	0	2	0	0	0	0	0	0	0	0	0
Sminthopsis hirtipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	0
Sminthopsis ooldea	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0
Sminthopsis youngsoni	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ctenophorus isolepis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1	0
Ctenotus dux	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ctenotus grandis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Ctenotus hanloni	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenotus helenae	0	0	0	0	1	0	0	0	0	0	0	1	0	3	0	0	1	0	1	0	0	0	0	0
Ctenotus leonhardii	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0
Ctenotus pantherinus	0	0	0	0	0	2	0	0	2	0	2	1	0	0	2	2	0	0	3	1	2	8	2	0
Ctenotus quat.	0	0	0	0	0	3	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0
Ctenotus saxatilis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenotus schomburgkii	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Demansia psammophis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Diplodactylus conspic.	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	1	5	2	1	0
Gehyra purpurescens	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Heteronotia binoei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lerista bipes	1	1	0	0	0	1	0	0	2	3	0	2	13	4	3	2	0	1	0	0	0	0	1	2
Lerista desertorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lerista labialis	0	0	0	0	0	0	0	0	2	2	1	3	0	0	2	1	0	0	0	0	0	0	0	0
Liopholis inornata	0	3	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Liopholis striata	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0
Lucasium sten.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Menetia greyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	2
Nephrurus levis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudonaja modesta	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ramphotyphlops end.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	4	0	0	0	0	0	0	1	0
Rhynchoedura ornata	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Simoselaps anomalus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Strophurus ciliaris	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Varanus eremius	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1

Table 8.3. Mean and standard deviations for species in the mulga woodland, mallee woodland and spinifex grassland sites at Uluṟu-Kata Tjuṯa National Park

	Mulga		**Mallee**		**Spinifex**	
Species	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Ningaui ridei	0	0	0.25	0.43	0.63	0.48
Notomys alexis	0	0	0.13	0.33	0	0
Pseudomys herm.	0.13	0.35	0.50	0.71	0	0
Sminthopsis hirtipes	0	0	0	0	0.63	1.32
Sminthopsis ooldea	0.25	0.46	0.13	0.33	0.25	0.66
Sminthopsis youngsoni	0.13	0.35	0.13	0.33	0	0
Ctenophorus isolepis	0	0	0.13	0.33	0.50	0.50
Ctenotus dux	0	0	0.13	0.33	0	0
Ctenotus grandis	0	0	0	0	0.25	0.66
Ctenotus hanloni	0	0	0.25	0.66	0	0
Ctenotus helenae	0.13	0.35	0.50	1.00	0.25	0.43
Ctenotus leonhardii	0	0	1.00	2.65	0	0
Ctenotus pantherinus	0.25	0.71	1.13	0.93	2.00	2.50
Ctenotus quat.	0.38	1.06	0.38	0.70	0	0
Ctenotus saxatilis	0	0	0.13	0.33	0	0
Ctenotus schomburgkii	0.25	0.46	0	0	0	0
Demansia psammophis	0	0	0.13	0.33	0	0
Diplodactylus conspic.	0	0	0.38	0.70	1.13	1.62
Gehyra purpurescens	0	0	0.13	0.33	0	0
Heteronotia binoei	0	0	0	0	0.13	0.33
Lerista bipes	0.38	0.52	3.63	3.71	0.50	0.71
Lerista desertorum	0	0	0.13	0.33	0	0
Lerista labialis	0	0	1.38	0.99	0	0
Liopholis inornata	0.38	1.06	0.25	0.43	0	0
Liopholis striata	0.13	0.35	0.50	0.87	0	0
Lucasium sten.	0	0	0.13	0.33	0	0
Menetia greyi	0	0	0	0	0.75	0.83
Nephrurus levis	0.13	0.35	0	0	0	0
Pseudonaja modesta	0.25	0.46	0.13	0.33	0	0
Ramphotyphlops end.	0	0	0.88	1.36	0.13	0.33
Rhynchoedura ornata	0.38	0.74	0	0	0.13	0.33
Simoselaps anomalus	0	0	0.13	0.33	0	0
Strophurus ciliaris	0.13	0.35	0	0	0.13	0.33
Varanus eremius	0	0	0.13	0.33	0.50	0.50

Analyses

H1: Mammal and reptile assemblages differ between the main habitat types.

i. Mammals and Reptiles

The PERMANOVA showed a significant difference between the fauna communities in the three habitat types (p=0.001) and therefore a CAP analysis was undertaken.

When mammals and reptiles were combined in a single analysis, the suite of fauna present was highly associated with habitat (Fig. 8.1a, Table 8.5). The first canonical axis had a canonical correlation of 0.98 and separated the habitats from mulga woodland on the left to spinifex grassland on the right (Fig. 8.1a). The second axis had a canonical correlation of 0.79 and separated the mallee woodland from the spinifex grassland and to a lesser extent the mulga woodland (Fig. 8.1a). The vector overlay shows that spinifex grasslands were characterized by *P. hermannsburgensis, N. ridei, D. conspicillatus, C. isolepis, C. pantherinus* and *V. eremius*. Mallee woodland was characterized by *R. endoterus, L. bipes* and *L. labialis*. Mulga woodland was characterized by *S. ciliaris* (Fig. 8.1a).

ii. Mammals

The PERMANOVA showed a significant difference between the mammal communities (P=0.001) and therefore a CAP analysis was also undertaken.

Mammal assemblages alone were also influenced by habitat (Fig. 8.1b, Table 8.5). The first canonical axis had a canonical correlation of 0.92 and separated the habitats from mulga woodland on the left to spinifex grassland on the right, with some overlap of the mulga and mallee woodland assemblages at some sites (Fig. 8.1b). The second axis had a canonical correlation of only 0.25 and played a small role in separating the assemblages from mallee woodland in the bottom to mulga woodland in the top (Fig. 8.1b). The vector overlay shows that spinifex grasslands were characterized by *P. hermannsburgensis* and *N. ridei*, and mulga woodland was characterized by *S. ooldea* (Fig. 8.1b).

Table 8.4. Averages and standard deviation for microhabitat variables measured at the surveyed habitats at UKTNP.

	Mulga		Mallee		Spinifex	
Microhabitat variable	Mean	SD	Mean	SD	Mean	SD
Centipedes (dry biomass g)	0.17	0.32	0.73	0.77	0.46	1.00
Spiders (dry biomass g)	0.07	0.09	0.09	0.20	0.03	0.03
Beetles (dry biomass g)	0.37	0.55	1.69	0.49	0.57	0.92
Scorpions (dry biomass g)	0.28	0.40	1.52	0.90	0.38	0.52
Seeds (g)	0.92	1.68	0.74	0.75	1.34	2.20
Dingo Activity	0.09	0.13	0.01	0.01	0.23	0.28
Fox Activity	0.02	0.03	0.01	0.01	0.01	0.01
Cat Activity	0.01	0.01	0.003	0.01	0.01	0.01
% Bare ground	53.44	26.76	44.75	17.65	41.13	10.88
Trees 15-30m high	1.50	2.60	0	0	0.17	0.37
Trees 5-15m high	7.00	0.50	7.00	0.82	2.17	2.73
Trees < 5m high	4.88	2.89	4.17	2.97	0.50	0.50
Shrubs 1.5-2.0m high	3.00	3.00	4.33	3.14	3.17	2.85
Grass (<50cm height)	6.38	2.69	7.33	1.37	7.50	1.50
Hummock grass	3.50	3.61	6.83	0.69	7.50	0.50

Table 8.5: Results from the canonical analysis of principal coordinates (CAP), summarising the chosen number of principal coordinate axes (m), the percentage variation explained by each ordination (% variation), and statistical significance (P). Statistical significance is taken at P ≤ 0.05 and significant P values are indicated in bold.

Model	M	% variation explained	*p*
Fauna/ habitat	8	89%	**0.001**
Mammals/ habitat	3	98%	**0.002**
Reptiles/habitat	3	67%	**0.001**
Fauna/environmental variables	4	61%	**0.025**
Mammals/ environmental variables	2	85%	0.183
Reptiles/ environmental variables	5	83%	**0.001**

iii. Reptiles

The PERMANOVA showed a significant difference between the reptile communities (P=0.001) and therefore a CAP analysis was undertaken.

Reptile assemblages were also highly dependent on habitat (Fig. 8.1c, Table 8.5). The first canonical axis had a canonical correlation of 0.93 and separated the habitats again from mulga woodland on the left, mallee woodland centrally and spinifex grassland on the right (Fig. 8.1c).

The second canonical axis had a canonical correlation of 0.71 and separated the reptile assemblage from mallee woodland in the top to spinifex grasslands in the bottom (Fig. 8.1c). The vector overlay shows that spinifex grasslands were characterized by *V. eremius, D. conspicillatus, C. pantherinus* and *C. isolepis*. Mallee woodlands were characterized by *L. labialis* and *L. bipes*, and mulga woodlands by *S. ciliaris* and *C. schomburgkii.* (Fig. 8.1c).

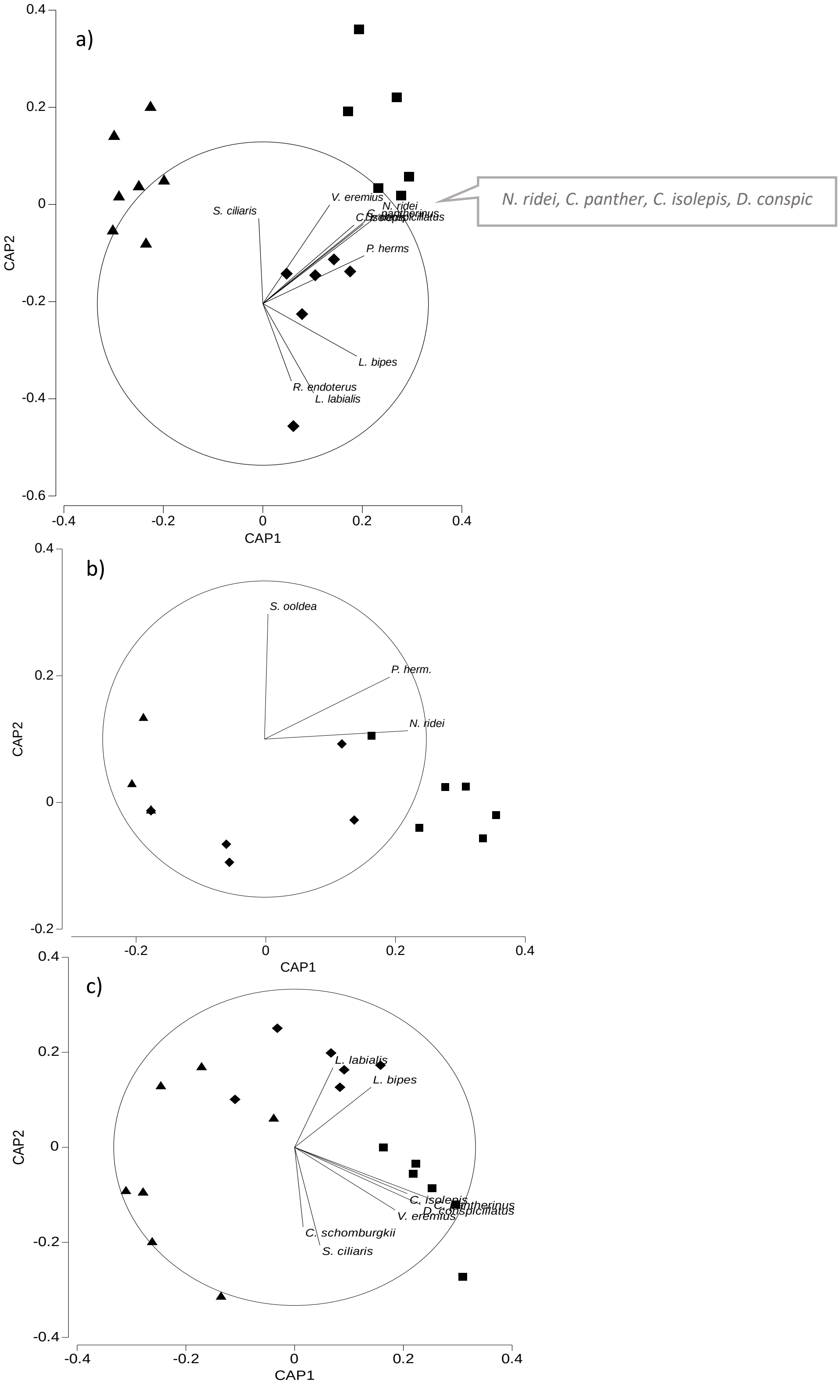


Figure 8.1. Results of canonical analysis of principal coordinates modelling the influence of mulga (triangles) and mallee (diamonds) woodland and spinifex grassland (squares) habitat types on mammal and reptile fauna assemblages combined (a) and for mammals (b) and reptiles (c) alone at UKTNP. Vectors corresponding to Pearson correlations (r > 0.5) of individual species superimposed to show which species contributed the most to within-group differences. D. conspic = *Diplodactylus conspicillatus*, P. herm. = *Pseudomys hermannsburgensis* and C. panther = *Ctenotus pantherinus*. The analyses are based on zero adjusted Bray-Curtis similarity matrices of square root transformed fauna abundance data.

H2: Mammal and reptile assemblage differences are driven by variation in resources and microhabitat characteristics.

i. *Mammals and Reptiles*

A second CAP analysis to model the effect of the environmental variable matrix on fauna assemblages showed that several components highly influenced both the mammal and reptile assemblages (Table 8.5). CAP axes 1 and 2 had canonical correlations of 0.99 and 0.97, respectively. CAP 1 separated species along a gradient of microhabitat variables with fox activity furthest to the left. CAP 2 separated species along a gradient of variables from spinifex hummocks in the top to trees < 5 m and the taller tree categories in the bottom of the graph (Fig. 8.2a). Fox activity and trees were the most influential factors for fauna assemblages in mulga woodlands. For mallee woodlands, spinifex hummocks were an important variable affecting fauna. In spinifex grasslands fox activity and spinifex hummocks were influential (Fig. 8.2a).

Fig. 8.2b shows the effect of these influential microhabitat variables on the fauna communities. Overlays of the Pearson correlations for species abundance data (capture rates) where correlations with the CAP axes were $r \geq 0.5$ showed that *N. ridei, C. isolepis, C. pantherinus*, *D. conspicillatus* and *L. bipes* were associated positively with spinifex hummocks. *C. schomburgkii* and *S. ciliaris* were associated negatively with fox activity, and *L. striata* and *N. levis* were negatively associated with trees.

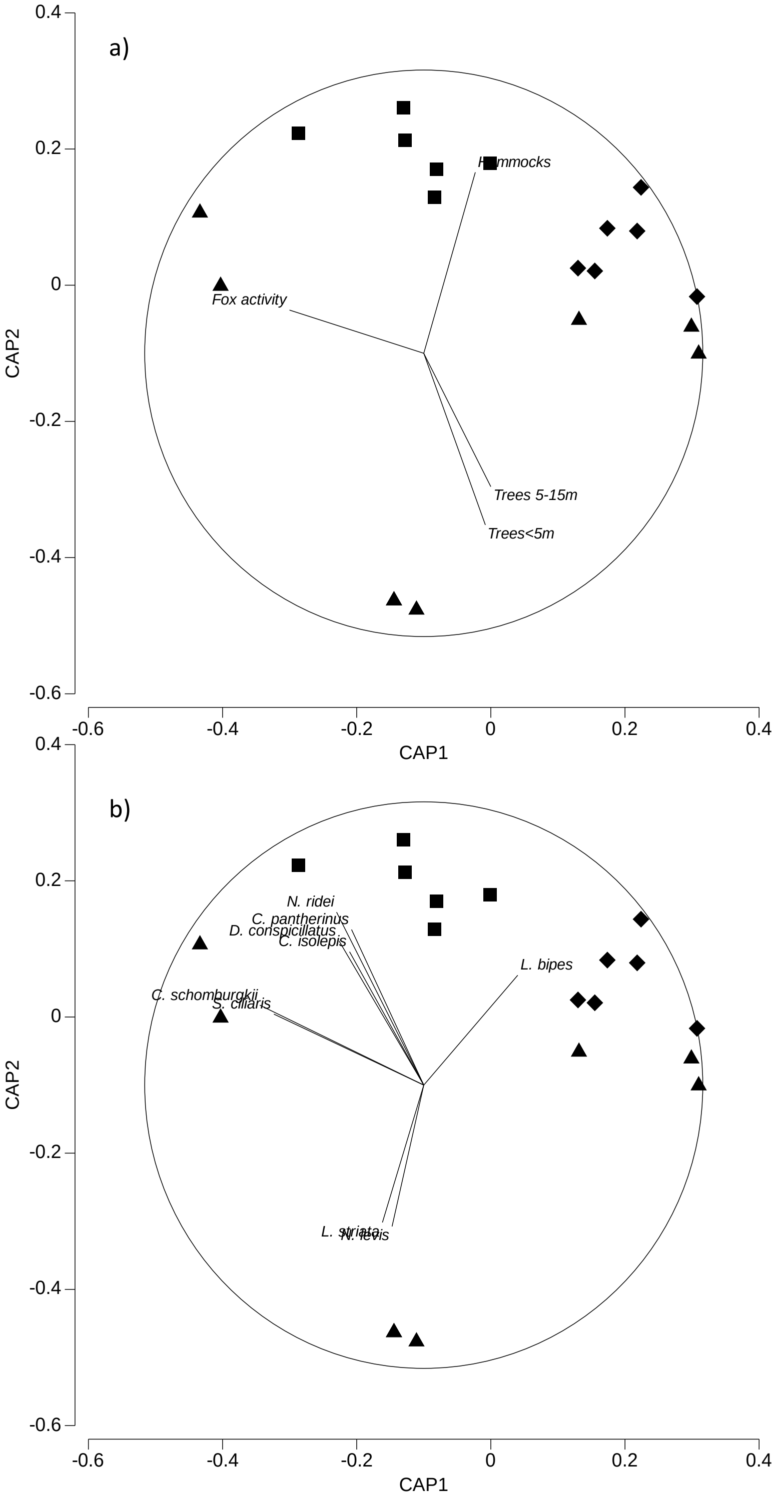


Figure 8.2 a. The effect of microhabitat and resource variables on fauna assemblages in mulga (triangles) and mallee (diamonds) woodland and spinifex grassland (squares). Of the variables examined, spinifex hummocks, fox activity, and trees < 5 m high were identified as contributing most to the variation in fauna. b. Species overlay shows which species are associated with the microhabitat variables (r ≥ 0.5).

i. *Mammals*

A CAP analysis incorporating the microhabitat and resource variable matrix showed that the microhabitat components of an area did not significantly influence mammal community assemblage (Table 8.5).

ii. *Reptiles*

Microhabitat variables were influential in driving reptile assemblage structure (Table 8.5). CAP axes 1 and 2 had canonical correlations of 1 and 0.99, respectively. CAP 1 separated species along a gradient of microhabitat variables with trees < 5 m high to the right and cat and fox activity to the left. CAP 2 separated species with trees < 5 m high as the only variable meeting the $r > 0.5$ requirement (Fig. 8.3a). Trees < 5 m high were the most influential driver of reptile assemblages in mulga and mallee woodland, although fox and cat activity also shaped the fauna assemblage at some mulga and mallee sites (Fig. 8.3a). In spinifex grasslands the reptile assemblage was associated primarily with cat and fox activity (Fig. 8.3a).

Figure 8.3b shows the effect of the microhabitat and resource variables on the fauna communities. Overlays of the Pearson correlations for species with $r \geq 0.5$ showed that *S. anomalus* and *L. inornata* were associated positively with tree cover, whereas negative associations occurred between fox and cat activity and the lizards *C. schomburgkii* and *S. ciliaris.*

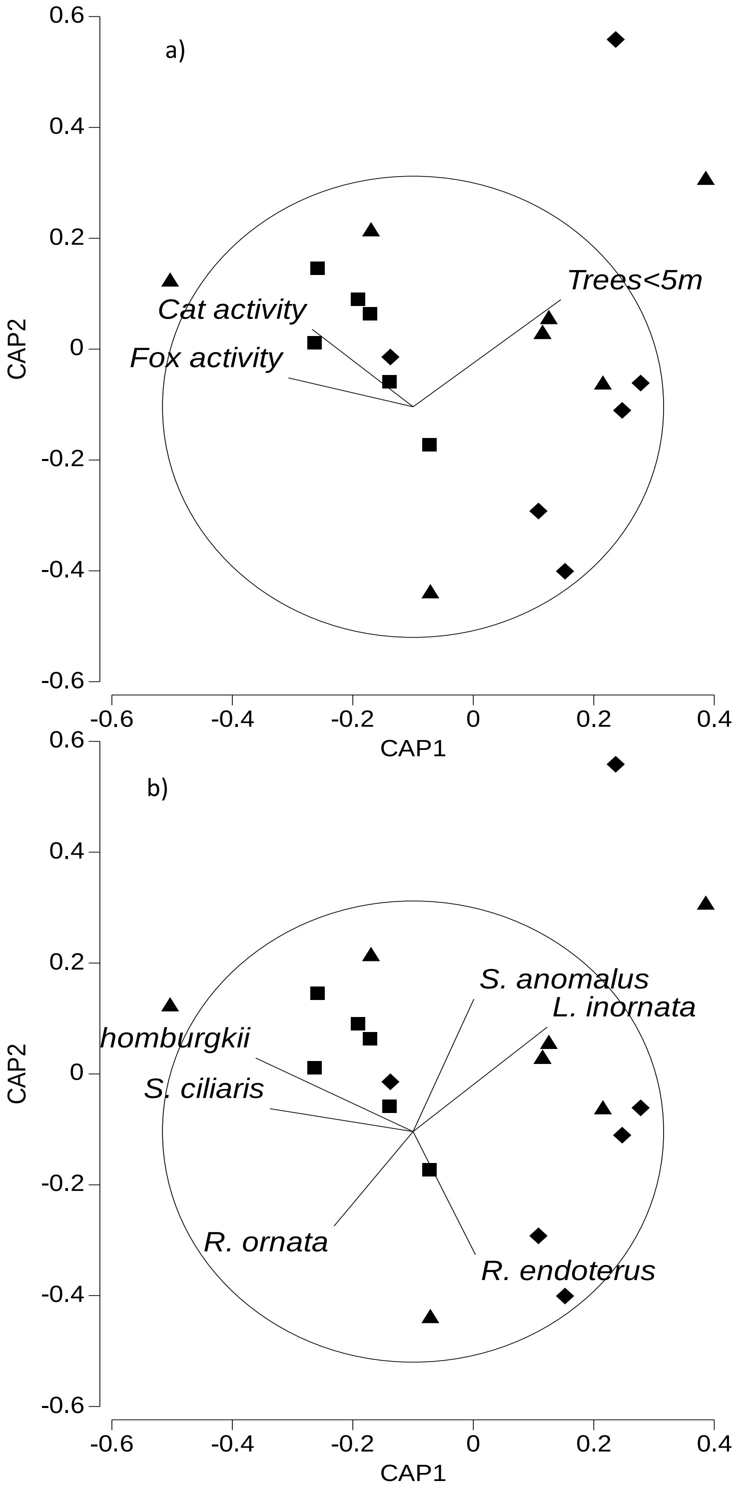


Figure 8.3 a. The effect of microhabitat and resource variables on reptile assemblages in mulga (triangles) and mallee (diamonds) woodland and spinifex grassland (squares). Of the variables examined, trees < 5 m high and 5-15 m high, cat and fox activity are identified as contributing to the variation in reptile fauna. 7.4. b. Species overlay shows which species are associated with the microhabitat variables (r ≥ 0.5).

Discussion

Variation in the accessibility and availability of food and shelter will influence an individual's health, ability to reproduce, and hence fitness, and across all individuals this will affect the success of the population to which the individuals belong. Food webs and the interaction between biotic and abiotic variables are complex and dynamic and thus, for this study, I chose to examine how a select subset of microhabitat and resource variables might affect the local activity of individual mammals and reptiles at sites in three different habitats in the study region. Although based on *a priori* assumptions about which variables might be most influential, I found that assemblages of mammals and reptiles within UKTNP were structured only partially by microhabitat and resource characteristics, with much variation, particularly among mammals, remaining unexplained. The results perhaps reflect the underlying complexity of the desert system. Despite this, some clear patterns emerged, although these differed both for the two target groups of vertebrates and for their constituent species.

The reptile and mammal assemblages in mulga and mallee woodland and spinifex grasslands, when grouped together, were very distinct, supporting the similar conclusion found in Chapters Two and Four. What has been illustrated very clearly in the present, better-replicated study, but was less obvious from previous chapters, is the clear distinction between the reptile fauna of spinifex grassland and mulga woodland. The data presented in this chapter clearly separate the fauna assemblages compared to earlier findings where species often overlapped between the two habitats, perhaps suggesting that there may be some movement of species between habitats when they are sampled over longer periods of time.

The availability of local environmental variables influenced species abundances in many cases. When examining reptiles and mammals together, and when looking at reptiles alone, there were significant associations between species assemblages and microhabitat variables within each habitat. Unsurprisingly, in both the woodlands, the abundance of trees shaped the fauna assemblage. Some of these associations were positive, with *S. anomalus* and *L. inornata* captures increasing with increasing tree cover. *Simoselaps* spp. such as *S. anomalus* shelter in loose sand under shrubs and leaf litter or beneath partly embedded stumps, which may explain their association with trees (Wilson 2012). Additionally, *S. anomalus* feeds almost entirely on *Lerista* spp. (Goodyear and Pianka 2008), a species group that generally regulates body temperature by seeking shade under vegetation like trees and shrubs (Wilson 2012). This may mean that predator and prey often share the same habitat and could explain the habitat choice of the small snake.

The association of *L. inornata* with increasing tree density revealed in this study contrasts with other research, which generally associates the species with open ground (Sass and Wilson 2006, Driscoll and Henderson 2008). However, this finding is consistent with those from Chapter Five of this thesis that also showed the species to prefer more complex structures. As discussed in Chapter Five, trees provide critical resources for some desert fauna. This may include nesting, resting and hiding sites (Melville and Schulte 2001) on the trees themselves or in the rings of loose bark and leaf litter that form at their base, such as the habitat preferred by *S. anomalus* (Wilson and Swan 2012). *Liopholis inornata* is a larger skink, living in multi-entranced burrows and bearing live young (Wilson and Swan 2012). As hypothesized earlier in this thesis, it may be that this fossorial species prefers areas of increasing tree density due to the soil properties of these areas improving the structural integrity of burrows.

Interestingly, at least two of the studied reptile species appeared to avoid trees, including *Liopholis striata* and *N. levis*. *N. levis* is known to prefer foraging on open ground. Wilson (2012) hypothesises that because *Nephrurus* spp. are known to include significant numbers of centipedes in their diet they may prefer open ground for foraging as centipedes (presumably as centipedes may be easier to hunt in the open), perhaps potentially explaining their negative association with the ‘islands of leaf litter’ (Wilson 2012) generated by trees and shrubs in woodlands. However, as the data from this chapter showed an increase percentage of bare ground in mallee and mulga woodlands compared to spinifex grasslands, this hypothesis is not well supported in this study. A radio-tracking study of *N. levis* in the Simpson Desert in western Queensland showed that individual geckoes avoided trees and instead hunted terrestrial prey such as scorpions and wolf spiders on open sand or under sparse shrub cover (Drury 1995). Similarly, Ferguson *et al.* 2015 note that the species forages on open areas between vegetation and found the only individual they captured inhabiting their grassland, rather than woodland sites, during a trapping study in 2007, 2008 and 2013. Further studies are needed to explain both species association with areas of less tree density.

In the grassland sites, hummock grass cover was, unsurprisingly, one of the most important variables associated with the capture of different fauna species, with many species significantly and positively associated with increasing density of spinifex hummocks. When the mammal and reptile fauna were examined as a single group, mammals that were associated with spinifex included the native rodent *P. hermannsburgensis* and the marsupial *N. ridei*. Although many studies suggest that small dasyurid marsupials generally prefer bare ground for hunting (Masters 1993, Dickman *et al.* 2001, Letnic 2002, 2003, Haythornthwaite and Dickman 2006), *N. ridei* is frequently associated with hummock grasses and appears to obtain small prey from within the hummocks (Fisher and Dickman 1993). *Pseudomys hermannsburgensis*, likewise, appears to forage within the vicinity of spinifex hummocks and, by remaining < 10 cm from hummocks most of the time, is able to take refuge within hummocks rapidly if threats appear (Murray and Dickman 1994b). Also associated with spinifex hummocks were reptiles including *C. isolepis, C. pantherinus*, *D. conspicillatus* and *L. bipes.* Spinifex hummocks provide protection from the harsh climate of central Australia, and an effective place of retreat from predation (Wilson 2012).

The use of spinifex hummocks to reduce predation risk was reinforced by the finding that indexes of predator activity were associated with the fauna assemblages. When both vertebrate fauna groups were analysed together, and when reptiles were examined alone, fox predation (former) and fox and cat predation (latter) were associated negatively with species abundance. For reptiles this was highlighted in spinifex habitats, but the relationship was apparent also in mulga and mallee woodlands and was a strong influence on the abundance of *C. schomburgkii* and *S. ciliaris*, perhaps explaining why *S. ciliaris* frequently lives in spinifex hummocks (Wilson 2012).

Some of the variability in faunal assemblage structure was not explained by the variables measured in this study, especially for mammals. The limitations of this study include the lack of a temporal perspective and also, especially for mammals, a small sample size. Deserts are dynamic environments, shaped at larger scales by fire and rainfall (Chapter Four), producing microhabitat variables that change in abundance, quality and distribution over time. It could be that some of the variables measured in this study are important determinants of fauna communities when they are more (or less, in the case of predators) abundant. However, the short timeframe in which this study was conducted could not demonstrate this connection.

The study may also have suffered from the lack of inclusion of one of the main food sources for desert fauna, termites (Colli *et al.* 2006, Abensperg-Traun 1994, Pianka and Goodyear 2012). Several of the species captured during this study are termite specialists and some authors argue that termites are a keystone species in arid Australia (Morton and James 1988), while others are not as convinced (Pianka 1989). It may be that variations in the availability of termites are another key to further understanding the structure of desert faunal assemblages.

Chapter Nine – Conclusion

This aim of this chapter is to synthesise and summarise the results of this study. The first section returns to the discussion of bottom up and top down drivers of arid ecosystems and places the findings into the context of this broader literature. The second section of the chapter revisits the main objectives and results of the study. Finally, the third component of the chapter suggests management actions based on these main findings.

Contribution of this study to the scientific field

Using historical and contemporary observational data from field sampling, and results obtained from experiments, my study began by examining the main habitat types within Uluṟu-Kata Tjuṯa National Park (UKTNP) and investigating the patterns of occurrence of small terrestrial vertebrates within and between these habitats. I then asked how and why native species are distributed as they are throughout the system to elucidate some of the processes that might help to shape the observed patterns. 'Top down' and 'bottom up' processes were examined as part these explorations, with a spotlight on the role of predation in driving the dynamics of the small vertebrate community.

Bottom up processes in Australian desert communities

Rainfall

As described in Chapter Two, rainfall is a powerful shaper of Australian desert systems, with summer rainfall predominating in northern arid regions and winter rainfall in southern arid regions. Pulse rainfall, which may occur at any time, generally stimulates further growth of perennial plants, the germination and growth of annual plants, and subsequent flowering and seeding (Nano and Pavey 2013). Increased productivity drives short-term increases in the abundance of primary and secondary consumers, including mammals and many lizards (Newsome and Corbett 1975, Masters 1993, Southgate and Masters 1996, Dickman *et al.* 1999a,b, 2001, 2010, 2011, Letnic 2003, Letnic *et al.* 2004, Letnic *et al.* 2005, Breed and Ford 2007, D'Souza *et al.* 2013, Greenville *et al.* 2013, Pavey and Nano 2013).

Chapter Two further outlined relevant literature showing that vertebrate responses to rainfall can be inconsistent, with several studies showing that rainfall does not always trigger increases in populations of mammals (Masters 1993, Dickman *et al.* 1999a, Paltridge and Southgate 2001, Letnic 2003, Letnic *et al.* 2004).

The present study found much support for rainfall as an important influencer of mammal communities in central Australia. Moreover, the timing of rainfall was important, with no association obvious between mammal captures and rainfall in the preceding 12 months, but with significant relationships emerging if rain fell within the immediately preceding 3- or 6-month period.

Importantly, this study contributed to our understanding of rainfall-driven responses by mammals, demonstrating that both groups—rodents and marsupials—fluctuate primarily according to rainfall, and do so in a broadly synchronous way. Rodents increased more sharply after rain and declined more severely during drought; however, I found evidence of marsupials also exhibiting the boom and bust pattern associated with rainfall in desert environments, a finding that emerged here perhaps because of the unusually long-term nature of the dataset that was available.

My study however also found that vertebrate responses are not always consistent within or among species groups. Rodents showed greater overall variability in capture rate in response to rainfall, but this varied widely between species. Marsupials too responded inconsistently to rainfall, with large fluctuations in the capture rates of *Ningaui ridei* and *Dasycercus blythi* as opposed to lower variability seen in Sminthopsis spp. Occasionally, populations even increased during drought and decreased after rainfall, demonstrating that other environmental or species factors must also influence the responses of the target species at times.

Primary productivity and primary consumerism

Chapter Two described how the structure and abundance of vegetation—forming the primary productivity of deserts—influences the composition of faunal communities in Australia's arid areas. This study supports these findings, showing that the faunal assemblages in the eucalypt woodland, mulga woodland and spinifex grassland sites surveyed at UKTNP were distinct. Different faunal assemblages were also found at the base of Uluṟu and Kata Tjuṯa, as well as on the transitional sand plain habitat that separates these major rock formations (the sand plain location is also known as the borefields as water for the local town is drawn from an underground aquifer in this area).

This study also demonstrated the dynamism, or indeed, in some habitats, the relative *lack* of dynamism, in the different vegetation communities of central Australia. The suite of fauna living at the base of Uluṟu, in mulga woodlands and on the borefields sand plain was consistent across time, suggesting that habitat characteristics, rather than environmental stochasticity, are likely to be at least partly responsible for the stable faunal composition of these areas. In contrast, the faunal assemblages in the eucalypt woodlands and spinifex grassland sites changed significantly over time, perhaps reflecting the operation of other (extrinsic) factors in driving these changes.

This study also uncovered some of the components of these environments that can affect the presence of individual species. The density of trees, particularly those < 5 m in height, in eucalypt and mulga woodlands influences the fauna present. There are species that are strongly associated with areas of increasing tree cover, for example the burrowing snake, *Simoselaps anomalus* and, in contrast, species that avoid areas with trees such as the ground-active gecko, *Nephrurus levis*. The density of hummock grass cover was also found to be an important microhabitat variable affecting where fauna live, with many species dependent on its presence.

Fire

The literature review from Chapter Two examined the known role of fire in shaping Australian desert ecosystems, proposing that fire can affect the composition of many desert ecological communities, especially the more flammable communities such as those dominated by hummock grassland. This study strongly supported this hypothesis for the small mammal communities of central Australia, finding that while rodent and marsupial abundance declined immediately after fire, both groups then preferred recently burned (approximately ≥ 2 years post burn) areas, presumably as key habitat and food resources regenerated.

Top down processes in Australian desert communities

Predation

Among mammals, the three most important predators in structuring Australian desert systems are the dingo (*Canis dingo / familiaris*), the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*). I found no evidence of predation, or rather fear of predation, caused by the presence of dingoes at UKTNP even though dingo activity on tracks was ubiquitous throughout the park, and particularly was high in the spinifex grassland sites. Foraging choices made by the rodent, *Notomys alexis*, were not influenced by the presence or absence of dingo activity near my experimental feeding stations and there was an inconsistent response between replicate sites, indicating that other unidentified factors were responsible for the choices that *N. alexis* made regarding choice of feeding locations and feeding duration. Proximity to tracks was also not a significant microhabitat variable directly influencing the composition of vertebrate faunal assemblages at UKTNP.

In contrast, the activity of feral cats and red foxes was probably a significant factor contributing to the structure of faunal assemblages, particularly reptiles and particularly in spinifex grasslands, but also to a lesser extent in the two woodland habitat types. Fox activity was also a key component helping to account for variation in reptile and mammal activity, particularly in mulga woodland.

Granivory

In Chapter Two I suggested that seed availability may affect the abundance and distribution of mammalian granivores and omnivores. However, there was no evidence from this study to support this proposition at UKTNP. The amount of seed in the soil was not a significant microhabitat variable influencing rodent populations at UKTNP in this study. The lack of any obvious relationship is surprising given that food has been found to be an important determinant of desert rodent dynamics elsewhere (e.g. Predavec 2000, Prevedello *et al.* 2013), and suggests either that food resources were not sampled reliably, or—more probably—that other factors such as predation and environmental influences were more important.

Mesopredator release theory

In Chapter Two I outlined the significant debate in Australia regarding the influence of dingoes on Australia's mesopredators, the feral cat and red fox. This study lends support to the argument that dingoes influence the local activity of both cats and foxes. Occupancy modelling showed that indices of dingo activity were the most important predictors of cat activity in all seasons, and of fox activity in autumn. However, patterns of temporal activity were similar for all species. These findings therefore allowed the conclusion that dingoes probably influence where, but not when, foxes and cats are active in UKTNP.

Summary of study findings

While the semi-arid landscape of UKTNP may appear initially to be uniform and homogeneous, there are rich faunal assemblages within and between different habitats so that the α (within-site diversity), β (between-site diversity) and γ (regional diversity) components of diversity are relatively high (Magurran 2013). The sites at the bases of Uluṟu and Kata Tjuṯa shelter different suites of vertebrate species to those that occur in the *Acacia* woodland site, and these in turn are distinct from the animals that live in the *Triodia*-dominated spinifex grasslands sites and *Eucalyptus* woodland site (Chapters Three, Five and Eight).

These differences are often distinguished by the presence or absence of a small number of species that characterise the fauna of a particular area or habitat (Chapter Five and Eight). Such differences would be expected, in part, owing to previous work within UKTNP that has demonstrated faunal affinities with very visually distinct areas (Reid *et al.* 1993). At the base of Uluṟu, for example, the rarely seen marsupial *Pseudantechinus macdonnellensis* shelters in the scree slopes, and granivorous birds congregate at semi-permanent water sources (Reid *et al.* 1993). However, similar species-led differences, while often subtle and associated with faunal components that can be detected only by targeted survey techniques, also occur across the three major study habitats. Species such as *Lerista bipes*, *Liopholis inornata*, *Sminthopsis ooldea* and *Sminthopsis youngsoni* drive assemblage change in UKTNP's woodlands and grasslands (e.g., Bennison *et al.* 2013, Chapter Five and Eight).

This study showed further that faunal assemblages in some habitats within UKTNP changed over time to a greater degree than others. The fauna of the mulga woodland sites, in particular, was relatively invariant, changing little despite periods of drought, fire and flood (Chapter Three, Five and Eight). Shaped largely by tree density and perhaps by fox activity, the mulga fauna group was relatively resistant to these forces of potential change that had greater influence in the other habitats (Chapter Eight). In contrast, the animals of the eucalypt woodland sites were in a more constant state of flux, changing regularly as tree cover, hummock grass density, rainfall and predators influenced the suitability of the habitat for different species (Chapter Eight). While the faunal assemblage of spinifex grassland sites was also influenced by these variables, they appeared to drive change to a lesser degree than that seen in eucalypt woodland (Chapter Eight). These patterns and processes are synthesised for visual appreciation in Fig. 9.1.

Pulses of rainfall and drought at UKTNP drove broadly synchronous boom and bust responses in both rodents and marsupials, with a greater magnitude of change seen in the fast breeding, primary productivity-consuming rodent group. However, rainfall was probably not the only agent driving change. This study also documented inconsistent responses by individual species in both mammal groups, with instances where populations increased after drought and decreased after rainfall: an indication that more than just rainfall drives change at UKTNP (Chapter Four). Fire was likely one such driver, with both marsupials and rodents declining after fire but returning after approximately two years and appearing to actively seek burned areas for the next 2-3 years (Chapter Four). Predator activity was also a significant factor influencing fauna in the woodlands and grasslands of UKTNP, with the activity of feral cats and red foxes having a negative influence on some faunal components, particularly reptiles (Chapter Eight).

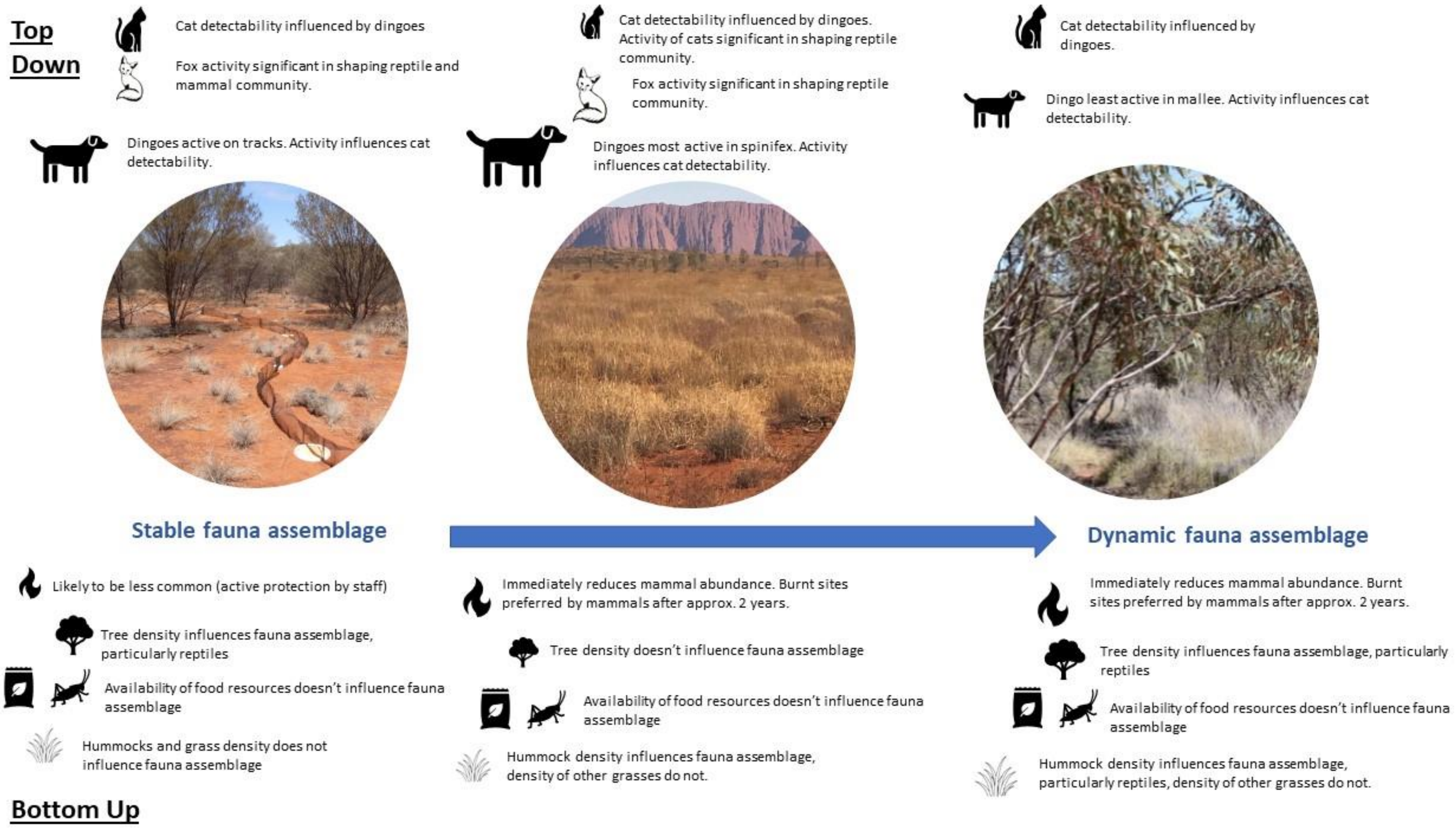
Although I did not study the actual diets of the three mammalian predators, their diets often show considerable overlap in sandy desert environments, with dingoes taking larger prey on average than the red fox and feral cat, and the cat tending to specialise more on small mammals than on reptiles and other taxa (Cupples *et al.* 2011, Spencer *et al.* 2014a). At UKTNP dingo activity did not have a significant influence on fauna assemblages in any of the study habitats, and high levels of dingo activity did not change the feeding behaviour of small mammals compared to areas where there was no dingo activity (Chapter Seven).

The dingo instead may play an important role in shaping fauna communities by changing where and how feral cats and red foxes interact with the landscape (Chapter Six). Thus, foxes and cats appear to avoid places with dingo activity (Chapter Six). While much about these relationships were beyond the capacity of this study to document, it does appear that dingoes disrupt the free movement of cats and foxes in some parts of UKTNP and therefore could possibly provide some protection for native fauna. While it was beyond the capacity of this study to document fauna responses in detail, this area is ripe for further research.

Management recommendations

The different habitats at UKTNP have different floristic and structural attributes, as well as faunas that differ in composition and temporal dynamics. For these reasons they should not be managed in the same way at the same time. Land management, including prescribed burning and feral animal control in mulga woodland, mallee woodland and spinifex grassland needs to be tailored to the dynamics of each habitat.

Fox and cats shape fauna communities at UKTNP particularly in spinifex and mulga woodlands and therefore control in these habitats should be a priority, especially in areas that contain rare or threatened species. Both species appear to avoid dingoes, being active at the same time but spatially separate. Therefore gaining a better understanding of peak dingo activity areas may help to target the placement of cat and fox control methods. Track based control methods would be suitable for foxes as most activity occurs on the tracks. Cats are roughly equally active on and off tracks and therefore, for this species, there is more flexibility available for trap placement. New trap designs are beginning to appear that operate optimally when placed along tracks and should be trialled for use at UKTNP. For example, the 'Felixer grooming trap' ejects a dose of 1080 toxin onto the shoulders or flanks of passing cats and foxes, achieving target specificity by activating only when a particular combination and sequence of infrared beams is broken (Read *et al.* 2019).



Top Down

Cat detectability influenced by dingoes

Fox activity significant in shaping reptile and mammal community.

Dingoes active on tracks. Activity influences cat detectability.

Cat detectability influenced by dingoes. Activity of cats significant in shaping reptile community.

Fox activity significant in shaping reptile community.

Dingoes most active in spinifex. Activity influences cat detectability.

Cat detectability influenced by dingoes.

Dingo least active in mallee. Activity influences cat detectability.

Stable fauna assemblage

Dynamic fauna assemblage

Likely to be less common (active protection by staff)

Tree density influences fauna assemblage, particularly reptiles

Availability of food resources doesn't influence fauna assemblage

Hummocks and grass density does not influence fauna assemblage

Immediately reduces mammal abundance. Burnt sites preferred by mammals after approx. 2 years.

Tree density doesn't influence fauna assemblage

Availability of food resources doesn't influence fauna assemblage

Hummock density influences fauna assemblage, density of other grasses do not.

Immediately reduces mammal abundance. Burnt sites preferred by mammals after approx. 2 years.

Tree density influences fauna assemblage, particularly reptiles

Availability of food resources doesn't influence fauna assemblage

Hummock density influences fauna assemblage, particularly reptiles, density of other grasses do not.

Bottom Up

Figure 9.1. The influence of top down and bottom up processes in mulga and mallee woodland and spinifex grassland at UKTNP

There is no evidence that small vertebrates perceive dingoes to be a threat at UKTNP and, while the diet of the dingo was not studied here, observations in the study area and dietary data from comparable desert environments elsewhere suggest that dingo predation is unlikely to impact the small vertebrate fauna of UKTNP. Dingoes appear to disrupt the activity and perhaps free movement of cats year-round and of foxes in autumn. Therefore, this study recommends that dingoes should remain persecution-free at UKTNP.

Fire should be carefully managed at UKTNP, particularly in spinifex grassland and mallee woodland, to produce a mosaic of fire ages. Mature hummock grasses support a diverse range of small vertebrates and provide refuge from predation and harsh environmental conditions, while frequently burned patches are preferred, probably for foraging. Therefore, a mix of fire ages is likely to provide both refuge and foraging opportunities. The woodlands of UKTNP should be managed to exclude fire and protect tree density as much as possible.

Literature

Abensperg-Traun, M., 1994. The influence of climate on patterns of termite eating in Australian mammals and lizards. *Australian Journal of Ecology,* 19(1), pp.65-71.

Abramsky, Z., 1983. Experiments on seed predation by rodents and ants in the Israeli desert. *Oecologia*, 57(3), pp.328-332.

Abramsky, Z., Rosenzweig, M.L. and Subach, A., 2001. The cost of interspecific competition in two gerbil species. *Journal of Animal Ecology,* 70(4), pp.561-567.

Algar D, Burrows ND., 2004. Feral cat control research: Western Shield review- February 2003, *Conservation Science Western Australia* 5:131–163.

Allan, G.E., 1984. Fire history and land units of Uluru. *Anticipating the Inevitable'.(Ed. EC Allan.) pp*, pp.13-24.

Allan, G. E., and R. I. Southgate., 2002. Fire regimes in the spinifex landscapes of Australia., in R.A. Bradstock, J. E. Williams and A. M. Gill, eds *Flammable Australia: the fire regimes and biodiversity of a continent* pp. 145-176. Cambridge University Press, Cambridge, United Kingdom.

Allen BL, Allen LR, Engeman RM, Leung LK-P., 2014. Sympatric prey responses to lethal top-predator control: predator manipulation experiments. *Frontiers in Zoology* 11:56.

Allen BL, Allen LR, Leung LK-P., 2015. Interactions between two naturalised invasive predators in Australia: are feral cats suppressed by dingoes? *Biological Invasions* 17: 761–776.

Allen BL, Engeman RM, Allen LR., 2011. Wild dogma: an examination of recent "evidence" for dingo regulation of invasive mesopredator release in Australia. *Current Zoology* 57: 568–583.

Allen BL, Fleming PJS., 2012. Reintroducing the dingo: the risk of dingo predation to threatened vertebrates of western New South Wales. *Wildlife Research*. 39: 35–50.

Anderson, M.J. and Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology,* 84(2), pp.511-525.

Anderson, M., Gorley, R. and Clarke, K.P., 2008. for *PRIMER: guide to software and statistical methods.* PRIMER-E, Plymouth, UK.

Aslin, H., 1995. Ooldea dunnart, in R.Strahan (ed.) *The mammals of Australia* pp. 152-153 Reed New Holland, New South Wales, Australia.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E. and Harris, A.T., 2004. Grazing systems, ecosystem responses, and global change. *Annual Review Environmental Resources*, 29, pp.261-299.

Aukema,J.E. and Martinez del Rio, C., 2002. Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. *Ecology* 83, 3489-3496.

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A. and Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia*, 141(2), pp.221-235.

Australian Bureau of Statistics. *Desert wildlife of Australia*. Retrieved on 1st August 2020. Available at https://www.abs.gov.au/ausstats/abs@.nsf/Previousproducts/1301.0Feature%20Article12006?opendocument&tabname=Summary&prodno=1301.0&issue=2006&num=&view=

Ayal, Y., 2007. Trophic structure and the role of predation in shaping hot desert communities. *Journal of Arid Environments*, 68(2), pp.171-187.

Báez, S., Collins, S.L., Lightfoot, D. and Koontz, T.L., 2006. Bottom-up regulation of plant community structure in an aridland ecosystem. *Ecology,* 87(11), pp.2746-2754.

Báez, S., Collins, S.L., Pockman, W.T., Johnson, J.E. and Small, E.E., 2013. Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. *Oecologia*, 172(4), pp.1117-1127.

Barrows, C.W., Allen, E.B., Brooks, M.L. and Allen, M.F., 2009. Effects of an invasive plant on a desert sand dune landscape. *Biological Invasions*, 11(3), pp.673-686.

Bates, J.M., 1992. Frugivory on Bursera microphylla (Burseraceae) by wintering Gray Vireos (*Vireo vicinior,* Vireonidae) in the coastal deserts of Sonora, Mexico. *The Southwestern Naturalist*, pp.252-258.

Bender, L.C. and Piasecke, J.R., 2015. Cervus elaphus foraging impacts on plants and soils at an ungrazed desert grass/shrubland in Northwestern New Mexico, USA. *International Journal of Ecology.*

Bennison, K., C.R. Dickman and R. Godfree., 2013. Habitat use and ecological observations of the Ooldea dunnart (*Sminthopsis ooldea*) at Uluru–Kata Tjuta National Park, Northern Territory. *Australian Mammalogy* 35:175-179.

Bennison, K., Godfree, R. and Dickman C.R., 2018. Synchronous boom-bust cycles in central Australian rodents and marsupials in response to rainfall and fire. *Journal of Mammalogy* 99: 1137-1148.

Bergallo, H.G. and Rocha, C.F.D., 1994. Spatial and trophic niche differentiation in two sympatric lizards (Tropidurus torquatus and Cnemidophorus ocellifer) with different foraging tactics. *Australian Journal of Ecology,* 19(1), pp.72-75.

Beschta RL., 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. *Ecological Applications* 13: 1295-1309.

Bisceglia, S.B.C., Pereira, J.A., Tetac, P., Quintana, R.D., 2011. Rodent selection by Geoffroy's cats in a semi-arid scrubland of central Argentina. *Journal of Arid Environments*, 75, 1024-1028.

Bleicher, S. S., and C.R. Dickman., 2016. Bust economics: foragers choose high quality habitats in lean times. *PeerJ* 4:e1609.

Bliege Bird, R., D. W. Bird, L. E. Fernandez, N. Taylor, W. Taylor, and D. Nimmo., 2018. Aboriginal burning promotes fine-scale pyrodiversity and native predators in Australia's western desert. *Biological Conservation* 219:110-118.

Borruel, N., Campos, C.M., Giannoni, S.M. and Borghi, C.E., 1998. Effect of herbivorous rodents (cavies and tuco-tucos) on a shrub community in the Monte Desert, Argentina. *Journal of Arid Environments*, 39(1), pp.33-37.

Bowers, MA., Jefferson, JL. and Kuebler ,MG., 1993. Variation in giving up densities of foraging chipmunks (*Tamias striatus*) and squirrels (*Sciurus carolinensis*). *Oikos* 66:229-236.

Brawata RL, Neeman T., 2011. Is water the key? Dingo management, intraguild interactions and predator distribution around water points in arid Australia. *Wildlife Research* ; 38: 426–436.

Breed, B., and F. Ford., 2007. *Native mice and rats*. CSIRO Publishing, Collingwood, Australia.

Brim Box, J.B., Nano, C.E., McBurnie, G., Waller, D.M., McConnell, K., Brock, C., Paltridge, R., McGilvray, A., Bubb, A. and Edwards, G.P., 2016. The impact of feral camels (Camelus dromedarius) on woody vegetation in arid Australia. *The Rangeland Journal*, 38(2), pp.181-190.

Brook, L.A., Johnson, C.N. and Ritchie, E.G., 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology,* 49(6), pp.1278-1286.

Brooks, M.L., 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. *The American Midland Naturalist*, 144(1), pp.92-108.

Brooks, M.L., Pyke, D.A., Galley, K.E.M. and Wilson, T.P., 2001. Invasive plants and fire in the deserts of North America. In *The First National Congress on Fire Ecology, Prevention, and Management*, San Diego, CA, Tall Timbers Research Station, Tallahassee, FL.

Brown, J.H., Grover, J.J., Davidson, D.W. and Lieberman, G.A., 1975. A preliminary study of seed predation in desert and montane habitats. *Ecology*, 56(4), pp.987-992.

Brown, G., 2002. Community composition and population dynamics in response to artificial rainfall in an undisturbed desert annual community in Kuwait. *Basic and Applied Ecology,* 3(2), pp.145-156.

Brown, J. S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22: 37–47.

Brown, J.H. and Heske, E.J., 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science,* 250(4988) pp.1705-1707.

Brown, J.H. and Munger, J.C., 1985, Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology,* 66(5), pp.1545-1563.

Brown, J.H., Reichman, O.J. and Davidson, D.W., 1979. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics*, 10(1), pp.201-227.

Brown, J.S., Kotler, B.P., Smith, R.J. and Wirtz, W.O., 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia*, 76(3), pp.408-415.

Bucher, E.H., 1987. Herbivory in arid and semi-arid regions of Argentina. *Revista Chilena de Historia Natural*, 60, pp.265-273.

Buckley, R., 1981. Soils and vegetation of central Australian sandridges II. Sandridge vegetation in the Uluru National Park Area, Northern Territory, Australia., *Australian Journal of Ecology,* (6)4, pp. 391-404.

Bureau of Meteorology 2010. *Climate Data Online*, from http://www.bom.gov.au/climate/data/

Bureau of Meteorology 2011. *Climate Data Online*, from http://www.bom.gov.au/climate/data/

Bureau of Meteorology 2017. *Climate Data Online* from http://www.bom.gov.au/climate/data/

Burnham KP, Anderson DR., 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Berlin, Germany: Springer.

Burrows, N.D., 2018. Feral Animals in the Semi-arid and Arid Regions of Australia: Origins, Impacts and Control, in *On the Ecology of Australia's Arid Zone* pp. 331-373. Springer, Cham.

Burrows, N.D., Algar, D., Robinson, A.D., Sinagra, J., Ward, B. and Liddelow, G., 2003. Controlling introduced predators in the Gibson Desert of Western Australia. *Journal of Arid Environments*, 55(4), pp.691-713.

Búrquez, A., Martínez-Yrízar, A., Felger, R.S. and Yetman, D., 1999. Vegetation and habitat diversity at the southern edge of the Sonoran Desert. *Ecology of Sonoran Desert plants and plant communities*, pp.36-67.

Calow, P.P., 2009. *Encyclopedia of ecology and environmental management*. John Wiley & Sons.

Campbell, G., Coffey, A., Miller, H., Read, J.L., Brook, A., Fleming, P.J., Bird, P., Eldridge, S. and Allen, B.L., 2019. Dingo baiting did not reduce fetal/calf loss in beef cattle in northern South Australia. *Animal Production Science,* 59(2), pp.319-330.

Capinera, J., 2011. *Insects and wildlife: arthropods and their relationships with wild vertebrate animals*. John Wiley & Sons.

Carrick, P.J., 2003. Competitive and facilitative relationships among three shrub species, and the role of browsing intensity and rooting depth in the Succulent Karoo, South Africa. *Journal of Vegetation Science,* 14(5), pp.761-772.

Carthey, A.J. and Banks, P.B., 2016. Naiveté is not forever: responses of a vulnerable native rodent to its long term alien predators. *Oikos*, *125*(7), pp.918-926.

Catling, P. C. & Burt, R. J., 1995. Why are red foxes absent from some Eucalypt forests in Eastern New South Wales? *Wildlife Research* 22, 535-546.

Chambers, J.C., Board, D.I., Roundy, B.A. and Weisberg, P.J., 2017. Removal of perennial herbaceous species affects response of Cold Desert shrublands to fire. *Journal of Vegetation Science,* 28(5), pp.975-984.

Chen, X., Dickman C.R. and Thompson, M.B., 1998. Diet of the mulgara, *Dasycercus cristicauda* (Marsupialia: Dasyuridae), in the Simpson Desert, central Australia. *Wildlife Research*, 25(3), pp.233-242.

Christensen, P. and Burrows, N., 1995. Project desert dreaming: experimental reintroduction of mammals to the Gibson Desert, Western Australia in *Reintroduction Biology of Australian and New Zealand Fauna*.(Ed. M. Serena.) pp.199-207.

Chung-MacCoubrey, A., H. L. Bateman, and D. M. Finch., 2009. Captures of Crawford's gray shrews (*Notiosorex crawfordi*) along the Rio Grande in central New Mexico. *Western North American Naturalist* 69:260-263.

Claridge, A.W. and Hunt, R., 2008. Evaluating the role of the dingo as a trophic regulator: additional practical suggestions. *Ecological Management & Restoration*, 9(2), pp.116-119.

Clarke K.R. and Warwick R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd edition. PRIMER-E, Plymouth.

Clarke, K.R. and Gorley, R.N., 2006. *Primer-e: user manual-tutorial*. PRIMER-E, Plymouth, UK.

Clarke, K.R., Somerfield, P.J. and Chapman, M.G., 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, *330*(1), pp.55-80.

Clayton, J. C. Pavey, C.R. Vernes, K. and Tighe, M., 2014. Review and analysis of Australian macropod translocations 1969, 2006 *Mammal Review*, 44 (2), pp. 109-123.

Cody, M.L., 1974. *Competition and the Structure of Bird Communities*. Princeton University Press, New Jersey.

Cody, M.L., 1994. Mulga bird communities. I. Species composition and predictability across Australia. *Australian Journal of Ecology* 19, 206-219.

Cogger, H.G., 2018. *Reptiles & amphibians*. CSIRO Publishing.

Colli, G.R., Constantino, R. and Costa, G.C., 2006. Lizards and termites revisited. *Austral Ecology,* 31(3), pp.417-424.

Commonwealth of Australia 2019. *Uluru – Kata Tjuta National Park*, Retrieved 24 January 2019
from http://www.environment.gov.au/topics/national-parks/uluru-kata-tjuta-national-park

Cooke, B.D., 2012. Rabbits: manageable environmental pests or participants in new Australian ecosystems?. *Wildlife Research*, 39(4), pp.279-289.

Corbalán, V., 2006. Microhabitat selection by murid rodents in the Monte desert of Argentina. *Journal of Arid Environments*, 65(1), pp.102-110.

Corbett, L.K., 1995. *The dingo in Australia and Asia*. Sydney, University of New South Wales Press.

Costa, G.C., Colli, G.R. and Constantino, R., 2008. Can lizard richness be driven by termite diversity? Insights from the Brazilian Cerrado. *Canadian Journal of Zoology*, *86*(1), pp.1-9.

Courchamp, F., Langlais, M. & Sugihara, G., 1999. Cats protecting birds: modelling the mesopredator release effect. *Journal of Animal Ecology,* 68, 282-292.

Cowan, M.A., 2004. *Preliminary analysis of fauna sampling for CALM's feral cat research program at Lorna Glen*. Department of Conservation & Land Management Report, Kalgoorlie, WA.

Cowlishaw, G., 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, 53(4), pp.667-686.

Craig, M.D., Withers, P.C. and Bradshaw, S.D., 2006. Patterns of diet and microhabitat use by four species of sympatric Ctenotus lizards: do they reveal foraging specialisation?. *Journal of the Royal Society of Western Australia*, 89, p.1.

Creel, S., 2001. Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, 15(1), pp.271-274.

Crooks, K. R. & Soule, M E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, 400, 563-566.

Cupples, J. B., Crowther, M. S., Story, G. L. and Letnic, M., 2011. Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? *Journal of Mammalogy* 92: 590–600.

Daly, B.G., Dickman C.R. and Crowther, M.S., 2007. Selection of habitat components by two species of agamid lizards in sandridge desert, central Australia. *Austral Ecology,* 32(7), pp.825-833.

Daly, B.G., Dickman C.R. and Crowther, M.S., 2008. Causes of habitat divergence in two species of agamid lizards in arid central Australia. *Ecology,* 89(1), pp.65-76.

Daly, M., Behrends, P.R., Wilson, M.I. and Jacobs, L.F., 1992. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, Dipodomys merriami. *Animal Behaviour*, 44(1), pp.1-9.

Davidson, A.D., Detling, J.K. and Brown, J.H., 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment*, 10(9), 477-486.

Davidson, D.W., 1977. Species diversity and community organization in desert seed-eating ants. *Ecology,* 58(4), pp.711-724.

Davidson, D.W., Inouye, R.S. and Brown, J.H., 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology,* 65(6), pp.1780 1786.

Davidson, D.W., Samson, D.A. and Inouye, R.S., 1985. Granivory in the Chihuahuan Desert: interactions within and between trophic levels. *Ecology,* 66(2), pp.486-502.

Davis, M.K., Cook, E.M., Collins, S.L. and Hall, S.J., 2015. Top-down vs. bottom-up regulation of herbaceous primary production and composition in an arid, urbanizing ecosystem. *Journal of Arid Environments*, 116, pp.103-114.

Dayton, G.H. and Fitzgerald, L.A., 2001. Competition, predation, and the distributions of four desert anurans. *Oecologia*, 129(3), pp.430-435.

de Casenave, J.L., Cueto, V.R. and Marone, L., 1998. Granivory in the Monte desert, Argentina: is it less intense than in other arid zones of the world?. *Global Ecology and Biogeography Letters*, pp.197-204.

Degen, A. A., 1997. *Ecophysiology of small desert mammals*. Springer, Berlin, Germany.

Del-Claro, K., Stefani, V., Nahas, L. and Torezan-Silingardi, H.M., 2017. Spiders as plant partners: complementing ant services to plants with extra-floral nectaries, in Viera C., Gonzaga M. (eds), *Behaviour and Ecology of Spiders*, pp. 215-226 Springer, Cham.

Dennis, A.J. (ed.), 2007. *Seed dispersal: theory and its application in a changing world*. CABI.

Dennison S, McAlpin S, Chapple DG, Stow AJ., 2015. Genetic divergence among regions containing the vulnerable great desert skink (*Liopholis kintorei*) in the Australian arid zone. *PloS ONE*. 10: e0128 74.

Department of the Environment 2015, *Conservation Management Zones of Australia-Arid Shrublands and Desert*. Retrieved 1st August 2020. Available at http://www.environment.gov.au/system/files/resources/a460eb8a-cd61-433f-9476-1562b78198b2/files/cmz-arid-shrublands-desert.pdf

Department of Environment and Energy 2019a, *Vegetation profiles: fact sheets of the major vegetation groups. MVG 13—Acacia open woodlands*. Retrieved 6th June 2019. Available at http://www.environment.gov.au/system/files/resources/2edcda80-d9b7-49d4-9e97-3623-b91e9f9/files/mvg13-nvis-acacia-open-woodlands.pdf

Department of Environment and Energy 2019b, *Vegetation profiles: fact sheets of the major vegetation groups. MGV 14 – Mallee woodlands and shrublands*. Retrieved 8th June 2019. Available at https://www.environment.gov.au/system/files/resources/2edcda80-d9b7-49d4-9e97-3623-b91e9f9/files/mvg14-nvis-mallee-woodlands-and-shrublands.pdf

Department of Natural Resources and Mines 2006. *A management program for the dingo (Canis lupus dingo) in the Northern Territory of Australia*.

Dickman C.R., M. Predavec, and F. J. Downey., 1995. Long-range movements of small mammals in arid Australia: implications for land management. *Journal of Arid Environments*, 31:441-452.

Dickman C.R., 1996a. Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology*, 2(3), pp.185-195.

Dickman C.R., 1996b. *Overview of the impacts of feral cats on Australian native fauna*. Canberra, Australia: Australian Nature Conservation Agency

Dickman C.R., Mahon, P.S., Masters, P. and Gibson, D.F., 1999a. Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildlife Research*, 26(4), pp.389-403.

Dickman C.R., Letnic, M. and Mahon, P.S., 1999b. Population dynamics of two species of dragon lizards in arid Australia: the effects of rainfall. *Oecologia* 119, 357-366.

Dickman C.R., A. S. Haythornthwaite, G. H. McNaught, P. S. Mahon, B. Tamayo, and M. Letnic., 2001. Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. *Wildlife Research* 28:493-506.

Dickman C.R., Glen AS, Letnic M., 2009. Reintroducing the dingo: can Australia's conservation wastelands be restored? In: Hayward MW, Somers MJ, editors. *Reintroduction of top-order predators*. Oxford, UK: Blackwell Publishing; pp. 238–269.

Dickman C.R., A. C. Greenville, C.-L. Beh, B. Tamayo, and G. M. Wardle., 2010. Social organization and movements of desert rodents during population “booms” and “busts” in central Australia. *Journal of Mammalogy* 91:798-810.

Dickman C.R., Greenville A. C., Tamayo B., Wardle G. M., 2011. Spatial dynamics of small mammals in central Australian desert habitats: the role of drought refugia. *BioOne*, 92(6): 1193 1209

Director of National Parks. 2010. *Uluru-Kata Tjuta National Park Management Plan 2010-2020,* Australian Government, Canberra, Australia.

Dittmer, D.E. and Bidwell, J.R., 2018. Herpetofaunal species presence in buffel grass (*Cenchrus ciliaris*) versus native vegetation-dominated habitats at Uluṟu-Kata Tjuṯa National Park. *Austral Ecology*, 43(2), pp.203-212.

Doblas-Miranda, E., Sánchez-Piñero, F. and González-Megías, A., 2009. Different microhabitats affect soil macroinvertebrate assemblages in a Mediterranean arid ecosystem. *Applied Soil Ecology,* 41(3), pp.329-335.

Doherty, T.S., Davis, N.E., Dickman C.R., Forsyth, D.M., Letnic, M., Nimmo, D.G., Palmer, R., Ritchie, E.G., Benshemesh, J., Edwards, G. and Lawrence, J., 2019. Continental patterns in the diet of a top predator: Australia's dingo. *Mammal Review*, 49(1), pp.31-44.

Doherty, T.S., Dickman C.R., Johnson, C.N., Legge, S.M., Ritchie, E.G. and Woinarski, J.C., 2017. Impacts and management of feral cats Felis catus in Australia. *Mammal Review*, 47(2), pp.83-97.

Donadio, E. and Buskirk, S. W., 2006. Diet, morphology, and interspecific killing in Carnivora. *American Naturalist* 167, 524-536.

Downey, F.J. and Dickman C.R., 1993. Macro-and microhabitat relationships among lizards of sandridge desert in central Australia. *Herpetology in Australia: A Diverse Discipline* (Eds D. Lunney and D. Ayers.) pp.133-138.

Drake, K.K., Bowen, L., Nussear, K.E., Esque, T.C., Berger, A.J., Custer, N.A., Waters, S.C., Johnson, J.D., Miles, A.K. and Lewison, R.L., 2016. Negative impacts of invasive plants on conservation of sensitive desert wildlife. *Ecosphere*, 7(10).

Driscoll, D.A. and Henderson, M.K., 2008. How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation*, 141(2), pp.460-471.

D'Souza, J. B., A. Whittington, C.R. Dickman and L. K.-P. Leung., 2013. Perfect storm: demographic responses of an irruptive desert mammal to prescribed burns following flooding rain. *Austral Ecology,* 38:765-776.

Edwards, G.P., De Preu, N.D., Shakeshaft, B.J. and Crealy, I.V., 2000. An evaluation of two methods of assessing feral cat and dingo abundance in central Australia. *Wildlife Research*, *27*(2), pp.143-149.

Edwards, G. P., De Preu, N., Crealy, I. V. & Shakeshaft, B. J., 2002. Habitat selection by feral cats and dingoes in a semi-arid woodland environment in central Australia. *Austral Ecology* 27, 26-31.

Eldridge, S. R., Shakeshaft, B. J. & Nano, T. J., 2002. *The impact of wild dog control on cattle, native and introduced herbivores and introduced predators in central Australia*. Unpublished report to the Bureau of Rural Sciences, Canberra.

English, P. 1998a, *Cainozoic Geology and Hydrogeology of Uluru – Kata Tjuta National Park*, Australian Geological Survey Organisation, Canberra.

English, P., 1998b, Palaeodrainage at Uluru - Kata Tjuta National Park and Implications for Water Resources, *Rangelands Journal*, vol.20, no.2., pp. 255-274.

Espinoza, J.J.O., Ayala, C.C., Castillón, E.E., Saldivar, F.G., Sauceda, J.U., Jurado, E., ChapaVargas, L., Jaramillo, E.M. and Hernández, E.O., 2017. Livestock effect on floristic composition and vegetation structure of two desert scrublands in northwest Coahuila, Mexico. *The Southwestern Naturalist*, 62(2), pp.138-145.

Estes, J. A., 1996. Predators and ecosystem management. *Wildlife Society Bulletin*, 24, 390-396.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B. and Marquis, R.J., 2011. Trophic downgrading of planet Earth. *Science,* 333(6040), pp.301-306.

Fedriani, J. M., Fuller, T. K., Sauvajot, R. M. & York, E. C., 2000. Competition and intraguild predation among three sympatric carnivores. *Oecologia* July:1-24.

Fennessy, J., 2009. Home range and seasonal movements of *Giraffa camelopardalis angolensis* in the northern Namib Desert. *African Journal of Ecology* 47:318-327.

Ferguson, D.J., Mathieson, M.T. and Eyre, T.J., 2015. Additional information on the beaded gecko (*'Lucasium damaeum'*) and smooth knob-tailed gecko (*'Nephrurus levis')* at their eastern limit in Southwest Queensland. Queensland Naturalist, 53(1/2/3), p.19.

Fisher, D. O. and Dickman C.R., 1993. Diets of insectivorous marsupials in arid Australia: selection for prey type, size or hardness? *Journal of Arid Environments* 25: 397-410.

Fleishman, E., McDonal, N., Nally, R.M., Murphy, D.D., Walters, J. and Floyd, T., 2003. Effects of floristics, physiognomy and non-native vegetation on riparian bird communities in a Mojave Desert watershed. *Journal of Animal Ecology*, *72*(3), pp.484-490.

Fleming, P. J. S., 1996. Ground placed baits for the control of wild dogs: Evaluation of a replacement baiting strategy in North-eastern New South Wales. *Wildlife Research* 23, 729-740.

Fleming, P., Corbett, L., Harden, R. & Thomson, P., 2001. *Managing the impacts of dingoes and other wild dogs.* Canberra, Australia. Bureau of Rural Science.

Fox, B. J., 2011. Review of small mammal trophic structure in drylands: resource availability, use, and disturbance. *Journal of Mammalogy* 92:1179 1192

Frank, A.S., Wardle, G.M., Greenville, A.C. and Dickman C.R., 2016. Cattle removal in arid Australia benefits kangaroos in high quality habitat but does not affect camels. *The Rangeland Journal*, 38(1), pp.73-84.

Franklin, D.C., Woinarski, J.C. and Noske, R.A., 2000. Geographical patterning of species richness among granivorous birds in Australia. *Journal of Biogeography*, 27(4), pp.829-842.

Free, C. L., G. S. Baxter, C.R. Dickman and L. K.-P. Leung. 2013. Resource pulses in desert river habitats: productivity-biodiversity hotspots, or mirages? *PloS ONE* 8:e7269

Free, C. L., G. S. Baxter, C.R. Dickman A. Lisle, and L. K.-P. Leung., 2015. Diversity and community composition of vertebrates in desert river habitats. *PloS ONE* 10:e1442 8.

Gardner, S.M., Cabido, M.R., Valladares, G.R. and Diaz, S., 1995. The influence of habitat structure on arthropod diversity in Argentine semi-arid Chaco forest. *Journal of Vegetation Science*, *6*(3), pp.349-356.

Geary, W.L., Ritchie, E.G., Lawton, J.A., Healey, T.R. and Nimmo, D.G., 2018. Incorporating disturbance into trophic ecology: Fire history shapes mesopredator suppression by an apex predator. *Journal of Applied Ecology,* 55(4), pp.1594 1603

Gehrt, S.D. and Clark, W.R., 2003. Racoons, coyotes, and reflections on the mesopredator release hypothesis. *Wildlife Society Bulletin* 31, 836-842.

Geiser, F., 2004. The role of torpor in the life of Australian arid zone mammals. *Australian Mammalogy* 26:125-134.

Geiser, F., and Körtner, G., 2010. Hibernation and daily torpor in Australian mammals. *Australian Zoologist* 35:204–215.

Geoscience Australia 2019. *Deserts* Accessed at: http://www.ga.gov.au/scientific-topics/national-location-information/landforms/deserts

Germano, D.J., Rathbun, G.B. and Saslaw, L.R., 2012. Effects of grazing and invasive grasses on desert vertebrates in California. *The Journal of Wildlife Management* 76(4), pp.670-682.

Gibb, H., Grossman, B.F., Dickman C.R. and Wardle, G., 2018. Over what timeframes do desert ants respond to variation in climate and resources? *Australian Zoologist* 39, 646-657.

Gibson, D. F., Lundie-Jenkins, G., Langford, D. G., Cole, J. R., Clarke, D. E. & Johnson, K. A., 1994. Predation by feral cats, Felis catus, on the rufous hare wallaby, Lagorchestes hirsutus, in the Tanami Desert. *Australian Mammology* 17, 103-107.

Gibson, L.A. and McKenzie, N.L., 2009. Environmental associations of small ground-dwelling mammals in the Pilbara region, Western Australia. *Records of the Western Australian Museum*, *78*, pp.91-122.

Gilfillan, S.L., 2001. An ecological study of a population of *Pseudantechinus macdonnellensis* (Marsupialia: Dasyuridae) in central Australia. I. Invertebrate food supply, diet and reproductive strategy. *Wildlife Research* : 469-480.

Gill, R.A., O'Connor, R.C., Rhodes, A., Bishop, T.B., Laughlin, D.C. and Clair, S.B.S., 2018. Niche opportunities for invasive annual plants in dryland ecosystems are controlled by disturbance, trophic interactions, and rainfall. *Oecologia*, pp.1-11.

Glen, A.S. and Dickman C.R., 2005. Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews*, 80(3), pp.387-401.

Glen, A.S., Dickman C.R., Soule, M.E. and Mackey, B.G., 2007. Evaluating the role of the dingo as a trophic regulator in Australian ecosystems. *Austral Ecology,* 32(5), pp.492-501.

Gonnet, J.M. and Ojeda, R.A., 1998. Habitat use by small mammals in the arid Andean foothills of the Monte Desert of Mendoza, Argentina. *Journal of Arid Environments*, 38(3), pp.349-357.

Goodyear, S.E. and Pianka, E.R., 2008. Sympatric ecology of five species of fossorial snakes (Elapidae) in Western Australia. *Journal of Herpetology*, 42(2), pp.279-285.

Gordon, C.E., Feit, A., Grüber, J. and Letnic, M., 2015. Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802), p.20142870.

Green, A.K., Ward, D. and Griffiths, M.E., 2009. Directed dispersal of mistletoe (*Plicosepalus acaciae*) by Yellow-vented Bulbuls *(Pycnonotus xanthopygos*). *Journal of Ornithology*, 150(1), pp.167-173.

Greenville, A.C. and Dickman C.R., 2009. Factors affecting habitat selection in a specialist fossorial skink. *Biological Journal of the Linnean Society* 97(3), pp.531-544.

Greenville, A. C., Dickman C.R., Wardle, G. M. and Letnic, M., 2009. The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. *International Journal of Wildland Fire* 18, 631-639.

Greenville, A. C., G. M. Wardle, and C.R. Dickman., 2012. Extreme climatic events drive mammal irruptions: regression analysis of 100-year trends in desert rainfall and temperature. *Ecology and Evolution* 2:2645 2658

Greenville, A. C., G. M. Wardle, and C.R. Dickman., 2013. Extreme rainfall events predict irruptions of rat plagues in central Australia. *Austral Ecology,* 38:754-764.

Greenville, A.C., Wardle, G.M., Tamayo, B. and Dickman C.R., 2014. Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. *Oecologia*, 175(4), pp.1349-1358.

Greenville, A. C., G. M. Wardle, V. Nguyen, and C.R. Dickman., 2016. Population dynamics of desert mammals: similarities and contrasts within a multispecies assemblage. *Ecosphere* 7:e0134.

Greenville, A.C., Wardle, G.M. and Dickman C.R., 2017. Desert mammal populations are limited by introduced predators rather than future climate change. *Royal Society Open Science* 4(11), 1703-4.

Griffin, M., 1990. A review of taxonomy and ecology of gerbilline rodents of the central Namib Desert, with keys to the species (Rodentia: Muridae). In M. K. Seely, (ed.) pp. 83-98 in *Namib ecology: 25 years of Namib research*. Transvaal Museum, Pretoria, South Africa.

Haby, N.A. and Brandle, R., 2018. Passive recovery of small vertebrates following livestock removal in the Australian rangelands. *Restoration Ecology,* 26(1), pp.174-182.

Hallett, J.G., 1982. Habitat selection and the community matrix of a desert small-mammal fauna. *Ecology*, *63*(5), pp.1400-1410.

Hamilton III, W.J. and Tilson, R.L., 1985. Fishing baboons at desert waterholes. *American Journal of Primatology*, 8(3), pp.255-257.

Hamilton, W.J., 1985. Demographic consequences of a food and water shortage to desert chacma baboons, Papio ursinus. *International Journal of Primatology*, 6(5), pp.451-462.

Hardin, G., 1960. The competitive exclusion principle. *Science* 131, 1292-1297

Hardman, B., Moro, D. and Calver, M., 2016. Direct evidence implicates feral cat predation as the primary cause of failure of a mammal reintroduction programme. *Ecological Management & Restoration*, 17(2), pp.152-158.

Haswell, P.M., Kusak, J. and Hayward, M.W., 2017. Large carnivore impacts are context-dependent. *Food Webs* 12, 3–13.

Haswell, P.M., Jones, K.A., Kusak, J. and Hayward, M.W., 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. *Oecologia*, pp.1-11.

Haythornthwaite, A.S. and Dickman C.R., 2006. Distribution, abundance, and individual strategies: a multi-scale analysis of dasyurid marsupials in arid central Australia. *Ecography*, 29(3), pp.285-300.

Haythornthwaite, A.S., 2005. Microhabitat use and foraging behaviour of *Sminthopsis youngsoni* (Marsupialia: Dasyuridae) in arid central Australia. *Wildlife Research*, 32(7), pp.609-615.

Hayward, M. W. and Marlow, N., 2014. Will dingoes really conserve wildlife and can our methods tell? *Journal of Applied Ecology* 51, 835-838.

Heffelfinger, L.J., Stewart, K.M., Bush, A.P., Sedinger, J.S., Darby, N.W. and Bleich, V.C., 2018. Timing of precipitation in an arid environment: Effects on population performance of a large herbivore. *Ecology and Evolution*, 8(6), pp.3354-3366.

Henke, S. E. & Bryant, F. C., 1999. Effects of coyote removal on the faunal community in western Texas. *Journal of Wildlife Management*, 63, 1066 1081

Henle, K., 1990. Population ecology and life history of three terrestrial geckos in arid Australia. *Copeia*, pp.759-781.

Hervert, J.J. and Krausman, P.R., 1986. Desert mule deer use of water developments in Arizona. *The Journal of Wildlife Management*, pp.670-676.

Heske, E.J., Brown, J.H. and Guo, Q., 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia*, 95(4), pp.520-524.

Heske, E.J., Brown, J.H. and Mistry, S., 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. *Ecology,* 75(2), pp.438-445.

Hines JE., 2006. *PRESENCE2– Software to estimate patch occupancy and related parameters*. USGS-PWRC. http://www.mbr_pwrc.usgs.gov/software/presence.html.

Hobbs, T.J., Morton, S.R., Masters, P. and Jones, K.R., 1994. Influence of pit-trap design on sampling of reptiles in arid spinifex grasslands. *Wildlife Research*, 21(5), pp.483-489.

Hódar, J.A., Pleguezuelos, J.M., Villafranca, C. and Fernández-Cardenete, J.R., 2006. Foraging mode of the Moorish gecko *Tarentola mauritanica* in an arid environment: inferences from abiotic setting, prey availability and dietary composition. *Journal of Arid Environments*, 65(1), pp.83-93.

Hohnen R, Tuft K, McGregor HW, Legge S, Radford IJ, Johnson CN., 2016. Occupancy of the invasive feral cat varies with habitat complexity. *PloS ONE*. 11: e0152 20.

Horn, K.J. and Clair, S.B.S., 2017. Wildfire and exotic grass invasion alter plant productivity in response to climate variability in the Mojave Desert. *Landscape Ecology,* 32(3), pp.635-646.

Huang, L. and Zhang, Z., 2016. Effect of rainfall pulses on plant growth and transpiration of two xerophytic shrubs in a revegetated desert area: Tengger Desert, China. *Catena*, 137, pp.269-276.

Hughes, J.J., Ward, D. and Perrin, M.R., 1994. Predation risk and competition affect habitat selection and activity of Namib Desert gerbils. *Ecology,* 75(5), pp.1397-1405.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L. and Schwinning, S., 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141(2), pp.254-268.

Idris, M., 2009. Eco-biodiversity of rodent fauna of the Thar Desert. In *Faunal Ecology and Conservation of the Great Indian Desert* (pp. 157-175). Springer, Berlin, Heidelberg.

Inouye, R.S., Byers, G.S. and Brown, J.H., 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology,* 61(6), pp.1344-1351

Jackson, S. and Groves, C., 2015. *Taxonomy of Australian mammals*. CSIRO publishing.

Jacob, J. and Brown, J. S., 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. - *Oikos* 91: 131-138.

James, C.D., 2003. Response of vertebrates to fenceline contrasts in grazing intensity in semi-arid woodlands of eastern Australia. *Austral Ecology,* 28(2), pp.137-151.

Jarman, P. J., Johnson, C. N., Southwell, C. J. & Stuart-Dick, R., 1987. Macropod studies at Wallaby Creek 1. The area and animals. *Wildlife Research* 14, 1-14.

Johnson C., 2006. *Australia's mammal extinctions: a 50,000 year history*. Melbourne, Australia: Cambridge University Press.

Johnson CN, Wallach AD., 2016. The virtuous circle: predator-friendly farming and ecological restoration in Australia. *Restoration Ecology* 24: 821–826.

Johnson KA, Gibson DF, Langford DG, Cole JR., 1996. Recovery of the mala Lagorchestes hirsutus: a 30-year unfinished journey. In: Stephens S, Maxwell S, editors. *Back from the brink: refining the threatened species recovery process*. Sydney, Australia: Surrey Beatty and Sons; pp. 155–161.

Johnson, K.A. and Burbidge, A.A., 2008. Rufous hare-wallaby Lagorchestes hirsutus Gould 1844 in *The Mammals of Australia*, eds S. Van Dyck and R. Strahan, Reed New Holland, Sydney, pp 317-319.

Jones, M.E., Apfelbach, R., Banks, P.B., Cameron, E.Z., Dickman C.R., Frank, A., McLean, S., McGregor, I.S., Müller-Schwarze, D., Parsons, M.H. and Sparrow, E., 2016. A nose for death: integrating trophic and informational networks for conservation and management. *Frontiers in Ecology and Evolution*, 4, p.124.

Jorgensen, E.E., 2001. Emission of volatile compounds by seeds under different environmental conditions. *The American Midland Naturalist* 145(2), 419-422.

Kämmerle, J.L., Coppes, J., Ciuti, S., Suchant, R. and Storch, I., 2017. Range loss of a threatened grouse species is related to the relative abundance of a mesopredator. *Ecosphere*, *8*(9), p.e01934.

Karasov, W.H., 1989. Nutritional bottleneck in a herbivore, the desert wood rat (*Neotoma lepida*). *Physiological Zoology*, 62(6), pp.1351-1382.

Kelly, L.T., Dayman, R., Nimmo, D.G., Clarke, M.F. and Bennett, A.F., 2013. Spatial and temporal drivers of small mammal distributions in a semi-arid environment: The role of rainfall, vegetation and life-history. *Austral Ecology,* 38(7), pp.786-797.

Kelt, D.A., 2011. Comparative ecology of desert small mammals: a selective review of the past 30 years. *Journal of Mammalogy* 92(6), 1158-1178.

Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R., Rogovin, K.A. and Shenbrot, G., 1996. Community structure of desert small mammals: comparisons across four continents. *Ecology,* 77(3), pp.746-761.

Kennedy, M., Phillips, B.L., Legge, S., Murphy, S.A. and Faulkner, R.A., 2012. Do dingoes suppress the activity of feral cats in northern Australia?. *Austral Ecology,* 37(1), pp.134-139.

Kennedy, T.A., Finlay, J.C. and Hobbie, S.E., 2005. Eradication of invasive Tamarix ramosissima along a desert stream increases native fish density. *Ecological Applications*, 15(6), pp.2072-2083.

Kerle, A., 1995, *Uluru, Kata Tjuta and Watarrka*, University of New South Wales Press, Sydney.

Kerley, G.I. and Whitford, W.G., 2000. Impact of grazing and desertification in the Chihuahuan Desert: plant communities, granivores and granivory. *The American Midland Naturalist*, 144(1), pp.78-91.

Kerley, G.I.H. and Whitford, W.G., 1994. Desert-Dwelling Small Mammals as Granivores-Intercontinental Variations. *Australian Journal of Zoology*, 42(4), pp.543-555.

Kinnear JE, Onus ML, Bromilow NR., 1988. Fox control and rock wallaby dynamics. *Australian Wildlife Research*, 15:435–450.

Klinger, R. and Brooks, M., 2017. Alternative pathways to landscape transformation: invasive grasses, burn severity and fire frequency in arid ecosystems. *Journal of Ecology,* 105(6), pp.1521-1533.

Kluever, B.M., Gese, E.M. and Dempsey, S.J., 2017. Influence of free water availability on a desert carnivore and herbivore. *Current zoology*, 63(2), pp.121-129.

Kotler, B.P., 1984. Risk of predation and the structure of desert rodent communities. *Ecology,* 65(3), pp.689-701.

Kotler, B.P., Brown, J.S. and Mitchell, W.A., 1994. The role of predation in shaping the behavior, morphology and community organization of desert rodents. *Australian Journal of Zoology*, 42(4), pp.449-466.

Kotler, B.P., Brown, J.S., Bleicher, S.S. and Embar, K., 2016. Intercontinental-wide consequences of compromise-breaking adaptations: the case of desert rodents. *Israeli Journal of Ecology & Evolution*, 62(3-4), pp.186-195.

Krebs, C.J., 1972. *The experimental analysis of distribution and abundance ecology*. New York: Harper and Row.

Krofel, M., Giannatos, G., Ćirovič, D., Stoyanov, S. and Newsome, T.M., 2017. Golden jackal expansion in Europe: a case of mesopredator release triggered by continent-wide wolf persecution? Hystrix: *Italian Journal of Mammalogy*, 28(1), pp.9-15.

Kurnath, P., Merz, N.D. and Dearing, M.D., 2016. Ambient temperature influences tolerance to plant secondary compounds in a mammalian herbivore. *Proceedings Royal Society Britain*, 283(1822), p.2015 387.

Kwok, A.B.C., Wardle, G.M., Greenville, A.C. and Dickman C.R., 2016. Long-term patterns of invertebrate abundance and relationships to environmental factors in arid Australia. *Austral Ecology* 41, 480-491.

Lambert, A.M., D'antonio, C.M. and Dudley, T.L., 2010. Invasive species and fire in California ecosystems. *Fremontia*, 38(2), p.38.

Latz, P.K., 1995. *Bushfires and bushtucker: Aboriginal plant use in Central Australia*. Alice Springs: IAD Press.

Layton, R., 1989. *Uluru – An Aboriginal History of Ayers Rock*, Aboriginal Studies Press, Canberra.

Leavesley, A., 2008. *The response of birds to the fire regimes of mulga woodlands in central Australia*. Doctoral dissertation, Australian National University.

Legge, S., Lindenmayer, D.B., Robinson, N.M., Scheele, B.C., Southwell, D.M. and Wintle, B.A., eds, 2018. *Monitoring Threatened Species and Ecological Communities*. CSIRO Publishing, Melbourne.

Legge, S., Murphy, B.P., McGregor, H., Woinarski, J.C.Z., Augusteyn, J., Ballard, G., Baseler, M., Buckmaster, T., Dickman C.R., Doherty, T. and Edwards, G., 2017. Enumerating a continental-scale threat: how many feral cats are in Australia?. *Biological Conservation*, 206, pp.293-303.

Leonard, B., 1976. The effect of forest fire on the ecology of leaf litter organisms. *Victorian Naturalist* 94:119-122.

Letnic, M., Dickman C.R. and McNaught, G., 2000. Bet-hedging and germination in the Australian arid zone shrub, Acacia ligulata. *Austral Ecology,* 25, 368-374.

Letnic, M., 2002., Long distance movements and the use of fire mosaics by small mammals in the Simpson Desert, central Australia. *Australian Mammology* 23: 125-134

Letnic, M., 2003. The effects of experimental patch burning and rainfall on small mammals in the Simpson Desert, Queensland. *Wildlife Research* 30: 547-563

Letnic M., Dickman C.R., Tischler M. K., Tamayo B., Beh C.L., 2004. The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments*, 59: 85-114.

Letnic M. Tamayo B. and Dickman C.R., 2005. The Responses of Mammals to La Nina (El Nino Southern Oscillation) Associated Rainfall. *Journal of Mammalogy* 86: 689-703.

Letnic M, Koch F, Gordon C, Crowther MS, Dickman CR., 2009. Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings Royal Society Britain*. 276: 3249- 3256.

Letnic, M. and Dickman C.R., 2010. Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews*, 85(3), pp.501-521.

Letnic, M., P. Story, G. Story, J. Field, O. Brown, and C.R. Dickman., 2011a. Resource pulses, switching trophic control, and the dynamics of desert small mammal assemblages in arid Australia. *Journal of Mammalogy* 92:1210-1222.

Letnic M, Greenville A, Denny E, Dickman C.R., Tischler M, Gordon C., 2011b. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? *Global Ecology and Biogeography* 20: 343–353.

Letnic, M., Ritchie, E.G. and Dickman C.R., 2012. Top predators as biodiversity regulators: the dingo Canis lupus dingo as a case study. *Biological Reviews*, 87(2), pp.390-413.

Letnic, M., M. Tischler, and C. Gordon., 2013. Desert small mammal responses to wildfire and predation in the aftermath of a La Niña driven resource pulse. *Austral Ecology,* 38:841-849.

Letnic, M. and Ripple, W.J., 2017. Large-scale responses of herbivore prey to canid predators and primary productivity. *Global Ecology and Biogeography*, 26(8), pp.860-866.

Letnic, M., Feit, A. and Forsyth, D.M., 2018. Strength of a trophic cascade between an apex predator, mammalian herbivore and grasses in a desert ecosystem does not vary with temporal fluctuations in primary productivity. *Ecosystems* 21(1), pp.153-165.

Li, F., Zhao, W. and Liu, H., 2013. The response of aboveground net primary productivity of desert vegetation to rainfall pulse in the temperate desert region of northwest China. *PloS ONE*, 8(9), p.e7300.

Li, F., Zhao, W. and Liu, H., 2015. Productivity responses of desert vegetation to precipitation patterns across a rainfall gradient. *Journal of Plant Research*, 128(2), pp.283-294.

Lima, M., S. K. Morgan Ernest, J. H. Brown, A. Belgrano, and N. C. Stenseth., 2008. Chihuahuan Desert kangaroo rats: nonlinear effects of population dynamics, competition, and rainfall. *Ecology* 89:2594-2603.

Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C.R. Dickman A. A. Hoffmann, D. A. Keith, M. J. Liddell, A. J. Lowe, D. J. Metcalfe, S. R. Phinn, J. Russell-Smith, N. Thurgate, and G. M. Wardle., 2012. Value of long-term ecological studies. *Austral Ecology* 37:745-757.

Litvaitis, J. A. & Villafuerte, R., 1995. Intraguild predation, mesopredator release and prey stability. *Conservation Biology*, 10, 676-677.

Lotan, A. and Izhaki, I., 2013. Could abiotic environment shape fleshy fruit traits? A field study of the desert shrub Ochradenus baccatus. *Journal of Arid Environments*, 92, pp.34-41.

Lu, A., 2011. Presence of the Dingo (Canis lupus dingo) on Risk Sensitive Foraging of Small Mammals in Forest Ecosystems.

Luna, C.A., Loayza, A.P. and Squeo, F.A., 2016. Fruit size determines the role of three scatter-hoarding rodents as dispersers or seed predators of a fleshy-fruited Atacama Desert shrub. *PloS ONE*, 11(11), p.e0166 24.

Lundie-Jenkins, G., Corbett, L. K. & Phillips, C. M., 1993. Ecology of the rufous hare- wallaby, Lagorchestes hirsutus Gould (Marsupialia: Macropodidae), in the Tanami Desert, Northern Territory. III. Interactions with introduced mammal species. *Wildlife Research* 20, 495-511.

Lyons, M.B., Mills, C.H., Gordon, C.E. and Letnic, M., 2018. Linking trophic cascades to changes in desert dune geomorphology using high-resolution drone data. *Journal of The Royal Society Interface*, 15(144), p.2018 327.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. and Hines, J.E., 2006. *Occupancy estimation and modelling: inferring patterns and dynamics of species occurrence*. London, UK: Elsevier.

Magurran, A. E., 2013. *Measuring Biological Diversity*. Blackwell Publishing, Oxford, UK.

Mahon PS, Banks PB, Dickman CR., 1998. Population indices for wild carnivores: a critical study in sand-dune habitat, south-western Queensland. *Wildlife Research* 25: 11–22.

Malo, J.E., González, B.A., Mata, C., Vielma, A., Donoso, D.S., Fuentes, N. and Estades, C.F., 2016. Low habitat overlap at landscape scale between wild camelids and feral donkeys in the Chilean desert. *Acta oecologica*, 70, pp.1-9.

Mares, M.A. and Rosenzweig, M.L., 1978. Granivory in North and South American deserts: rodents, birds, and ants. *Ecology,* 59(2), pp.235-241.

Mares, Michael A. *Encyclopedia of Deserts*, University of Oklahoma Press, 1999, ProQuest Ebook Central, https://ebookcentral-proquest-com.ezproxy1.library.usyd.edu.au/lib/usyd/detail.action?docID=4784 49.

Marlow, N.J., Thomas, N.D., Williams, A.A., Macmahon, B., Lawson, J., Hitchen, Y., Angus, J. and Berry, O., 2015. Cats (*Felis catus*) are more abundant and are the dominant predator of woylies (*Bettongia penicillata*) after sustained fox (*Vulpes vulpes*) control. *Australian Journal of Zoology*, 63(1), pp.18-27.

Marone, L. and Horno, M.E., 1997. Seed reserves in the central Monte Desert, Argentina: implications for granivory. *Journal of Arid Environments*, 36(4), pp.661-670.

Marone, L., Cueto, V.R., Milesi, F.A. and Casenave, J.L.D., 2004. Soil seed bank composition over desert microhabitats: patterns and plausible mechanisms. *Canadian Journal of Botany*, 82(12), pp.1809-1816.

Marone, L., De Casenave, J.L. and Cueto, V.R., 2000. Granivory in southern South American deserts: conceptual issues and current evidence. *AIBS Bulletin*, 50(2), pp.123-132.

Marsack, P. and Campbell, G., 1990. *Feeding behaviour and diet of dingoes in the Nullarbor region, Western Australia*. Australian Wildlife Research (Australia) – agris.fao.org.

Marshal, J.P., Bleich, V.C. and Andrew, N.G., 2008. Evidence for interspecific competition between feral ass *Equus asinus* and mountain sheep *Ovis canadensis* in a desert environment. *Wildlife Biology*, 14(2), pp.228-236.

Martin, G.R., Twigg, L.E. and Robinson, D.J., 1996. Comparison of the diet of feral cats from rural and pastoral Western Australia. *Wildlife Research*, 23(4), pp.475-484.

Masters, P., 1993. The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park, Northern Territory. *Wildlife Research* 20:803-813.

Masters, P., 1998. The mulgara *Dasycercus cristicauda* (Marsupialia: Dasyuridae) at Uluru National Park, Northern Territory. *Australian Mammalogy* 20:403-407.

Masters, P., 1996. The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. *Wildlife Research*, 23(1), pp.39-47.

Masters, P., and C.R. Dickman., 2012. Population dynamics of *Dasycercus blythi* (Marsupialia: Dasyuridae) in central Australia: how does the mulgara persist? *Wildlife Research* 39:419-428.

McAuliffe, J.R., 1986. Herbivore-Limited Establishment of a Sonoran Desert Tree, *Cerciduium Microphyllum*. *Ecology,* 67(1), pp.276-280.

McDonald, J.H., 2009. Handbook of biological statistics. Retrieved regularly between 2014 and 2018 from http://www.biostathandbook.com/index.html

McDonald, P.J., Griffiths, A.D., Nano, C.E., Dickman, C.R., Ward, S.J. and Luck, G.W., 2015. Landscape-scale factors determine occupancy of the critically endangered central rock-rat in arid Australia: the utility of camera trapping. *Biological Conservation* 191: 93–100.

McDonald, P.J., Luck, G.W., Dickman C.R., Ward, S.J. & Crowther, M.S., 2015. Using multiple-source occurrence data to identify patterns and drivers of decline in arid-dwelling Australian marsupials. *Ecography*: 1090-1100.

McDonald, P.J., Stewart, A., Schubert, A.T., Nano, C.E., Dickman, C.R. and Luck, G.W., 2016. Fire and grass cover influence occupancy patterns of rare rodents and feral cats in a mountain refuge: implications for management. *Wildlife Research* 43: 121–129.

McDonald, P.J., Nano, C.E., Ward, S.J., Stewart, A., Pavey, C.R., Luck, G.W. and Dickman, C.R., 2017. Habitat as a mediator of mesopredator-driven mammal extinction. *Conservation Biology* 31: 1183-1191.

McDonald, P.J., Brim-Box, J., Nano, C.E., Macdonald, D.W. and Dickman C.R., 2018. Diet of dingoes and cats in central Australia: does trophic competition underpin a rare mammal refuge?. *Journal of Mammalogy* 99(5), pp.1120-1127.

McGregor, H., S. Legge, M. E. Jones, and C. N. Johnson., 2015. Feral cats are better killers in open habitats, revealed by animal-borne video. *PloS ONE* 10:e1339 5.

McKenzie, N. L. and J. R. Cole., 1995. Lesser hairy footed dunnart, in R. Strahan (ed.) *The Mammals of Australia* pp. 152-153 Reed New Holland, New South Wales, Australia.

Meek, P. D. & Shields, J., 2001. Positive dingo management: how to not throw the baby out with the bath water. In Dickman C.R. & Lunney, D (eds), *A Symposium on the Dingo*, Royal Zoological Society of New South Wales, Mosman, NSW.

Melville, J. and Schulte Ii, J.A., 2001. Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards. *Austral Ecology*, *26*(6), pp.660-669.

Meserve, P. L., D. A. Kelt, M. A. Previtali, W. B. Milstead, and J. R. Gutiérrez., 2011. Global climate change and small mammal populations in north-central Chile. *Journal of Mammalogy* 92:1223-1235.

Meyer, M.D. and Valone, T.J., 1999. Foraging under multiple costs: the importance of predation, energetic, and assessment error costs to a desert forager. *Oikos*, pp.571-579.

Michel, V.T., Jiménez‐Franco, M.V., Naef‐Daenzer, B. and Grüebler, M.U., 2016. Intraguild predator drives forest edge avoidance of a mesopredator. *Ecosphere*, 7(3), p.e0122.

Mills, C.H. and Letnic, M., 2018. Reversing functional extinction of mammals prompts a rethink about seed fate in arid Australia. *Royal Society Open Science* 5, 1719 7.

Mills, M. G. L. & Biggs, H. C., 1993. Prey appointment and related ecological relationships between large carnivores in Kruger National Park. *Symposium of Zoological Society of London* 65, 253-268.

Mills, M. G. L. & Gorman, M. L., 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology*, 11, 1397 1406

Milstead, W. B., P. L. Meserve, A. Campanella, M. A. Previtali, D. A. Kelt, and J. R. Gutiérrez., 2007. Spatial ecology of small mammals in north-central Chile: role of precipitation and refuges. *Journal of Mammalogy* 88:1532-1538.

Mitchell, B.D. and Banks, P.B., 2005. Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. *Austral Ecology* 30: 581–591.

Mitchell, D., Henschel, J.R., Hetem, R.S., Wassenaar, T.D., Strauss, W.M., Hanrahan, S.A. and Seely, M.K., 2019. Fog and fauna of the Namib Desert: past and future. *Ecosphere*, in press.

Molyneux, J., 2017. *Fauna assemblages of the spinifex sand plains in central Australia: response to climate, fire and predation*. Doctoral dissertation, Charles Darwin University.

Molyneux, J., Pavey, C.R., James, A.I. and Carthew, S.M., 2018. Small mammal and reptile persistence in desert grasslands during a period of low rainfall–Part 1. *Journal of Arid Environments* 157, pp.27-38.

Monasmith, T. J., 1997. *Fire effects on small mammals and vegetation of the northern Chihuahuan Desert*. M.S. thesis, Texas Tech University, Lubbock, Texas.

Moore, P., 2005. *A Guide to Plants of Inland Australia*, Reed New Holland, Sydney

Morton, S. R., 1978. Torpor and nest-sharing in free-living *Sminthopsis crassicaudata* (Marsupialia) and Mus musculus (Rodentia). *Journal of Mammalogy* 59:569-575.

Morton, S.R. and Davies, P.H., 1983. Food of the zebra finch (*Poephila guttata*), and an examination of granivory in birds of the Australian arid zone. *Australian Journal of Ecology,* 8(3), pp.235-243.

Morton, S.R. and James, C.D., 1988. The diversity and abundance of lizards in arid Australia: a new hypothesis. *American Naturalist* 132, 237-256.

Morton, S.R., 1985. Granivory in arid regions: comparison of Australia with North and South America. *Ecology,* 66(6), pp.1859-1866.

Morton, S.R., Gillam, M.W., Jones, K.R. and Fleming, M.R., 1988. Relative efficiency of different pit-trap systems for sampling reptiles in spinifex grasslands. *Wildlife Research*, 15(5), pp.571-577.

Morton, S.R., Stafford Smith, D.M., Dickman C.R., Dunkerley, D.L., Friedel, M.H., McAllister, R.R.J., Reid, J.R.W., Roshier, D.A., Smith, M.A., Walsh, F.J., Wardle, G.M., Watson, I.W. and Westoby, M., 2011. A fresh framework for the ecology of arid Australia. *Journal of Arid Environments* pp.313-329.

Moseby, K.E., Crowther, M.S. and Letnic, M., 2018. Ecological Role of an Apex Predator Revealed by a Reintroduction Experiment and Bayesian Statistics. *Ecosystems* pp.1-13.

Moseby, K.E., Read, J.L., Paton, D.C., Copley, P., Hill, B.M. and Crisp, H.A., 2011. Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation*, 144(12), pp.2863-2872.

Munro, N.T., Moseby, K.E. and Read, J.L., 2009. The effects of browsing by feral and re-introduced native herbivores on seedling survivorship in the Australian rangelands. *The Rangeland Journal*, 31(4), pp.417-426.

Murray, B. R. and Dickman C.R., 1994a. Food preferences and seed selection in two species of Australian desert rodents. *Wildlife Research* 21: 647-655.

Murray, B. R. and Dickman C.R., 1994b. Granivory and microhabitat use in Australian desert rodents: are seeds important? *Oecologia* 99: 216-225.

Murray, B. R., C.R. Dickman C. H. S. Watts, and S. R. Morton., 1999. The dietary ecology of Australian desert rodents. *Wildlife Research* 26:421-437.

Mutze, G., 2017. Barking up the wrong tree? Are livestock or rabbits the greater threat to rangeland biodiversity in southern Australia? *The Rangeland Journal* 38(6) pp.523-531.

Meyer, M.D. and Valone, T.J., 1999. Foraging under multiple costs: the importance of predation, energetic, and assessment error costs to a desert forager. *Oikos,* pp.571-579.

Nafus, M.G., Germano, J.M., Perry, J.A., Todd, B.D., Walsh, A. and Swaisgood, R.R., 2015. Hiding in plain sight: a study on camouflage and habitat selection in a slow-moving desert herbivore. *Behavioral Ecology* 26(5) pp.1389-1394.

Nafus, M.G., Tuberville, T.D., Buhlmann, K.A. and Todd, B.D., 2017. Precipitation quantity and timing affect native plant production and growth of a key herbivore, the desert tortoise, in the Mojave Desert. *Climate Change Responses*, 4(1) p.4.

Nano, C.E.M. and Pavey, C.R., 2013. Refining the ‘pulse-reserve’ model for arid central Australia: seasonal rainfall, soil moisture, and plant productivity in sand ridge and stony plain habitats of the Simpson Desert, Australia. *Austral Ecology*, 741–753.

Newsome, A. E., and L. K. Corbett., 1975. Outbreaks of rodents in semi-arid and arid Australia: causes, preventions, and evolutionary considerations, in I. Prakash, and P. K. Ghosh, (eds) *Rodents in desert environments*. pp. 117-151, Dr. W. Junk, The Hague, Netherlands.

Newsome AE, Corbett LK, Catling PC, Burt RJ., 1983. The feeding ecology of the dingo I. Stomach contents from trapping in south-eastern Australia, and the non-target wildlife also caught in dingo traps. *Australian Wildlife Research*, 10: 477–486.

Newsome, A., Pech, R., Smyth, R., Banks, P. & Dickman C., 1997. *Potential impacts on Australian native fauna of rabbit calicivirus disease*. Biodiversity Group, Environment Australia. Canberra.

Newsome, A. E., Catling, P. C., Cooke, B. D. & Smyth, R., 2001. Two ecological universes separated by the dingo barrier fence in semi-arid Australia: Interactions between landscapes, herbivory and carnivory, with and without dingoes. *Rangelands Journal* 23, 71-98

Newsome, T.M., Stephens, D., Ballard, G.A., Dickman C.R. and Fleming, P.J., 2013. Genetic profile of dingoes (*Canis lupus dingo*) and free-roaming domestic dogs (*C. familiaris*) in the Tanami Desert, Australia. *Wildlife Research*, 40(3), pp.196-206.

Newsome, T.M., Ballard, G.A., Crowther, M.S., Dellinger, J.A., Fleming, P.J., Glen, A.S., Greenville, A.C., Johnson, C.N., Letnic, M., Moseby, K.E. and Nimmo, D.G., 2015. Resolving the value of the dingo in ecological restoration. *Restoration Ecology* 23(3), pp.201-208.

Newsome, T. M., Greenville, A. C., Ćirović, D., Dickman C.R., Johnson, C. N., Krofel, M., Letnic, M., Ripple, W. J., Ritchie, E. G., Stoyanov, S. and Wirsing, A. J., 2017. Top predators constrain mesopredator distributions. *Nature Communications* 8: 1546

Nguyen, V., Greenville, A.C., Dickman C.R. and Wardle, G.M., 2015. On the validity of visual cover estimates for time series analyses: a case study of hummock grasslands. *Plant Ecology*, 216(7), pp.975-988.

Nimmo, D.G., Kelly, L.T., Spence-Bailey, L.M., Watson, S.J., Taylor, R.S., Clarke, M.F. and Bennett, A.F., 2013. Fire mosaics and reptile conservation in a fire-prone region. *Conservation Biology*, 27(2) pp.345-353.

O'Neill A., 2002. *Living with the dingo*. Annandale, Sydney, Australia: Envirobook.

O'Connell, M.A. and Hallett, J.G., 2019. Community ecology of mammals: deserts, islands, and anthropogenic impacts. *Journal of Mammalogy* in press.

Ojeda, R. A., S. Tabeni, and V. Corbalán., 2011. Mammals of the Monte Desert: from regional to local assemblages. *Journal of Mammalogy* 92:1236-1244.

Palomares, F. and Caro, T.M., 1999. Interspecific killing among mammalian carnivores. *The American Naturalist*, 153(5), pp.492-508.

Palomares, F., Gaona, P., Ferreras, P. & Delibes, M., 1994. Positive effects on game species of top predators by controlling smaller predator populations: An example with lynx, mongooses and rabbits. *Conservation Biology*, 9, 295-305.

Paltridge, R., 2002. The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research*, 29(4), pp.389-403.

Paltridge, R., Gibson, D. and Edwards, G., 1997. Diet of the feral cat (Felis catus) in central Australia. *Wildlife Research*, 24(1), pp.67-76.

Paltridge, R., R. Southgate., 2001. The effect of habitat type and seasonal conditions on fauna in two areas of the Tanami Desert. *Wildlife Research* 28:247-260.

Pasanen-Mortensen, M., Elmhagen, B., Lindén, H., Bergström, R., Wallgren, M., van der Velde, Y. and Cousins, S.A., 2017. The changing contribution of top-down and bottom-up limitation of mesopredators during 220 years of land use and climate change. *Journal of Animal Ecology*, *86*(3), pp.566-576.

Pastro, L. A., C.R. Dickman and M. Letnic., 2011. Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. *Ecological Applications* 21:3238-3253.

Pastro, L.A., Dickman, C.R. and Letnic, M., 2013. Effects of wildfire, rainfall and region on desert lizard assemblages: the importance of multi-scale processes. *Oecologia*, *173*(2), pp.603-614.

Pavey, C.R. and Nano, C.E., 2013. Changes in richness and abundance of rodents and native predators in response to extreme rainfall in arid Australia. *Austral Ecology,* 38(7), pp.777-785.

Pavey, C.R. and Nano, C.E.M., 2009. Bird assemblages of arid Australia: vegetation patterns have a greater effect than disturbance and resource pulses. *Journal of Arid Environments*: 634-642.

Pavey, C.R., J. Addison, R. Brandle, C.R. Dickman P. J. McDonald, K. E. Moseby, and L. I. Young., 2017. The role of refuges in the persistence of Australian dryland mammals. *Biological Reviews* 92:647-664.

Pavey, C.R., J. R. Cole, P. J. McDonald, and C. E. M. Nano., 2014. Population dynamics and spatial ecology of a declining desert rodent, *Pseudomys australis*: the importance of refuges for persistence. *Journal of Mammalogy* 95:615-625.

Pavey, C.R., S. R. Eldridge, and M. Heywood., 2008. Population dynamics and prey selection of native and introduced predators during a rodent outbreak in arid Australia. *Journal of Mammalogy* 89:674-683.

Pedler, R.D., Brandle, R., Read, J.L., Southgate, R., Bird, P. and Moseby, K.E., 2016. Rabbit biocontrol and landscape-scale recovery of threatened desert mammals. *Conservation Biology*, 30(4), pp.774-782.

Peinetti, H.R., Fredrickson, E.L., Peters, D.P., Cibils, A.F., Roacho-Estrada, J.O. and Laliberte, A.S., 2011. Foraging behavior of heritage versus recently introduced herbivores on desert landscapes of the American Southwest. *Ecosphere*, 2(5), pp.1-14.

Penteriani, V., Kuparinen, A., del Mar Delgado, M., Palomares, F., López-Bao, J.V., Fedriani, J.M., Calzada, J., Moreno, S., Villafuerte, R., Campioni, L. and Lourenço, R., 2013. Responses of a top and a meso predator and their prey to moon phases. *Oecologia*, *173*(3), pp.753-766.

Perrin, M.R. and Boyer, D.C., 1994. The effect of rodents on plant recruitment and production in the dune fields of the Namib Desert. *Tropical Zoology*, 7(2), pp.299-308.

Pettigrew, J. D., 1993, A burst of feral cats in the Diamantina- a lesson for the management of pest species? *Cat Management Workshop Proceedings-1993*, Queensland Department of Environment and Heritage.

Pianka, E.R., 1989. Desert lizard diversity: additional comments and some data. *American Naturalist* 134, 344-364.

Pianka, E.R. and Goodyear, S.E., 2012. Lizard responses to wildfire in arid interior Australia: Long-term experimental data and commonalities with other studies. *Austral Ecology,* 37(1), pp.1-11.

Pianka, E.R. and Pianka, H.D., 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia*: 125-142.

Pianka, E.R., 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology*: 1055-1059.

Pianka, E.R., 1969. Habitat specificity, speciation, and species density in Australian desert lizards. *Ecology*: 498-502.

Pianka, E.R., 2017. *Ecology and natural history of desert lizards: analyses of the ecological niche and community structure*. Princeton University Press.

Piovia-Scott, J., Yang, L.H. and Wright, A.N., 2017. Temporal variation in trophic cascades. *Annual Review of Ecology, Evolution, and Systematics* 48, 281–300.

Plomley, N. J. B., 1972. Some notes on plagues of small mammals in Australia. *Journal of Natural History* 6:363-384.

Polis, G.A., 1993. Scorpions as model vehicles to advance theories of population and community ecology: the role of scorpions in desert communities. *Memoirs of the Queensland Museum* 33, 401–410.

Poulos, H.M. and Camp, A.E., 2010. Topographic influences on vegetation mosaics and tree diversity in the Chihuahuan Desert Borderlands. *Ecology*, *91*(4), pp.1140-1151.

Ponce-Guevara, E., Davidson, A., Sierra-Corona, R. and Ceballos, G., 2016. Interactive effects of black-tailed prairie dogs and cattle on shrub encroachment in a desert grassland ecosystem. *PloS ONE*, 11(5), p.e0154 48.

Potter, T.I., Greenville, A.C. and Dickman C.R., 2018. Assessing the potential for intraguild predation among taxonomically disparate micro-carnivores: marsupials and arthropods. *Royal Society Open Science,* 5(5), p.1718 2.

Predavec, M., 1997. Seed removal by rodents, ants and birds in the Simpson Desert, central Australia. *Journal of Arid Environments*, 36(2), pp.327-332.

Predavec, M., 2000. Food limitation in Australian desert rodents: experiments using supplementary feeding. *Oikos*, 91(3), pp.512-522.

Prevedello, J. A., Dickman, C. R., Vieira, M. V. & Vieira, E. M., 2013. Population responses of small mammals to food supply and predators: a global meta-analysis. *Journal of Animal Ecology* 82: 927-936.

Previtali, M. A., M. Lima, P. L. Meserve, D. A. Kelt, and J. R. Gutiérrez., 2009. Population dynamics of two sympatric rodents in a highly variable environment: rainfall, resource availability, and predation. *Ecology* 90:1996-2006

Previtali, M. A., P. L. Meserve, D. A. Kelt, W. B. Milstead, and J. R. Gutiérrez., 2010. Effects of more frequent and prolonged El Niño events on life-history parameters of the degu, a long-lived and slow-reproducing rodent. *Conservation Biology* 24:18-28.

Price, M.V., 1978. The role of microhabitat in structuring desert rodent communities. *Ecology,* 59(5), pp. 910-921.

Price, M.V. and Joyner, J.W., 1997. What resources are available to desert granivores: seed rain or soil seed bank? *Ecology,* 78(3), pp.764-773.

Purdie, R., 1984. Land systems of the Simpson Desert region.

Quinn, G.P. and Keough, M.J., 2002. *Experimental design and data analysis for biologists.* Cambridge University Press.

Read, J. and Bowen, Z., 2001. Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildlife Research*, 28(2), pp.195-203.

Read, J.L., 1995. Subhabitat variability: a key to the high reptile diversity in chenopod shrublands. *Australian Journal of Ecology,* 20(4), pp.494-501.

Read, J.L., Bowden, T., Hodgens, P., Hess, M., McGregor, H. and Moseby, K., 2019. Target specificity of the Felixer Grooming "Trap". *Wildlife Society Bulletin* 43: 112-120.

Read, J.L., Dagg, E. and Moseby, K.E., 2019. Prey selectivity by feral cats at central Australian rock-wallaby colonies. *Australian Mammalogy*, 41(1), pp.132-141.

Rees, J.D., Kingsford, R.T. and Letnic, M., 2017. In the absence of an apex predator, irruptive herbivores suppress grass seed production: Implications for small granivores. *Biological Conservation*, 213, pp.13-18.

Rees, J.D., Kingsford, R.T. and Letnic, M., 2018. Changes in desert avifauna associated with the functional extinction of a terrestrial top predator. *Ecography*, 42(1), pp.67-76.

Reichman, O.J., 1979. Desert granivore foraging and its impact on seed densities and distributions. *Ecology,* 60(6), pp.1085-1092.

Reid, J. R. W., J. A. Kerle, and S. R. Morton., 1993, *Uluru fauna: the distribution and abundance of vertebrate fauna of Uluru (Ayers Rock-Mount Olga) National Park, N.T.*, Australian National Parks and Wildlife Service, Canberra, Australia.

Reid, J.R.W., Kerle, J.A., Morton, S.R. 1993, *Kowari 4: Uluru Fauna. The distribution and abundance of vertebrate fauna of Uluru (Ayers Rock- Mount Olga) National Park, NT,* Australian National Parks and Wildlife Service, Canberra.

Reynolds, J.F., Kemp, P.R., Ogle, K. and Fernández, R.J., 2004. Modifying the 'pulse–reserve'paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, 141(2), pp.194-210.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G. and Hebblewhite, M.l., 2014. Status and ecological effects of the world's largest carnivores. *Science*. 343: 1241 84.

Ripple, W. J. and Beschta, R. L., 2004. Wolf reintroduction, predation risk and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*, 184, 299-313.

Ripple, W. J. and Larsen, E. J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation*, 95, 361-370.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P. and Schmitz, O.J., 2014. Status and ecological effects of the world's largest carnivores. *Science,* 343(6167, p.1241-84)

Ripple, W.J., Wirsing, A.J., Wilmers, C.C. and Letnic, M., 2013. Widespread mesopredator effects after wolf extirpation. *Biological Conservation*, 160, pp.70-79.

Risbey, D.A., Calver, M.C., Short, J., Bradley, J.S. and Wright, I.W., 2000. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research*, 27(3), pp.223-235.

Rogstad, A., Bean, T.M., Olsson, A. and Casady, G.M., 2009. Fire and invasive species management in hot deserts: resources, strategies, tactics, and response. *Rangelands*, 31(3), pp.6-13.

Rohner, C. and Ward, D., 1997. Chemical and mechanical defence against herbivory in two sympatric species of desert Acacia. *Journal of Vegetation Science,* 8(5), pp.717-726.

Rojas-Martinez, A.E., Pavón, N.P. and Castillo, J.P., 2015. Effects of seed ingestion by the lesser long-nosed bat Leptonycteris yerbabuenae on the germination of the giant cactus Isolatocereus dumortieri. *The Southwestern Naturalist,* 60(1), pp.85-89.

Roschlau, C. and Scheibler, E., 2016. Foraging behaviour of a desert rodent community: habitat or moon–which is more influential? *Ethology Ecology & Evolution*, 28(4), pp.394-413.

Rosenzweig, M.L. and Winakur, J., 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology,* 50(4), pp.558-572.

Rudzinski, D. R., Graves, H. B., Sargeant, A. B. and Storm, G. L., 1982, Behavioural interactions of penned red and arctic foxes. *Journal of Wildlife Management*, 46, 877-884.

Ryerson, D.E. and Parmenter, R.R., 2001. Vegetation change following removal of keystone herbivores from desert grasslands in New Mexico. *Journal of Vegetation Science,* 12(2), pp.167-180.

Samson, D.A., Philippi, T.E. and Davidson, D.W., 199. Granivory and competition as determinants of annual plant diversity in the Chihuahuan desert. *Oikos*, pp.61-80.

Sass, S. and Wilson, A., 2006. Effects of fire on lizard communities in the mallee shrublands of western New South Wales. *Herpetofauna,* 36(2), pp.106-111.

Schachtschneider, K. and February, E.C., 2013. Impact of Prosopis invasion on a keystone tree species in the Kalahari Desert. *Plant Ecology,* 214(4), pp.597-605.

Schade, J.D., Kyle, M., Hobbie, S.E., Fagan, W.A. and Elser, J.J., 2003. Stoichiometric tracking of soil nutrients by a desert insect herbivore. *Ecology Letters,* 6(2), pp.96-101.

Schaller, G. B., 1972. *The Serengeti lion: a study of predator-prey relations*, in G. B. Schaller, (ed.) Wildlife behaviour and ecology series, University of Chicago Press, Chicago.

Schleicher, J., Wiegand, K. and Ward, D., 2011. Changes of woody plant interaction and spatial distribution between rocky and sandy soil areas in a semi-arid savanna, South Africa. *Journal of Arid Environments*, 75(3), pp.270-278.

Schlesinger, C., White, S. and Muldoon, S., 2013. Spatial pattern and severity of fire in areas with and without buffel grass (*Cenchrus ciliaris*) and effects on native vegetation in central Australia. *Austral Ecology* 38(7), 831-840.

Schlesinger, C.A., 2007. Does vegetation cover affect the rate of capture of ground-active lizards in pitfall traps?. *Wildlife Research*, 34(5), pp.359-365.

Schlesinger, C.A., Noble, J.C. and Weir, T., 1997. Fire studies in mallee (Eucalyptus spp.) communities of western New South Wales: Reptile and beetle populations in sites of differing fire history. *The Rangeland Journal*, 19(2), pp.190-205.

Schlesinger, W.H. and Pilmanis, A.M., 1998. Plant-soil interactions in deserts. *Biogeochemistry*, 42(1-2), pp.169-187.

Schlesinger, W.H., Raikes, J.A., Hartley, A.E. and Cross, A.F., 1996. On the Spatial Pattern of Soil Nutrients in Desert Ecosystems: Ecological Archives E077-002. *Ecology,* 77(2), pp.364-374.

Schooley, R.L., Sharpe, P.B. and Horne, B.V., 1996. Can shrub cover increase predation risk for a desert rodent?. *Canadian Journal of Zoology*, 74(1), pp.157-163.

Schroeder, T., Lewis, M.M., Kilpatrick, A.D. and Moseby, K.E., 2015. Dingo interactions with exotic mesopredators: spatiotemporal dynamics in an Australian arid-zone study. *Wildlife Research*, 42(6), pp.529-539.

Schwinning, S. and Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141(2), pp.211-220.

Schwinning, S., Sala, O.E., Loik, M.E. and Ehleringer, J.R., 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia*, 141 pp.191-193.

Shenbrot, G., 2014. Population and community dynamics and habitat selection of rodents in complex desert landscapes. *Mammalia* 78:1-10.

Shenbrot, G., B. Krasnov, and S. Burdelov., 2010. Long-term study of population dynamics and habitat selection of rodents in the Negev Desert. *Journal of Mammalogy* 91:776-786.

Short, J., 1998. The extinction of the rat-kangaroos in New South Wales, Australia. *Biological Conservation* 86, 365-377.

Short, J. and Smith, A., 1994. Mammal decline and recovery in Australia. *Journal of Mammalogy*, 75(2), pp.288-297.

Short, J., Calver, M.C. and Risbey, D.A., 1999. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. I. Exploring potential impact using diet analysis. *Wildlife Research*, 26(5), pp.621-630.

Short, J., Kinnear, J.E. and Robley, A., 2002. Surplus killing by introduced predators in Australia—evidence for ineffective anti-predator adaptations in native prey species? *Biological Conservation*, 103(3), pp.283-301.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016, 2016 guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.

Smith, A. P. & Quin, D. G., 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* 77, 243-267.

Smith, A.L., Bull, C.M. and Driscoll, D.A., 2013. Successional specialization in a reptile community cautions against widespread planned burning and complete fire suppression. *Journal of Applied Ecology,* 50(5), pp.1178-1186.

Smith, S.D., Huxman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Coleman, J.S., Fenstermaker, L.K., Seemann, J.R. and Nowak, R.S., 2000. Elevated CO 2 increases productivity and invasive species success in an arid ecosystem. *Nature*, 408(6808, p.79).

Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Sorice, J. and Hill, S., 1988. Reconstructed dynamics of rapid extinctions of chapparal-requiring birds in urban habitat islands. *Conservation Biology* 2: 75–92.

Soule, M. K., Estes, J. A., Miller, B. & Honnold, D. L., 2005. Strongly interacting species: Conservation policy, management and ethics. *BioScience* 55, 168-176.

Southgate, R., and P. Masters., 1996. Fluctuations of rodent populations in response to rainfall and fire in a central Australian hummock grassland dominated by *Plectrachne schinzii*. *Wildlife Research* 23:289-303.

Southgate, R., and S. Carthew., 2008. Post-fire ephemerals and spinifex-fuelled fires: a decision model for bilby habitat management in the Tanami Desert, Australia. *International Journal of Wildland Fire* 16:741-754.

Southgate, R., Paltridge, R., Masters, P. and Ostendorf, B., 2007. Modelling introduced predator and herbivore distribution in the Tanami Desert, Australia. *Journal of Arid Environments*, 68(3), pp.438-464.

Spencer, E. E., Crowther, M. S. and Dickman C.R., 2014a. Diet and prey selectivity of three species of sympatric mammalian predators in central Australia. *Journal of Mammalogy* 95: 1278-1288.

Spencer, E. E., Crowther, M. S. and Dickman C.R., 2014b. Risky Business: Do Native Rodents Use Habitat and Odor Cues to Manage Predation Risk in Australian Deserts? *Oikos* 9 (2).

Spencer, E. E., Newsome, T. M. and Dickman C.R., 2017. Prey selection and dietary flexibility of three species of mammalian predator during an irruption of non-cyclic prey. *Royal Society Open Science* 4: 1703 7.

Sponseller, R.A., 2007. Precipitation pulses and soil CO2 flux in a Sonoran Desert ecosystem. *Global Change Biology*, 13(2), pp.426-436.

Strong, D.R., Kaya, H.K., Whipple, A.V., Child, A.L., Kraig, S. and Bondonno, M., 1996. Entomopathogenic nematodes: natural enemies of root-feeding caterpillars on bush lupine. *Oecologia*. 108: 167–173.

Sutherland, E. F., and C.R. Dickman., 1999. Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildlife Research* 26:405-419.

Sweet, I.P. and Crick, I.H., 1992. *Uluru and Kata Tjuta - A geological history*, Australian Geological Survey Organisation, Canberra.

Tabeni, S., Marcos, N., Rosi, M.I., Bender, B., 2012. Vulnerability of small and medium sized prey mammals in relation to their habitat preferences, age classes and locomotion types in the temperate Monte Desert, *Argentinian Mammalian Biology*, 77, 90–96.

Taraborelli, P., Borruel, N. and Mangeaud, A. 2009. Ability of murid rodents to find buried seeds in the Monte Desert. *Ethology* 115(3), 201-209.

Taraborelli, P., Corbalán, V., Giannoni, S., 2003. Locomotion and escape modes in rodents of the Monte Desert (Argentina). *Ethology*, 109, 475–485.

Tews, J., Moloney, K. and Jeltsch, F., 2004. Modelling seed dispersal in a variable environment: a case study of the fleshy-fruited savanna shrub Grewia flava. *Ecological Modelling*, 175, 65–76.

Thibault, K. M., S. K. Morgan Ernest, E. P. White, J. H. Brown, and J. R. Goheen., 2010. Long-term insights into the influence of precipitation on community dynamics in desert rodents. *Journal of Mammalogy* 91:787-797.

Thompson S.D., 1982. Structure and species composition of desert heteromyid rodent species assemblages. Effects of a simple habitat manipulation. *Ecology*, 63(5), pp. 1313-1321.

Thompson, D.B., Brown, J.H. and Spencer, W.D., 1991. Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. *Ecology,* 72(3), pp.852-863.

Thomson, P. C., 1992. The behavioural ecology of dingoes in North-western Australia II, III and IV. Hunting and feeding behaviour and diet. *Wildlife Research* 19, 531-541.

Tilson, R.L. and Henschel, J.R., 1986. Spatial arrangement of spotted hyaena groups in a desert environment, Namibia. *African Journal of Ecology,* 24(3), pp.173-180.

Tischler, M., Dickman C.R. and Wardle, G.M., 2013. Avian functional group responses to rainfall across four vegetation types in the Simpson Desert, central Australia. *Austral Ecology*: 809-819.

Uluru - Kata Tjuta Board of Management and Parks Australia 2000. *Uluru - Kata Tjuta National Park Plan of Management 2000* Director of National Parks, Canberra.

Uluru - Kata Tjuta Board of Management and Director of National Parks 2010. *Uluru - Kata Tjuta National Park Plan of Management 2010-2020* Director of National Parks, Canberra.

Upham, N.S., Hafner, J.C., 2013. Do nocturnal rodents in the Great Basin Desert avoid moonlight? *Journal of Mammalogy*, 94 (1), 59–72.

Vander Wall, S.B. and Longland, W.S., 2005. Diplochlory: are two seed dispersers better than one? Trends in *Ecology and Evolution* 19(3), 155-161.

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

Vidiella, P.E., Armesto, J.J. and Gutiérrez, J.R., 1999. Vegetation changes and sequential flowering after rain in the southern Atacama Desert. *Journal of Arid Environments*, 43(4), pp.449-458.

Vinton, M.A. and Burke, I.C., 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology,* 76(4), pp.1116 1133

Walker, R.S., Novaro, A.J., Perovic, P., Palacios, R., Donadio, E., Lucherini, M., Pia, M. and López, M.S., 2007. Diets of three species of Andean carnivores in high-altitude deserts of Argentina. *Journal of Mammalogy*, 88(2), pp.519-525.

Wallach AD, Ramp D, O'Neill AJ., 2017. Cattle mortality on a predator-friendly station in central Australia. *Journal of Mammalogy*. 98: 45–52.

Wang, Y. and Fisher, D.O., 2012. Dingoes affect activity of feral cats, but do not exclude them from the habitat of an endangered macropod. *Wildlife Research*, 39(7), pp.611-620.

Ward, D. and Saltz, D., 1994. Forging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. *Ecology,* 75(1), pp.48-58.

Ward, D., 2016. *The biology of deserts*. Oxford University Press.

Watts, C. H. S. and Aslin, H. J., 1981. *The Rodents of Australia*. Sydney, Angus and Robertson.

Waudby, H.P. and Petit, S., 2015. Small Australian desert vertebrate responses to grazing intensity during La Niña. *Ecological research*, 30(4), pp.715-722.

Wesche, K., Ronnenberg, K., Retzer, V. and Miehe, G., 2010. Effects of large herbivore exclusion on southern Mongolian desert steppes. *Acta Oecologica*, 36(2), pp.234-241.

Whitehouse, M.E., Shochat, E., Shachak, M. and Lubin, Y., 2002. The influence of scale and patchiness on spider diversity in a semi-arid environment. *Ecography*, 25(4), pp.395-404.

Whitford, W. G., 2002. *Ecology of desert systems*. Academic Press, San Diego, California.

Whitney, K.D., 2004. Experimental evidence that both parties benefit in a facultative plant–spider mutualism. *Ecology,* 85(6), pp.1642 1650

Wilson, S., 2012. *Australian lizards: a natural history*. CSIRO Publishing.

Wilson, S.K. and Swan, G., 2012. *A complete guide to reptiles of Australia*. Sydney: Reed New Holland.

Woinarski, J.C., Burbidge, A.A. and Harrison, P.L., 2015. Ongoing unravelling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences* p 7301

Woinarski, J.C., South, S.L., Drummond, P., Johnston, G.R. and Nankivell, A., 2018. The diet of the feral cat (*Felis catus*), red fox (*Vulpes vulpes*) and dog (*Canis familiaris*) over a three-year period at Witchelina Reserve, in arid South Australia. *Australian Mammalogy*, 40(2), pp.204-213.

Woinarski, J.C.Z., Murphy, B.P., Legge, S.M., Garnett, S.T., Lawes, M.J., Comer, S., Dickman C.R., Doherty, T.S., Edwards, G., Nankivell, A. and Paton, D., 2017. How many birds are killed by cats in Australia?. *Biological Conservation*, 214, pp.76-87.

Woolley, P. A., 1984. Reproduction in *Antechinomys laniger* (‘*spenceri’* form) (Marsupialia: Dasyuridae): field and laboratory observations. *Australian Wildlife Research* 11:481–489.

Wright, B.R. and Fensham, R.J., 2017. Relationships between fire severity and recruitment in arid grassland dominated by the obligate-seeding soft spinifex (Triodia pungens). *International Journal of Wildland Fire*, 25(12), pp.1264 -272.

Wysong, M.L., 2016. *Predator ecology in the arid rangelands of Western Australia: spatial interactions and resource competition between an apex predator, the dingo Canis dingo, and* *an introduced mesopredator, the feral cat Felis catus* Ph. D. thesis. University of Western Australia, Perth.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence., 2010. A meta-analysis of resource pulse-consumer interactions. *Ecological Monographs* 80:125-151.

Zhang, R., Wang, Z., Han, G., Schellenberg, M.P., Wu, Q. and Gu, C., 2018. Grazing induced changes in plant diversity is a critical factor controlling grassland productivity in the Desert Steppe, Northern China. *Agriculture, Ecosystems & Environment*, 265, pp.73-83.

Appendix 1

Pooled numbers of mammals, birds and reptiles recorded in surveys at eight sites (S1–S8) in Uluṟu Kata Tjuṯa National Park between 1994 and 2010.

	Site							
Species	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**
Dasycercus blythi	0	0	0	2	0	0	34	0
Ningaui ridei	2	0	19	19	15	10	29	0
Pseudantechinus macdonnellensis	11	0	0	0	0	0	0	0
Sminthopsis hirtipes	0	0	0	4	0	3	1	0
Sminthopsis ooldea	6	9	3	4	2	11	1	0
Sminthopsis youngsoni	1	1	22	24	35	14	4	4
Mus musculus	469	24	44	19	8	14	47	103
Notomys alexis	37	22	67	115	26	37	63	7
Pseudomys desertor	100	3	9	2	1	3	12	1
Pseudomys hermannsburgensis	142	60	138	227	87	95	353	95
Gowidon longirostris	0	1	0	0	0	0	0	0
Ctenophorus isolepis	0	0	15	10	19	8	19	0
Ctenophorus nuchalis	2	0	3	6	2	2	1	6
Diporiphora winneckei	0	0	5	4	1	1	0	0
Moloch horridus	0	0	9	2	1	0	0	0
Pogona minor	1	3	2	1	5	5	1	3
Diplodactylus conspicillatus	21	27	23	35	17	29	14	26
Gehyra variegata	2	2	3	6	8	5	0	1
Heteronetia binoei	0	0	1	1	0	0	0	3
Lucasium stenodactylum	0	2	22	14	11	10	15	0
Nephrurus laevissimus	0	0	31	10	25	6	1	0
Nephrurus levis	0	1	1	4	0	3	2	1
Rhynchoedura ornata	2	2	37	34	11	53	11	6
Strophurus ciliaris	4	7	11	10	9	10	0	17
Strophurus elderi	3	2	2	1	2	0	2	2
Varanus brevicauda	0	0	1	0	0	1	8	0
Varanus eremius	0	0	7	4	2	4	4	1
Varanus gilleni	0	2	1	0	1	1	0	1
Varanus gouldii	0	0	1	1	3	2	0	0
Varanus tristis	0	0	0	0	0	0	0	1
Delma butleri	6	0	0	0	2	0	1	0
Delma desmosa	6	0	0	0	2	0	0	3
Delma haroldi	1	0	0	3	0	6	0	0
Delma nasuta	4	0	0	1	4	0	7	0
Lialis burtonis	0	0	3	2	1	1	0	1

Pygopus nigriceps	0	5	6	8	0	7	2	0
Carlia tricantha	0	0	0	0	0	0	0	18
Cryptoblepharus plagiocephalus	3	0	0	0	0	0	0	0
Ctenotus brooksi	0	0	42	33	28	0	1	0
Ctenotus dux	0	0	12	3	4	3	0	0
Ctenotus hanloni	0	0	0	0	0	0	20	0
Ctenotus leae	0	0	32	0	11	0	0	0
Ctenotus nasutus	0	1	14	10	9	0	1	0
Ctenotus piankai	0	1	7	16	2	6	35	0
Ctenotus septenarius	0	0	0	0	0	0	0	44
Ctenotus calurus	0	0	16	25	14	7	66	0
Ctenotus grandis	0	0	3	2	0	0	12	0
Ctenotus helenae	17	2	17	25	9	8	8	3
Ctenotus leonhardii	88	41	0	1	2	18	14	22
Ctenotus pantherinus	0	0	15	32	7	7	61	1
Ctenotus schomburgkii	0	4	10	13	0	8	0	0
Ctenotus quatturodecimlineatus	1	0	53	45	32	62	1	0
Cyclodomorphus melanops	0	0	5	2	4	0	0	0
Liopholis inornata	0	22	0	1	15	31	0	0
Liopholis striata	0	3	0	0	0	0	9	0
Eremiascinus phantasmus	0	0	10	3	13	0	0	0
Lerista bipes	0	0	77	44	106	17	51	0
Lerista desertorum	11	2	2	3	1	2	0	19
Lerista labialis	1	9	6	2	1	1	3	36
Lerista xanthura	0	0	1	1	0	0	0	0
Menetia greyii	12	11	14	19	2	16	49	14
Morethia ruficauda	0	3	0	4	11	0	0	1
Notoscincus ornatus	0	0	4	0	0	0	7	0
Tiliqua multifasciata	0	0	0	1	2	3	1	0
Tiliqua occipitalis	0	0	0	0	0	1	0	0
Ramphotyphlops endoterus	0	3	23	19	28	5	0	10
Ramphotyphlops grypus	0	0	1	1	0	0	2	0
Brachyurophis fasciolatus	0	0	0	0	1	0	0	0
Brachyurophis semifasciatus	1	0	0	1	0	0	0	8
Demansia psammophis	2	0	0	0	0	1	0	1
Parasuta monachus	0	1	0	0	1	0	1	1
Pseudechis australis	1	0	0	1	0	0	0	0
Pseudonaja modesta	0	1	1	1	2	2	3	0
Pseudonaja nuchalis	0	1	0	0	0	1	0	0

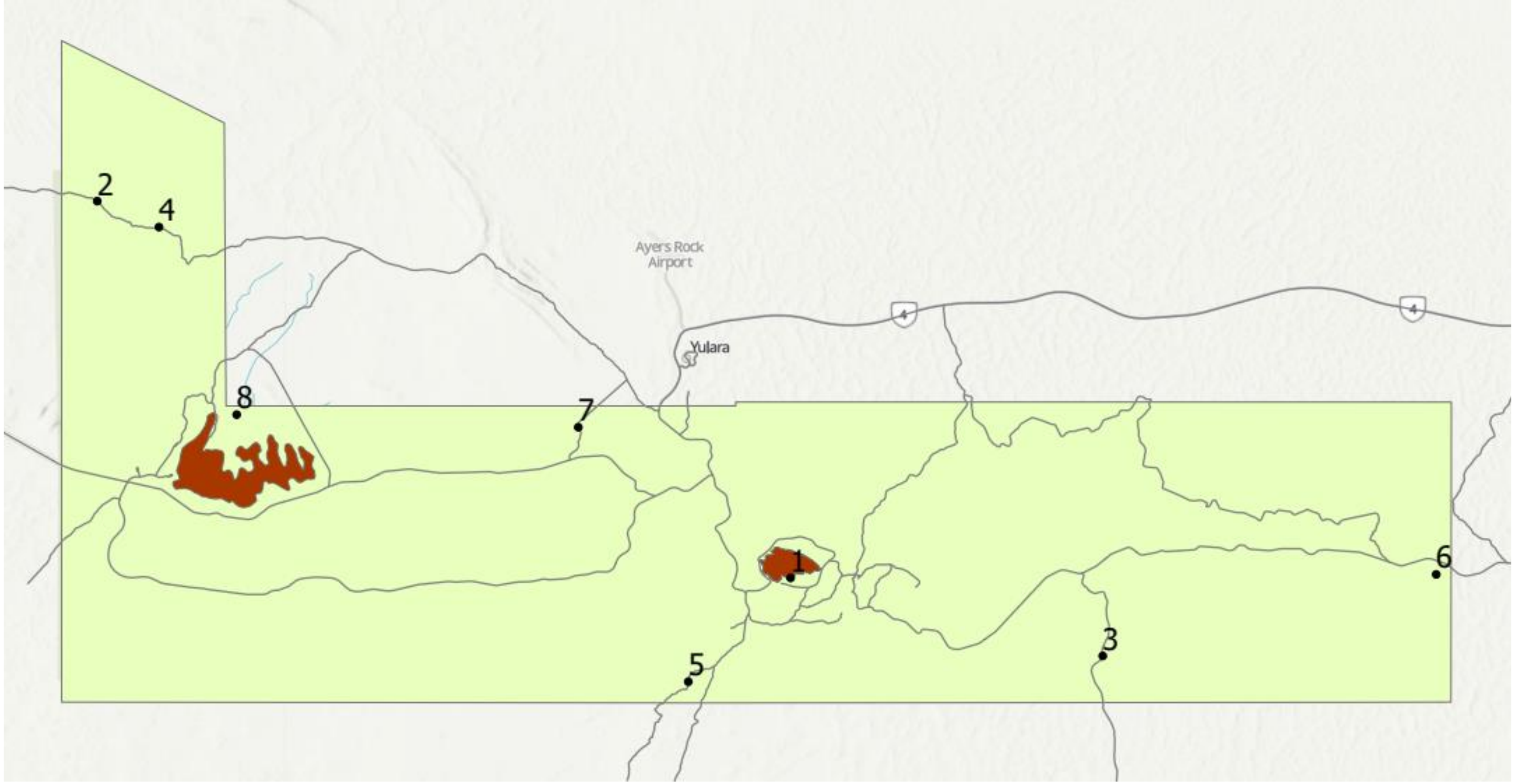
Simoselaps anomalus	0	0	19	6	16	0	0	0
Accipiter fasciatus	0	0	0	0	0	0	0	0
Accipiter cirrocephalus	17	14	0	1	0	1	0	4
Elanus axillaris	3	0	0	0	0	0	1	0
Aquila audax	3	0	0	0	0	0	0	0
Hieraaetus morphnoides	0	0	0	0	0	1	0	0
Hamirostra melanosternon	1	0	0	0	0	0	0	0
Milvus migrans	0	0	0	0	0	1	0	0
Circus assimilis	1	0	0	0	0	0	1	0
Cincloramphus mathewsi	165	0	0	0	0	1	0	75
Cincloramphus cruralis	0	0	0	0	0	0	19	0
Apus pacificus	0	0	26	0	0	0	0	0
Artamus minor	90	0	0	0	0	0	0	0
Cracticus nigrogularis	106	2	18	16	13	1	1	53
Artamus cinereus	150	30	436	226	171	207	324	98
Gymnorhina tibicen	53	0	20	32	7	5	24	43
Artamus personatus	42	57	779	498	679	376	352	155
Cracticus torquatus	1	17	7	8	93	59	4	6
Coracina novaehollandiae	90	1	5	0	13	1	1	55
Lalage sueurii	69	19	118	90	176	161	1	44
Coracina maxima	0	2	6	13	0	0	3	0
Eurostopodus argus	0	4	0	0	1	0	0	0
Aegotheles cristatus	0	0	0	0	0	1	0	0
Psophodes occidentalis	4	29	0	0	0	0	0	109
Cinclosoma castaneothorax	0	0	0	0	0	0	0	5
Geopelia cuneata	51	4	0	6	11	9	0	53
Phaps chalcoptera	7	0	0	2	4	0	0	18
Ocyphaps lophotes	22	0	3	2	16	0	19	51
Corvus orru	16	7	18	10	8	24	27	61
Corvus bennetti	0	0	1	2	0	4	4	0
Chalcites osculans	0	0	0	1	0	8	0	0
Chalcites basalis	0	1	2	0	11	11	1	1
Cuculus pallidus	3	0	7	0	16	8	0	3
Dicaeum hirundinaceum	14	2	0	0	1	1	0	14
Rhipidura fuliginosa	0	7	0	0	0	4	0	0
Rhipidura leucophrys	127	44	51	106	125	162	47	129
Dromaius novaehollandiae	0	0	0	0	1	0	0	2
Falco cenchroides	22	1	5	10	1	2	11	8
Falco berigora	8	8	17	3	6	29	1	31
Falco peregrinus	2	0	0	0	0	0	0	0

Falco longipennis	0	0	0	0	0	0	1	1
Todiramphus pyrrhopygia	29	0	2	0	1	0	0	14
Hirundo ariel	792	0	3	2	0	0	0	20
Cheramoeca leucosternus	0	0	2	7	0	0	0	4
Hirundo nigricans	5	0	0	0	0	0	0	0
Cheramoeca leucosternus	0	0	1	4	0	0	0	0
Malurus splendens	2	93	0	2	0	228	0	7
Malurus leucopterus	0	18	165	9	0	0	149	12
Malurus lamberti	16	62	33	96	42	11	2	175
Amytornis striatus	0	0	8	0	0	0	0	0
Lichenostomus keartlandi	596	0	0	0	0	0	0	47
Acanthagenys rufogularis	304	94	54	109	389	351	36	69
Manorina flavigula	67	13	175	190	209	92	11	63
Lichenostomus virescens	231	236	391	506	33	73	243	336
Epthianura tricolor	31	38	492	24	59	77	86	109
Phylidonyris albifrons	3	4	199	38	97	47	1	12
Certhionyx variegatus	26	6	88	52	42	64	21	30
Lichenostomus plumulus	0	0	1	0	545	0	0	0
Lichenostomus penicillatus	18	0	1	0	0	0	0	642
Certhionyx niger	3	7	32	4	18	11	0	2
Lichmera indistincta	0	0	0	0	0	0	0	1
Merops ornatus	161	4	2	4	22	0	0	71
Anthus novaeseelandiae	22	0	0	0	0	0	25	22
Daphoenositta chrysoptera	4	0	38	26	0	0	0	5
Ardeotis australis	0	1	3	0	1	0	2	0
Colluricincla harmonica	45	17	7	19	112	80	2	64
Oreoica gutturalis	62	264	149	192	240	228	120	101
Pachycephala rufiventris	87	467	0	25	303	314	0	139
Pardalotus rubricatus	4	0	0	1	2	0	0	15
Smicronis brevirostris	0	0	0	0	22	0	0	0
Aphelocephala leucopsis	7	34	0	7	0	2	0	62
Acanthiza apicalis	5	104	0	36	65	228	5	14
Acanthiza robustirostris	0	119	3	34	17	138	0	12
Acanthiza uropygialis	0	59	0	23	8	74	0	23
Acanthiza chrysorrhoa	38	17	0	9	2	11	0	48
Pyrrholaemus brunneus	0	39	0	0	0	37	0	0

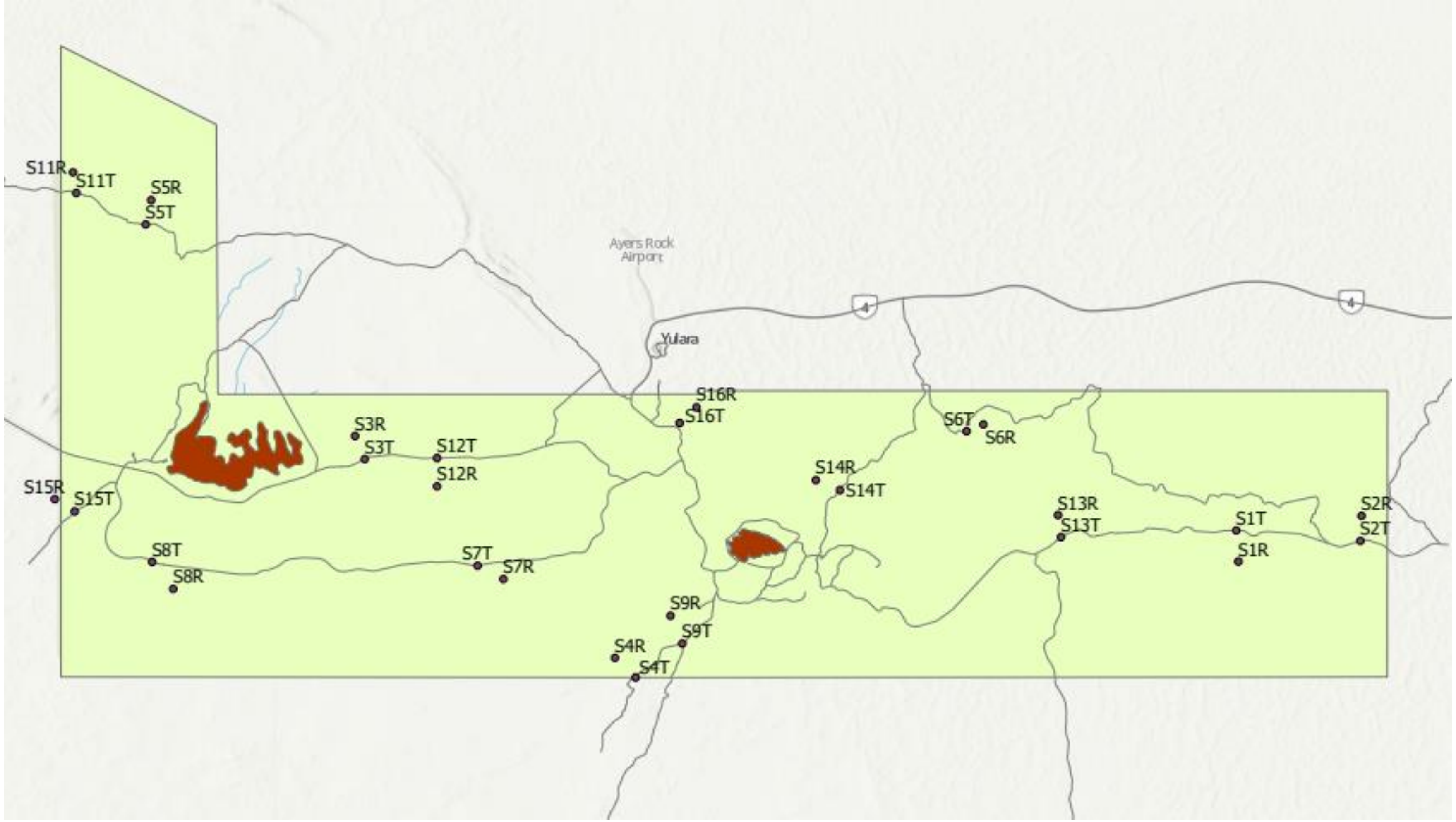
Gerygone fusca	0	16	0	3	4	17	0	0
Aphelocephala nigricincta	0	0	189	21	0	0	54	0
Pardalotus striatus	3	0	0	0	0	0	0	0
Petroica goodenovii	7	210	1	16	17	186	0	11
Melanodryas cucullata	6	18	2	9	21	0	15	72
Microeca fascinans	0	0	0	0	13	0	0	0
Coturnix ypsilophora	2	0	0	0	0	0	0	0
Barnadius zonarius	0	3	4	21	31	30	2	78
Psephotus varius	3	20	4	40	51	18	4	36
Neopsephotus bourkii	1	9	0	0	2	7	0	0
Melopsittacus undulatus	204	980	735	681	860	709	1807	434
Nymphicus hollandicus	0	0	31	7	9	2	3	15
Neophema splendida	0	0	0	0	7	2	0	0
Taeniopygia guttata	983	67	382	153	29	35	723	1565
Emblema pictum	0	0	0	0	0	0	0	2
Podargus strigoides	0	0	0	0	0	1	0	0
Pomatostomus superciliosus	22	130	3	26	42	105	7	145
Eolophus roseicapillus	0	0	14	0	2	10	1	0
Cacatua leadbeateri	0	0	0	2	4	4	2	0
Chlamydera guttata	0	0	0	1	0	0	0	19
Chlamydera maculata	0	0	0	0	1	0	0	6
Turnix velox	11	8	6	6	1	5	9	24

Appendix 2

Map of Uluru-Kata Tjuta National Park with locations of the historical fauna survey sites



Map of Uluru-Kata Tjuta National Park with locations of the contemporary fauna survey sites



Sites 1-6 (mulga woodland), Site 7,8,9 and 11 (mallee woodland) and sites 12-16 (spinifex grassland).

Appendix 3

Dietary preference (Diurnal generalist/diurnal specialist/nocturnal generalist/nocturnal specialist) of reptiles at three sites in Uluṟu Kata Tjuṯa National Park between 1994 and 2010.

Species	**Dietary preference**
Varanus brevicauda	Diurnal generalist
Varanus eremius	Diurnal generalist
Varanus gilleni	Diurnal generalist
Varanus gouldii	Diurnal generalist
Varanus tristis	Diurnal generalist
Amphibolurus longirostris	Diurnal generalist
Ctenotis brooksi	Diurnal generalist
Ctenotis dux	Diurnal generalist
Ctenotis hanloni	Diurnal generalist
Ctenotis leae	Diurnal generalist
Ctenotis nasutus	Diurnal generalist
Ctenotis piankai	Diurnal generalist
Ctenotis septenarius	Diurnal generalist
Ctenotis calurus	Diurnal generalist
Ctenotis grandis	Diurnal generalist
Ctenotis helenae	Diurnal generalist
Ctenotis leonhardii	Diurnal generalist
Ctenotis schomburgkii	Diurnal generalist
Ctenotus quattuordecimlinaetus	Diurnal generalist
Menetia greyii	Diurnal generalist
Morethia ruficauda	Diurnal generalist
Notoscincus ornatus	Diurnal generalist
Egernia inornata	Diurnal generalist
Egernia striata	Diurnal generalist
Tiliqua multifasciata	Diurnal generalist
Tiliqua occipitalis	Diurnal generalist
Ctenophorus nuchalis	Diurnal generalist
Diporiphora winneckei	Diurnal generalist
Pogona minor	Diurnal generalist
Cryptoblepharus plagiocephalus	Diurnal generalist
Ctenophorus isolepis	Diurnal specialist
Moloch horridus	Diurnal specialist
Demansia psammophis	Diurnal specialist
Lialis burtonis	Diurnal specialist
Ctenotis pantherinus	Diurnal specialist
Pseudechis australis	Nocturnal generalist
Pseudonaja nuchalis	Nocturnal generalist
Gehyra variegata	Nocturnal generalist
Heteronetia binoea	Nocturnal generalist
Lucasium stenodactylum	Nocturnal generalist
Nephurus laevissimus	Nocturnal generalist
Nephurus levis	Nocturnal generalist
Strophurus ciliaris	Nocturnal generalist
Strophurus elderi	Nocturnal generalist

Delma butleri	Nocturnal generalist
Delma desmosa	Nocturnal generalist
Delma haroldi	Nocturnal generalist
Delma nasuta	Nocturnal generalist
Carlia tricantha	Nocturnal generalist
Cyclodomorphus melanops	Nocturnal generalist
Eremiascinus fasciolatus	Nocturnal generalist
Lerista bipes	Nocturnal generalist
Lerista desertorum	Nocturnal generalist
Lerista labialis	Nocturnal generalist
Lerista xanthura	Nocturnal generalist
Ramotyphlops endoterus	Nocturnal generalist
Ramotyphlops grypus	Nocturnal generalist
Pseudonaja modesta	Nocturnal specialist
Diplodactylus conspicillatus	Nocturnal specialist
Rhynchoedura ornata	Nocturnal specialist
Pygopus nigriceps	Nocturnal specialist
Brachyurophis fasciolatus	Nocturnal specialist
Brachyurophis semifasciatus	Nocturnal specialist
Parasuta monachus	Nocturnal specialist
Simoselaps anomalus	Nocturnal specialist