Ecology of the savanna glider (*Petaurus ariel*) in tropical northern Australia

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Savanna glider in salmon gum (*Eucalyptus tintinnans*) in Nitmiluk National Park (artwork by volunteer Aline Gibson Vega).

Thesis Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university, and to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis, nor does this thesis contain any material that infringes copyright.

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Acknowledgements

I was once told, when first considering a PhD, that undertaking Honours is like running a sprint but completing a PhD is like running a marathon. Never has an analogy been more accurate. The peaks and troughs in completing this PhD have been significant, the endurance required substantial and at point of submission I am overwhelmed by both exhaustion and an amazing sense of achievement. Like completing a marathon, there has been a team of people that have helped me get here. It has been an amazing journey, and together, I hope we have ensured the future conservation of the remarkable creature.

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This thesis is the culmination of:

> **4** flat tyres,
> while working in **4** National Parks,
> and staying at **15** different remote field locations,
> joined by **50** amazing volunteers,
> together trapping **118** savanna gliders,
> over **360** field days,
> driving **31,627** km,
> suffering **1000**s of mosquito bites,
> all the while creating a million memories.

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Thesis Abstract

Widespread declines of a small, arboreal mammals in the drier regions of northern Australia are of global concern. These declines have been variously attributed to either disruption of resource availability or increased predation pressure from invasive species. The aims of my study were to identify the factors that influence the distribution, abundance and ecology of an arboreal marsupial, the savanna glider (*Petaurus ariel*) in the tropical savannas of northern Australia; including whether this species is in decline. My study forms the first targeted ecological research on this species, which was formerly considered a subspecies of the sugar glider, *P. breviceps*.

My research reveals significant variation in the abundance and ecology of *P. ariel* across its geographic range within the tropical savannas. I found that the dramatic north–south climatic gradient within northern Australia has an overarching influence on the distribution, abundance, density, home range size and fine-scale habitat use of *P. ariel*. Interestingly, I found a 50% increase in *P. ariel* body mass and a ten-fold increase in *P. ariel* home range size in areas of low resource availability. The variable ecology of *P. ariel* has enabled the species to adapt to varied environmental conditions, including areas of naturally low resource availability at the southern edge of the species' distribution. Importantly, my research shows evidence of a 35% decline in the geographic distribution of *P. ariel*, primarily in the southern end of its geographic range; emphasising the need to

understand fundamental aspects of the species' ecology for future conservation efforts.

Overall, my findings highlight the influence of variation in resource availability on an arboreal marsupial in the tropical savannas of northern Australia. My thesis contributes to our understanding of the drivers of the ecology of this, and other, arboreal mammal species inhabiting the region, and helps explain underlying patterns of decline.

Notes on Text

The data chapters of this thesis are formatted as manuscripts, in the style of the scientific journal to which each has been (or will be) submitted. Consequently, there is some repetition, particularly in the Introduction and Methods sections, and there are also stylistic differences between chapters. The list below describes author contributions for all data chapters.

Chapter Two. This chapter has been accepted for publication with the journal *Biodiversity and Conservation*. The authors listed on this publication are: Alyson M. Stobo-Wilson, Brett P. Murphy, Teigan Cremona and Susan M. Carthew. The idea for this chapter was conceived by Brett Murphy, Teigan Cremona, Susan Carthew and I. I collected all data for this chapter, completed all the analyses and wrote the draft of the chapter. Brett Murphy, Teigan Cremona and Susan Carthew also provided editorial comments on the chapter.

Chapter Three. This chapter has been prepared for submission to the *Journal of Biogeography*. The authors listed on this publication are: Alyson M. Stobo-Wilson, Teigan Cremona, Brett P. Murphy and Susan M. Carthew. The idea for this chapter was conceived by Teigan Cremona, Brett Murphy, Susan Carthew and I. Teigan collected all the Petaurid skull data used for this chapter. I collected all other data, completed all the analyses and wrote the draft of the chapter. Teigan Cremona, Brett Murphy and Susan Carthew also provided editorial comments on the chapter.

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Chapter Five. This chapter has been submitted to the journal *Remote Sensing in Ecology and Conservation*. The authors listed on this publication are: Alyson M. Stobo-Wilson, Shaun R. Levick, Teigan Cremona, Brett P. Murphy and Susan M. Carthew. The idea for this chapter was conceived by Teigan Cremona, Brett Murphy, Susan Carthew and I. Shaun Levick collected all LiDAR data for this chapter and assisted with data processing. I collected all other data for this chapter, completed all the analyses and wrote the draft of the chapter. Shaun Levick, Teigan Cremona, Brett Murphy, and Susan Carthew also provided editorial comments on the chapter.

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Chapter One cover page is of a sunrise on Melville Island taken after checking traps in the morning

Introduction

Earth is currently experiencing its sixth 'mass extinction' event, with rapidly declining biodiversity at a global scale (Ceballos *et al.*, 2015), which is in turn driving the loss of important ecosystem services and ecosystem function (Ostfeld & LoGiudice, 2003; Sweeney *et al.*, 2004; Potts *et al.*, 2010). To prevent further biodiversity decline we require an improved knowledge of biodiversity patterns and processes in both natural and modified landscapes (Tscharntke *et al.*, 2012). This requires landscape-scale studies that incorporate both field ecology (focusing on local mechanisms), and biogeography (describing spatial patterns over a regional to global scale). Recently, there has been a globally significant decline of small mammals in the tropical savannas of northern Australia (Woinarski *et al.*, 2015). These declines first occurred in the drier regions of northern Australia, with arboreal mammals being more notably affected. Research to identify the causes of small mammal declines has highlighted insufficient knowledge of the underlying environmental drivers of mammal abundance and diversity within the region, and the ecology and associated habitat requirements of mammal species. Such research gaps have hampered our ability to explain patterns of mammal decline and protect essential resources for declining species. In this thesis, I describe landscape-scale research to provide fundamental information on the ecology of an arboreal, gliding marsupial in the tropical savannas of northern Australia. This work fills some of the critical gaps in our knowledge of the ecology of arboreal mammals in the tropical savannas and provides necessary information to help mitigate further mammal decline.

The tropical savannas of northern Australia

Northern Australia comprises the world's largest expanse of tropical savanna, covering an estimated 1.9 million km^2 (Bradshaw, 2012). These savannas remain relatively undeveloped, and have been integral to protecting Australia's biodiversity, as they act as a refugia for a range of fauna that have suffered marked declines elsewhere in the country (Woinarski & Braithwaite, 1990; Williams *et al.*, 1996; Bradshaw *et al.*, 2009). The tropical savannas of northern Australia occur at locations above the 600 mm rainfall isohyet and are typically dominated by a discontinuous woody overstorey of eucalypts (*Eucalyptus* and *Corymbia* spp.) and occasionally *Acacia*, with an understorey of annual and/or perennial grasses (Williams *et al.*, 1996).

Significant spatial and temporal variation in rainfall across the tropical savannas of northern Australia has an overarching influence on habitat structure and fire regimes (including the frequency, seasonality and intensity of fire) in the region. There is a strong rainfall gradient throughout the region (Figure 1.1), that drives variation in the habitat structure of the savannas, with areas of higher rainfall in the north having greater productivity, woody biomass and vegetation structural complexity relative to areas of low rainfall in the south (Woinarski, 1992; Woinarski *et al.*, 1999). The tropical savannas are also characterised by a distinct wet season (December–April) which encompasses a large part of the years' rainfall, and an almost rainless dry season (May-November) which coincides with the region's fire season (Russell-Smith *et al.*, 2003a). This temporal variation in rainfall influences the region's fire regimes, as it determines the annual cycle of grasses growing then senescing, producing a highly flammable fuel layer each year (Russell-Smith *et al.*, 2003b).

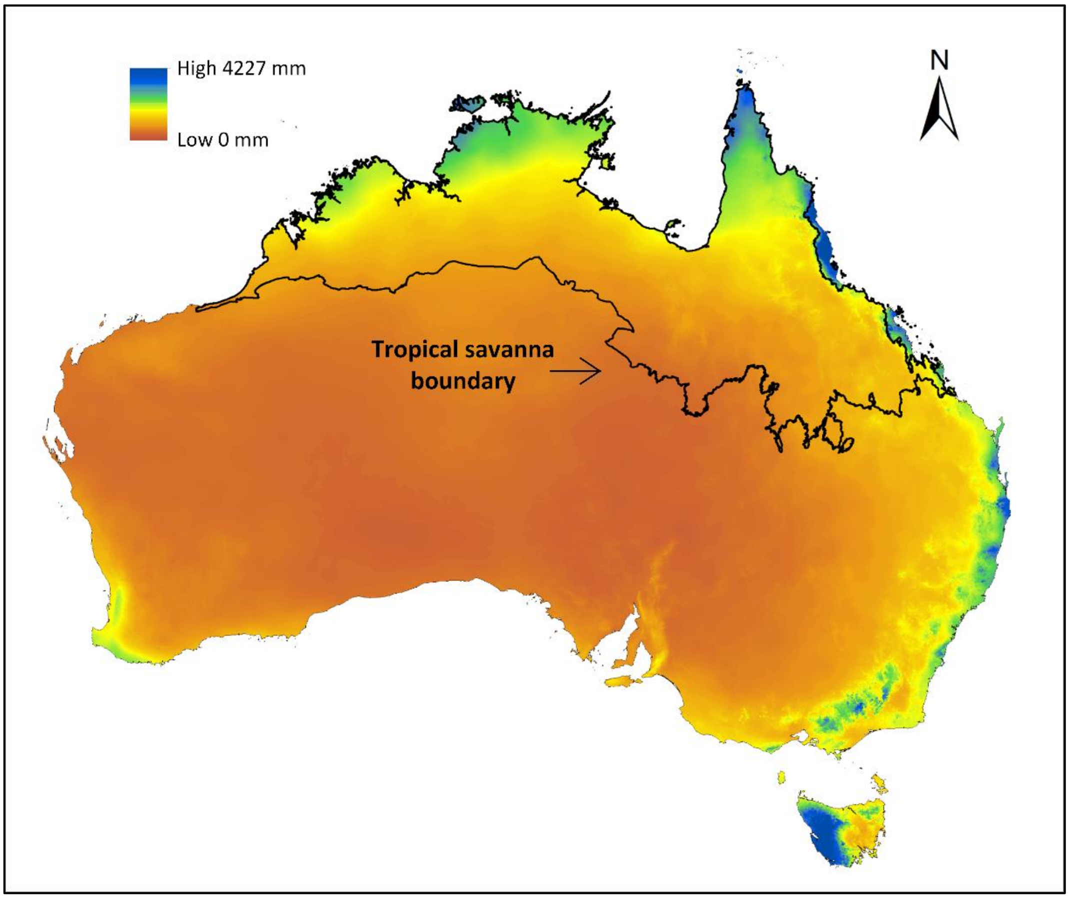

Figure 1.1: Mean annual rainfall across Australia and extent of Australia's tropical savanna landscapes (Fox *et al.*, 2001).

For millennia, tropical savanna fires have been a prominent feature of northern Australia's dry season (May–September) (Russell-Smith *et al.*, 2003b). They are often ignited by humans as well as by lightning associated with the onset of the summer wet season (typically November–December) (Russell-Smith *et al.*, 2003b). Landscape fire management in northern Australia has been an integral part of traditional Aboriginal society for up to 50,000 years (Bowman, 1998; Russell-Smith *et al.*, 2003b). Traditional burning practices consisted of burning small patches of areas as the grass cured, which created a mosaic of burnt and unburnt patches throughout the landscape (Russell-Smith *et al.*, 2003b). However, disruption to traditional burning practices after European settlement in the 19th Century is believed to have led to an increase in the frequency and extent of late dry season fires (Andersen *et al.*, 2012). Despite efforts to restore traditional burning practices, patchiness is substantially lacking under current management regimes (Russell-Smith *et al.*, 2003b), and there is a general paucity of long unburnt habitat available to fire-sensitive savanna species (Andersen *et al.*, 2005).

Small mammal declines in northern Australia

A recent long-term fauna monitoring program in the savannas of the Northern Territory has revealed a rapid and catastrophic decline in populations of small mammals (Woinarski *et al.*, 2010; Woinarski *et al.*, 2011). It has been difficult to determine the key drivers of these declines as many ecological processes within the region have been altered since European settlement (Russell-Smith *et al.*, 2003b; Woinarski *et al.*, 2011). These include altered fire regimes and land use and the introduction of invasive flora and fauna (Russell-Smith *et al.*, 2003b; Setterfield *et al.*, 2010; Legge *et al.*, 2011). Additionally, determining the onset of these declines has been made difficult by the limited availability of historical data due to inaccessibility to a large part of the region and a lack of historical fauna survey effort in northern Australia. Thus, it is difficult to determine what events coincided with the initial decline of small mammals across northern Australia.

Many causes have been suggested to explain small mammal decline in northern Australia, including changes to resource availability, predation by feral cats, poisoning by cane toads (*Bufo marinus*) and novel disease (Woinarski *et al*., 2011). Variation in resource availability has been linked to habitat simplification due to changed fire regimes (Pardon *et al*., 2003; Russell-Smith *et al*., 2003b), over-grazing by herbivores (Legge *et al*., 2011), and the introduction of weeds (Setterfield *et al*., 2010). Of these potential causes, there is more consistent evidence that changed fire regimes (i.e. increased fire frequency and fire intensity) are associated with low mammal abundance (Friend & Taylor, 1985; Friend, 1987; Andersen *et al*., 2005; Woinarski *et al*., 2010; Ziembicki *et al*., 2013b; Lawes *et al*., 2015a). However, in northern Australia there has also been a notable decline of mammals within the 'critical weight range' (35-5500 g) (Burbidge & McKenzie, 1989; Johnson & Isaac, 2009; Murphy & Davies, 2014; Woinarski, 2015). This pattern is reminiscent of earlier mammal declines in Australia which were attributed to increased predation pressure from the introduction of the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*) (Johnson & Isaac, 2009; Fisher *et al*., 2014). In the absence of the red fox, the decline of small mammals in northern Australia suggests predation pressure from the feral cat is also a likely driver of decline. Certainly, increased predation pressure through the introduction of feral cats has been directly linked to the decline of some mammal species in northern Australia (Frank *et al*., 2014; Leahy *et al*., 2016; Davies *et al*., 2017b), with dietary studies on feral cats further suggesting a significant proportion of mammals are likely to be susceptible to feral cat predation (Stokeld *et al*., 2018).

There is strong evidence to support both changed fire regimes and predation by the feral cat as drivers of small mammal decline in northern Australia (Pardon *et* *al.*, 2003; Firth *et al.*, 2010; Frank *et al.*, 2014; Davies *et al.*, 2017b). However, most of the current literature surrounding mammal declines in northern Australia overlooks two other patterns of decline. Firstly, that small mammal decline in northern Australia seems to have followed a trend from south to north, as many species have first declined in their southern extent in areas of lower rainfall, with a resulting contraction to the mesic end of their former distribution (Firth *et al.*, 2010; Start *et al.*, 2012; Ziembicki *et al.*, 2013b). Secondly, that six of the nine mammal species with the most marked declines across northern Australia are at least partially arboreal (Fitzsimons *et al.*, 2010; Woinarski *et al.*, 2010; Ziembicki *et al.*, 2013b). Critical evaluation of the underlying drivers of such patterns will better enable conservation managers to mitigate further declines of small mammals in northern Australia.

While there have been several studies on small mammal declines and the likely causes in northern Australia, there is an over-representation of localised studies and few landscape-scale studies in the literature. There is also a paucity of ecological studies on northern Australia's arboreal mammals that consider in detail their ecology and habitat requirements. Alarmingly, recent research has shown that contraction of mammal distributions has continued to extend into areas of high rainfall at the northern extremities of the tropical savannas (Davies *et al.*, 2017b; Davies *et al.*, 2018). As arboreal mammals in the tropical savannas of northern Australia continue to decline at alarming rates, it is important that we describe the environmental drivers underlying small mammal decline in northern

Australia and identify common patterns in either behaviour or resource use which has made arboreal mammals more susceptible to decline.

Petaurid gliders: A diverse group of arboreal mammals in Australia

In contrast to northern Australia, significant research effort has been allocated to describing the ecology and habitat use of arboreal mammals in southern and eastern Australia (Goldingay, 2011; Berry *et al.*, 2015; Lindenmayer *et al.*, 2017) and identifying their key threats. Threats to arboreal mammals throughout eastern Australia have been relatively conspicuous, with declines primarily attributed to habitat fragmentation, habitat loss (due to agriculture and forestry) and fire (Lindenmayer *et al.*, 1990; Lindenmayer *et al.*, 1997; van der Ree, 2002; Lindenmayer *et al.*, 2013; Berry *et al.*, 2016), all of which reduce the quality and quantity of habitat available for arboreal mammals. One group of arboreal mammals subjected to these threats are the gliding marsupials (Jackson, 1999; Goldingay *et al.*, 2016), most of which belong to the family Petauridae.

Petaurid gliders are arguably the most 'arboreal' non-volant mammals in Australia as they shelter, forage and move almost exclusively within the canopy (Goldingay, 1990; Sharpe & Goldingay, 1998; Jackson, 2001). The ecology of Australia's Petaurid gliders and their habitat requirements have been particularly well studied, with four species of Petaurid glider currently recognised in Australia (Table 1.1). In order of increasing body size, they are the sugar glider (*Petaurus breviceps*), squirrel glider (*P. norfolcensis*), mahogany glider (*P. gracilis*) and yellow-bellied glider (*P. australis*). Petaurid gliders are all nocturnal, obligate hollow-dwellers and have a predominantly exudivorous diet but can be opportunistically insectivorous (Goldingay & Jackson, 2004; Jackson, 2012). All species have a gliding membrane from wrist to ankle, which enables them to glide between trees so that they rarely come to ground (albeit some species have been found to forage in low shrubs) (Jackson, 2012). Petaurid gliders also have a long-furred prehensile tail that allows them to steer their glide, and strong lower incisors that are important for sap feeding (Jackson, 2012).

Studies have been undertaken on the habitat use, social structure, population dynamics, diet and home-range of most of Australia's Petaurid gliders throughout various parts of each species' geographic range (e.g. *P. breviceps*: Suckling, 1984; Quin, 1995; Jackson, 2000; *P. norfolcensis*: Quin, 1995; van der Ree, 2002; Smith and Murray, 2003; Sharpe and Goldingay, 2007, 2010; *P. gracilis*: Jackson, 2000; *P. australis*: Craig, 1985; Goldingay and Kavanagh, 1993; Goldingay and Possingham, 1995; Carthew *et al.*, 1999). To date, considerable variation has been found in the morphology and general ecology both within and between species (Jackson, 2012). For example, both *P. australis* and *P. norfolcensis* show variation in their mating system and home range size depending on regional resource availability (Goldingay, 1992; Quin, 1995; Sharpe & Goldingay, 2007). *Petaurus norfolcensis*, *P. breviceps* and *P. australis* also exhibit variation in fine-scale habitat preferences (Bennett *et al.*, 1991; Quin, 1995; Goldingay, 2011). Variation in the ecology of Petaurids both within and between species highlights that information from one species, or from one location, is not necessarily transferable to another.

Table 1.1: Comparison of body mass, home range area, density and social structure for Australia's gliding Petauridae species (Goldingay & Jackson, 2004; Jackson, 2012); in order of increasing body size. *Petaurus ariel*, the subject of this thesis, is not included in this list.

Body mass (range)	Home range area (range)	Density (range)	Social structure
Petaurus breviceps			
60 – 150 g	0.2 – 10 ha	0.23 – 6.10 per ha^{-1}	Polygynous
Petaurus norfolcensis			
150 – 300 g	0.7 – 10.5 ha	0.35 – 1.54 per ha^{-1}	Socially monogamous to polygynous
Petaurus gracilis			
310 – 500 g	10.0 – 34.0 ha	0.15 – 0.24 per ha^{-1}	Polygynous
Petaurus australis			
435 – 727 g	25.0 – 120.0 ha	0.04 – 0.16 per ha^{-1}	Monogamous or polygynous depending on resource availability

Discovering the savanna glider, *Petaurus ariel*

Although the ecology of Petaurid gliders has seemingly been well-studied within Australia, a recent phylogenetic analysis of *P. breviceps* highlighted a need for further investigation into the taxonomy of gliders in northern Australia (Malekian *et al.*, 2010). While it has always been recognised that a marsupial glider occurs in the tropical savannas of northern Australia, preliminary taxonomic work by Malekian *et al.* (2010) suggested that the northwestern subspecies of sugar glider (*Petaurus breviceps ariel*; Figure 1.2) has much closer affiliations with *P. norfolcensis* and *P. gracilis*, which are found in eastern Australia, than the more ubiquitous *P. breviceps*. A recent targeted study using genetics and morphometrics, has reclassified *P. ariel* as a separate species (T. Cremona and S. Carthew unpublished data). The ecology and habitat requirements of this species were largely unknown prior to the present study. The recent discovery of a distinct species of marsupial glider in northern Australia's tropical savannas further highlights the gaps in our knowledge of arboreal mammals in northern Australia. Throughout this thesis I use the new, albeit not formally published, nomenclature, which considers *P. breviceps ariel* a distinct species – *P. ariel* (Figure 1.3).

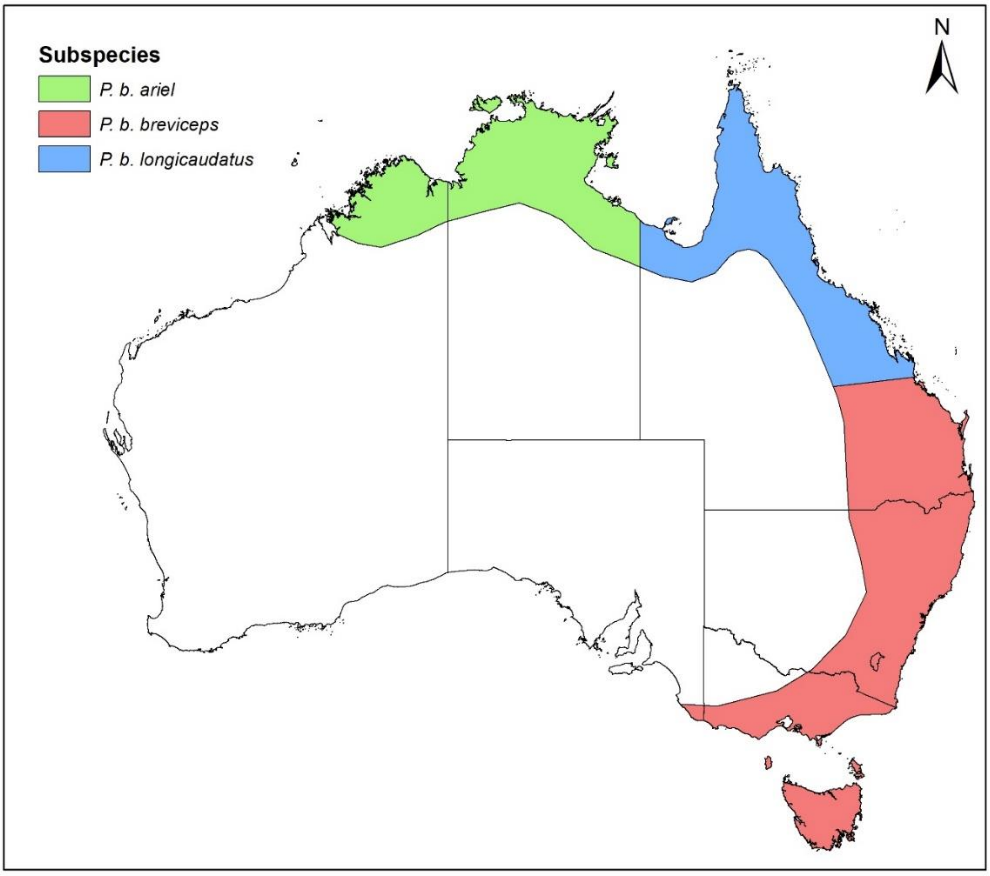

Figure 1.2: Original recorded distribution of formally recognised subspecies *Petaurus breviceps* within Australia (modified from Smith, 1973). Although yet to be formally described, *P. b. ariel* is considered a distinct species, *P. ariel*.

To date, there has been no targeted research on the ecology or conservation status of *P. ariel*. However, existing studies have noted the potential susceptibility of *P. ariel* to frequent high-intensity fires (Corbett *et al.*, 2003) and a high prevalence of *P. ariel* in feral cat scats (Stokeld *et al.*, 2018). Furthermore, fauna surveys undertaken across northern Australia have noted low detectability of *P. ariel* using traditional ground-based survey methods (Einoder *et al.*, 2018). Despite the susceptibility of *P. ariel* to the perceived drivers of mammal decline in northern Australia and low detectability of the species in standard fauna surveys, *P. ariel* is generally not considered to be declining (Woinarski *et al.*, 2010; Woinarski *et al.*, 2014). In view of the disproportionate decline of arboreal mammals in northern Australia there is an obvious need to understand the ecology of *P. ariel* and accurately assess its conservation status.

Figure 1.3: Photograph of savanna glider (*Petaurus ariel*) taken in bushland surrounding Darwin, Northern Territory ; photo credit Amanda Lilleyman.

Thesis aims and scope

My thesis was developed with three observations in mind. Firstly, small mammals first declined in the southern, drier parts of the tropical savannas gradually contracting into northern, mesic regions. Secondly, a large proportion of small mammals which have declined in northern Australia are arboreal, and these groups have been largely under-represented in fauna surveys in northern Australia. Thirdly, *P. ariel* is arguably the least studied and most strictly arboreal mammal in northern Australia, yet there is a concerning assumption that this species is not declining, unlike most other similar-sized mammals in the tropical savannas.

Therefore, the broad aim of this thesis was to **identify the factors that influence the distribution, abundance and ecology of *P. ariel* in the tropical savannas of northern Australia**. This thesis forms the first ecological study focusing on this species. It comprises an investigation on the broad distribution patterns of *P. ariel* over northern Australia's rainfall gradient and details the fine-scale habitat use by *P. ariel* at the climatic extremes of the species' geographic range (Figure 1.4). This thesis addresses whether *P. ariel* is vulnerable to decline and will guide future conservation management of the species in northern Australia.

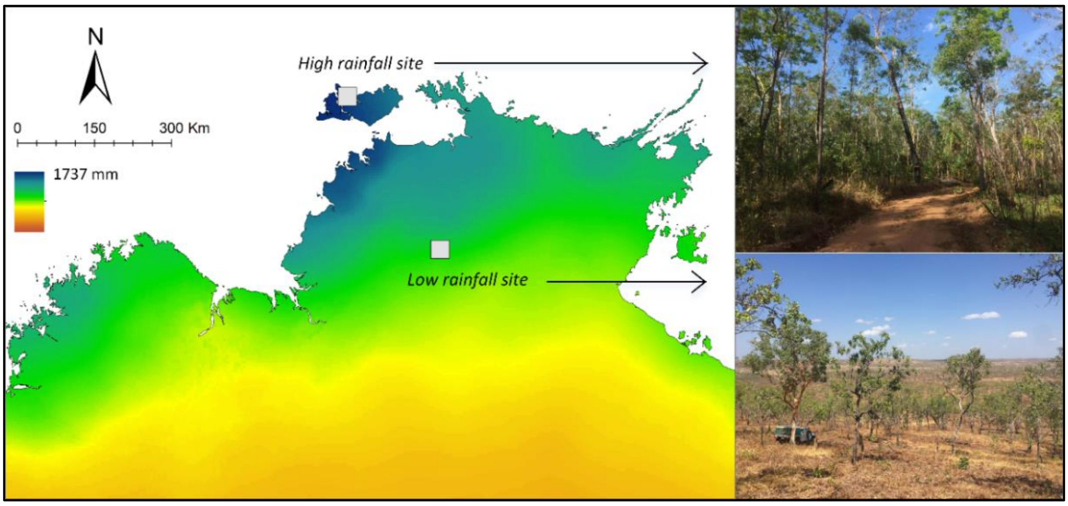

Figure 1.4: Location of the two primary study sites in the Northern Territory referred to in this thesis, representing an area of high and low rainfall (grey squares; 1685 mm and 1074 mm, respectively). Images on the right are of the general habitat structure at each location.

Thesis outline

In **Chapter Two**, I document historical changes in the distribution of *P. ariel* within north and northwestern Australia, and compare them to another arboreal marsupial, the common brushtail possum (*Trichosurus vulpecula*). I also identify broad-scale environmental drivers of the contemporary distribution for each species. I ask the question of whether relatively sparse mammal data from northern Australia can map the known decline of *T. vulpecula*, and if so, also reveal changes in the distribution of *P. ariel*.

In **Chapter Three**, I begin to explore how the environmental gradients in northern Australia influence the ecology of *P. ariel*. Specifically, I look at drivers of variation in *P. ariel* body size (using skull length as a surrogate for body size) throughout the species' geographic range. To strengthen the findings of this chapter I also model variation in body size of three other Petaurid gliders and *T. vulpecula*.

In **Chapter Four** and **Chapter Five** I detail aspects of fine-scale habitat use by *P. ariel* in populations at the climatic extremes of the species' geographic range. In **Chapter Four,** I focus on variation in the home range size and density of *P. ariel* between the two study sites, and in **Chapter Five** I describe variation in den selection between the two sites.

Finally, in **Chapter Six**, I provide a general discussion that evaluates the findings of the study, and make recommendations for future research on *P. ariel*, and more broadly, arboreal mammals in the tropical savannas of northern Australia.

Chapter 2 :

Contrasting patterns of decline in two arboreal marsupials from northern Australia

Brushtail possum (left) and savanna glider (right) observed during spotlight surveys in the Katherine region

Chapter Two cover page photo credit Jenny Davies

Abstract

Widespread declines of small- to medium-sized, semi-arboreal mammals in the drier regions of northern Australia are of global concern. These declines have been variously attributed to either disruption of available resources or increased predation pressure. We aimed to clarify causes of mammal decline in northern Australia using a comparative methods approach, examining historical changes in the distribution of two arboreal mammals, the common brushtail possum (*Trichosurus vulpecula*) and the savanna glider (*Petaurus ariel*), and model drivers of their current abundance. We used single-season occupancy models to describe changes in the geographic range of *P. ariel* and *T. vulpecula* based on multiple-source occurrence data, from before and after 1993. We conducted spotlighting surveys in 2016 across the mesic savannas of the Northern Territory to identify environmental correlates of the current abundance of each species. Our results show that, within northwestern Australia, the geographic range (area where the probability of occupancy was ≥5%) has declined by 72% for *T. vulpecula* and 35% for *P. ariel*, between the historical and contemporary periods (before and after 1993, respectively). The abundance of each species varied substantially across the study area, but high *T. vulpecula* abundance was associated with high shrub density. We propose that areas with high shrub density are providing refuge for *T. vulpecula*, due to an increase in protection from predation by feral cats (*Felis catus*). Regardless of the driver, conservation management within northern Australia should concentrate efforts on maintaining or increasing shrub abundance in tropical savannas. Our findings should also be viewed as an indicator of early stages of *P. ariel* decline and prompt targeted monitoring efforts.

Keywords

Arboreal marsupial, comparative methods, distribution, disturbance, mammal decline, occupancy model, *Petaurus ariel*, presence data, *Trichosurus vulpecula*

Introduction

Modelling patterns and drivers of species decline has never been so important. Globally, there has been a rapid loss of biodiversity over the last century, suggesting we are witnessing Earth's sixth 'mass extinction' event (Ceballos *et al.*, 2015). However, there is a severe deficit of long-term monitoring data for the vast majority of species globally. Thus, we are not only limited in our ability to detect the early stages of species decline but also to infer causes of decline. Since European settlement, Australia has experienced an extremely high rate of decline and extinction of its native mammal fauna (Short & Smith, 1994; McKenzie *et al.*, 2007; Woinarski *et al.*, 2015), and we are failing to mitigate ongoing declines. Most notably, mammals are declining at an alarming rate in the vast tropical savannas of northern Australia, a region once considered a stronghold for mammal groups lost from the arid and temperate regions of Australia (McKenzie *et al.*, 2007). It has been difficult to determine the key drivers of the northern Australian mammal declines, as many ecological processes within the region have been altered since European settlement (Russell-Smith *et al.*, 2003b; Woinarski *et al.*, 2011). Additionally, the relative lack of historical fauna survey effort in northern Australia and the region's vast area and inaccessibility has made it difficult to determine the onset of these declines.

Evidence suggests that disruptions to key ecological processes in northern Australia may have resulted in reduced availability of resources and increased predation pressure. Habitat simplification through changed fire regimes (Pardon *et al.*, 2003; Russell-Smith *et al.*, 2003b), over-grazing by herbivores (Legge *et al.*, 2011) and the introduction of weeds (Setterfield *et al.*, 2010), have all been suggested as possible drivers of mammal decline, due to disruption of resource availability (food and shelter) (Legge *et al.*, 2011; Woinarski *et al.*, 2011; Lawes *et al.*, 2015b). Increased predation pressure through the introduction of feral cats has also been linked to the decline of mammal species in northern Australia (Leahy *et al.*, 2016; Davies *et al.*, 2017b). Overall, targeted studies on drivers of mammal decline primarily support both resource availability (Pardon *et al.*, 2003; Firth *et al.*, 2010) and predation pressure (Frank *et al.*, 2014; Davies *et al.*, 2017b) as the significant drivers. Additionally, recent studies have shown feral cats are more likely to occur in areas with a simplified habitat structure (McGregor *et al.*, 2015; Hohnen *et al.*, 2016; McGregor *et al.*, 2016), suggesting a complex interplay could be occurring between changes in resource availability and predation pressure.

There are distinct similarities in the traits of species that have declined in northern Australia that can be used to identify drivers of decline. Increased predation pressure from the introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) (Johnson & Isaac, 2009; Fisher *et al.*, 2014) has resulted in the disproportionate decline and extinction of mammals that fall within a 'critical weight range' (35-5500 g) (Burbidge & McKenzie, 1989). This trend is evident throughout mainland Australia, including northern Australia (Johnson & Isaac, 2009; Murphy & Davies, 2014; Woinarski, 2015). The continued pattern of decline of mammals in the critical weight range further suggests increased predation pressure is an underlying driver of mammal decline in northern Australia, regardless of the absence of the red fox.

Despite reviews into correlates of decline in both rodents (Lawes *et al.*, 2015b) and marsupials (Fisher *et al.*, 2014) in northern Australia, there are key patterns in the decline of mammals in northern Australia that have seemingly been overlooked. For example, six out of the nine mammals that have experienced ‘marked declines’ in northern Australia are semi-arboreal and arboreal. There has also been little synthesis of research to explain why the onset of declines in northern Australia has occurred in areas of lower rainfall for some species, with a resulting contraction to the mesic ends of their former distribution (Firth *et al.*, 2010; Start *et al.*, 2012; Ziembicki *et al.*, 2013b). Alarmingly, recent research has shown that the contraction of mammal distributions has continued to extend into areas of high rainfall at the northern extremities of the continent (Davies *et al.*, 2017b; Davies *et al.*, 2018). The continued loss of species from their mesic refuges further highlights the need to understand the drivers behind mammal declines in northern Australia. Emphasis should be placed on linking patterns in mammal decline, and similarities in the traits of declining species, to ecological processes, such as increased predation pressure and changed resource availability, to determine key drivers of mammal decline in northern Australia.

Here, we use a comparative methods approach (Fisher & Owens, 2004) to identify historical changes in the distribution of two arboreal mammals in the critical weight range, *Trichosurus vulpecula* Kerr and *Petaurus ariel* (formerly *P. breviceps* subsp. *ariel*

Gould), and model the influence of resource availability as a potential driver of their current abundance. We chose these study species as field-based surveys (Woinarski *et al.*, 2010) suggest *T. vulpecula* has experienced a marked decline in the region (Fitzsimons *et al.*, 2010), while *P. ariel* is (anecdotally) believed to be the only widespread mammal within the critical weight range not to have declined. However, no formal analysis has been undertaken on the extent of decline of either species in the region. Additionally, both study species have sufficient historical occurrence records and can be readily surveyed with conventional survey methods (i.e. spotlight surveys).

Materials and methods

Study species

Neither *T. vulpecula* or *P. ariel* are currently listed as threatened by the IUCN or Australian Government. *Petaurus ariel* is reported to be 'stable' (Woinarski *et al.*, 2014) but has only recently been taxonomically reclassified as a separate species (formerly *P. breviceps* subsp. *ariel*) (T. Cremona, A. Baker, S. Cooper, R Montague-Drake, A. Stobo-Wilson, S. Carthew unpublished data), thus making this the first formal assessment of the distribution and conservation status of *P. ariel*.

Trichosurus vulpecula and *P. ariel* are nocturnal arboreal marsupials that primarily den in tree hollows. Both species have similar and relatively high fecundity; they can carry up to two young in their pouch and are able to reproduce twice within a year . Both species fall within the critical weight range of mammals highly susceptible to decline. However, *T. vulpecula* is noticeably larger in body size (1300–1625 g; Kerle 1998) than

P. ariel (65–140 g; A. Stobo-Wilson, unpublished data), thus there are likely to be differences in the physiological demands of each species (i.e. food and water requirements). There are also minor differences in the diet of each species: *T. vulpecula* are folivorous, while Petaurid gliders are more exudivorous and insectivorous (Jackson & Johnson, 2002; Goldingay & Jackson, 2004). As a Petaurid glider with a patagium, *P. ariel* can glide between trees and therefore may spend very little time on the ground.

Data collection

Geographic range

To map and compare the historical and current geographic range of *T. vulpecula* and *P. ariel* in northwestern Australia we used occurrence records from several sources from the period of 1840 to 2017. Records were sourced from the online database Atlas of Living Australia (http://www.ala.org.au), supplemented by data from Woinarski *et al.* (2014) and surveys undertaken by the Western Australian Department of Biodiversity, Conservation and Attractions (I. Radford, pers. comm.) and Kerle and Burgman (1984). We also used occurrence records from our own field surveys during 2016. Records were split into two time periods, 'before 1993' and 'after (and including) 1993', to align with the time periods examined by Woinarski *et al.* (2014). We defined our study area as northwestern Australia (116–141˚E and 11–21˚S ; shown in Fig. 1), where the geographic range of both study species overlaps. We removed apparent duplicate records with the same latitude, longitude and year, resulting in 1,654 *T. vulpecula* and 432 *P. ariel* records (Fig. 2.1). For both species, there were greater numbers of records available for the period since 1993 (275 and 171 records before 1993, 1379 and 261 records after 1993, for *T. vulpecula* and *P. ariel* respectively).

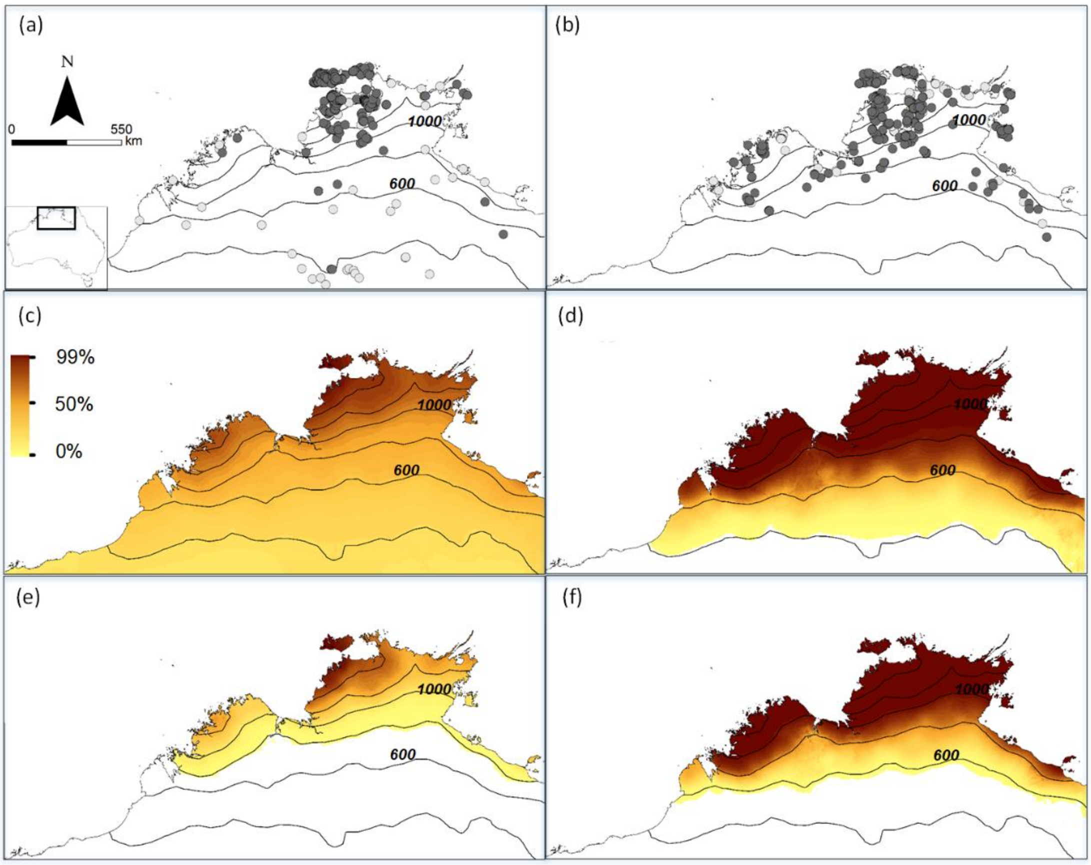

Figure 2.1: Location of the study area and occurrence records for (a) *Trichosurus vulpecula* and (b) *Petaurus ariel* in north and northwestern Australia. Light grey circles represent records before 1993 and dark grey circles represent records after 1993. Black lines represent 200 mm isohyet contours, with 600 and 1000 mm isohyets indicated. The location of the study area relative to Australia is shown in the inset. The modelled geographic range changes for Trichosurus vulpecula (c) before 1993, and (e) after 1993 and Petaurus ariel (d) before 1993, and (f) after 1993, based on the predicted occupancy (≥5%) generated from single-season occupancy models using occurrence records. Areas of darker shading indicate higher predicted abundance. The white areas indicate where predicted occupancy for the respective species is <5%.

Within the defined study area, we assigned each occurrence record to a 50 × 50 km cell using ARCMAP 10.2.2 (ESRI, Redlands, CA). We created separate detection histories for *T. vulpecula* and *P. ariel* based on occurrence records before and after 1993. Detection histories were generated for each cell (considered here as a site) across the entire survey period (1840 to 2017). For each given year '1' indicated the presence of the species and '0' indicated an absence. We also captured occurrence records for all non-flying terrestrial mammals from the study area (from Woinarski et al. 2014) to represent a measure of sampling effort. We tallied the number of records for all mammals (36,700 records in total), including observation records for *T. vulpecula* and *P. ariel*, from within each cell to create a measure of sampling effort for each year. Cells that did not include any observation records in either time period were removed from analysis as they were deemed to be an unsurveyed area (29% of all cells; see Supplementary information, Fig. S2.1). Before proceeding with analysis, we first mapped the spatial-temporal pattern of sampling effort to ensure there was no underlying pattern that would bias our findings (see Supplementary information, Fig. S2.1).

Current abundance

To characterise the current patterns of abundance of *T. vulpecula* and *P. ariel*, we surveyed 39 sites across the mesic, coastal regions of the Northern Territory (Fig. 2.2). All sites were surveyed between March and July 2016, with one exception (Bulman, Arnhem Land), which was opportunistically sampled in November 2016. Site selection was based on the historical distribution of *P. ariel*, habitat suitability and accessibility. To detect arboreal mammals, we undertook spotlight surveys on foot, using head torches (1000 lumens output; Ledlenser, Solingen, Germany). We walked 750-m transects over 45 min each, scanning all habitat and trees either side of the transect. Due to the low vegetation density of the tropical savannas relative to forested areas of southern Australia, spotlighting at a pace of 1km per hour was deemed sufficient for detecting the study species. Up to three sites were surveyed within a night, with no site surveyed more than once in a night. Each site was surveyed at 0.5, 2.5 and 4 h after sunset. The total count of *T. vulpecula* and *P. ariel* recorded from each spotlight site (i.e. the sum of the three surveys) were tallied and used as an index of abundance for that site.

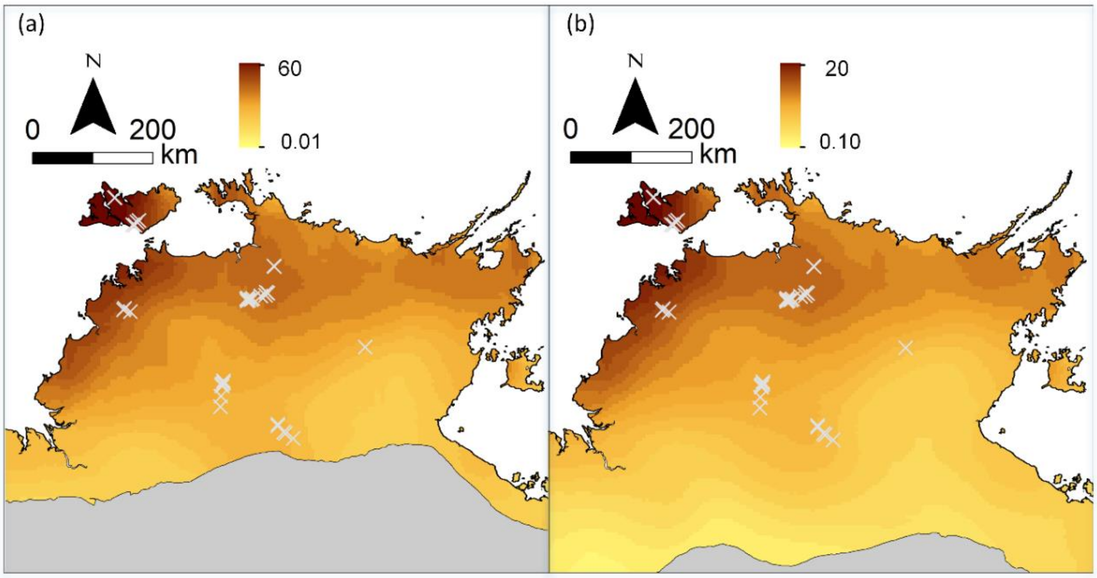

Figure 2.2: Location of 39 sites surveyed for arboreal mammals in 2016 across the mesic savannas of the Northern Territory. The yellow–brown shading indicates the predicted abundance (total number of detections per site over three transects) of (a) Trichosurus vulpecula and (b) Petaurus ariel, generated from the best negative binomial generalised linear model using geographic and site-based variables. Areas of darker brown shading indicate higher predicted abundance. Grey shaded areas indicate where predicted occupancy for the respective species is <5%, generated from single-season occupancy models using occurrence records from after 1993 (Table 2.3; Figure 2.1).

Data analysis

All analyses were conducted in the program R (R Core Team, 2017) unless otherwise stated.

Change in geographic range

We used single-season occupancy models to determine the historical and recent (before and after 1993, respectively) geographic range of *T. vulpecula* and *P. ariel*. To account for the spatial and temporal variation in sampling effort over the study area, probability of detection was modelled as a function of both mean annual rainfall and sampling effort. Probability of occupancy was modelled as a function of mean annual rainfall and time-period (before and after 1993), including an interaction term of mean annual rainfall with time-period to account for the onset of decline in areas of relatively low rainfall. Single-season occupancy modelling was performed using the 'unmarked' package. We used Akaike's Information Criterion (AIC) to identify the most parsimonious models (Burnham & Anderson, 2003). The model with the lowest AIC by >2AIC in the candidate set was deemed the top model. The top model was used to predict the occupancy of each species for each time-period, by using the 'predict' function in the 'spatial tools' package. We used the 'raster' package to map our models over the study area. Any area that had a predicted occupancy of ≥5% was considered part of the species geographic range. For both time periods, we calculated the maximum (95% predicted occupancy) and core geographic range (50% predicted occupancy) of *T. vulpecula* and *P. ariel* to highlight the extent in which each species distribution has changed.

Correlates of current abundance

To model spatial patterns of abundance of *T. vulpecula* and *P. ariel*, we examined both geographic (two) and site-based (10) predictor variables for fire, rainfall, canopy cover, topographic wetness, tree diameter and shrub density (Table 2.1). We also included Julian day (i.e. day of the year) of the survey because of the potential for seasonal variation in the detectability of each species.

We used generalized linear models to investigate whether abundances of *T. vulpecula* and *P. ariel* were correlated with the 13 predictor variables. Modelling was conducted using the 'mass' package. Prior to analyses, predictor variables were centred and standardised by subtracting the mean and dividing by the standard deviation. Data exploration was carried out following the protocol described in Zuur *et al.* (2010). We checked for collinearity between predictor variables and excluded variables that had an r ≥0.5. After initial data exploration, several variables were eliminated from analysis (due to multi-collinearity) with only two geographic variables and three site-based variables included in the final model set. Due to the underlying influence of geographic variables, we modelled site-based predictor variables independently of geographic variables to determine site-based correlates of species abundance. The negative binomial error family was chosen for the GLMs of abundance as there were large numbers of zeros for the count of each species and the data were over-dispersed. We used a model averaging approach to identify important predictor variables (Grueber *et al.*, 2011), using the 'mumin' package. Predictor variables were deemed significant if they had a relative variable importance ≥ 0.73; equivalent to an AIC difference of 2, a common 'rule-of-thumb' to indicate a significant effect (Richards, 2005).

Table 2.1: Description and source of the predictor variables used in analyses of correlates of abundance for *Trichosurus vulpecula* and *Petaurus ariel* in the mesic savannas of the Northern Territory.

Predictor variable	Description and source
(a) Geographic variables (broad-scale)	
Rainfall	Mean annual rainfall based on a standard 30-year climatology (1961 – 1990) (Bureau of Meteorology, www.bom.gov.au).
Topographic wetness index (TWI)	Topographic wetness index is calculated as log_e (specific catchment area/slope) and estimates the relative wetness within a catchment (CSIRO, http://data.csiro.au).
(b) Site-based variables (fine-scale)	
Diameter at breast height	Average diameter at breast height of all trees, recorded within two 5 * 100 m transects from either side of each spotlight transect.
Shrub abundance (>100 cm height)	A count of the number of shrubs (diameter at breast height < 5 cm) greater than or equal to 100 cm height, recorded within two 1 * 100 m transects from either side of each spotlight transect.
Shrub abundance (<100 cm height)	A count of the number of shrubs (diameter at breast height < 5 cm) less than 100 cm height, recorded within two 1 * 100m transects from either side of each spotlight transect.
Canopy cover	Persistent green fraction at spotlight location, derived from Landsat data as an index of woody cover (TERN AusCover, www.auscover.org.au)
Total basal area	Total basal area of all trees that had a diameter at breast height greater than or equal to 5 cm, recorded with two 5 * 100 m transects from either side of each spotlight transect.
Eucalypt basal area	Total basal area of *Eucalypts* (including both *Eucalyptus* and *Corymbia* spp.), that had a diameter at breast height greater than 5 cm, recorded within from two 5 * 100 m transects from either side of each spotlight transect.
Non-eucalypt basal area	Total basal area of all trees excluding Eucalypt species, that had a diameter at breast height greater than 5 cm, recorded with two 5 * 100 m transects from either side of each spotlight transect.
Late fire frequency	Numbers of years burnt between 2000 – 2016 late in the season (after July 31st) at spotlight location, derived from Landsat data (North Australia and Rangelands Fire Information, www.firenoth.org.au).
Years since last burnt	Number of years since last burnt between 2000 – 2016, at spotlight location, derived from Landsat data (North Australia and Rangelands Fire Information, www.firenoth.org.au).
Fire frequency	Numbers of years burnt between 2000 – 2016, at spotlight location, derived from Landsat data (North Australia and Rangelands Fire Information, www.firenoth.org.au).
(c) Other	
Julian day	The Julian day of the calendar year that the spotlighting survey was undertaken.

Results

Change in geographic range

Using presence-only occurrence records we found the geographic range of both *T. vulpecula* and *P. ariel* in northwestern Australia has significantly reduced since 1993 (Table 2.2). However, we found a much greater decrease in the geographic range of *T. vulpecula* compared to *P. ariel*. The predicted occupancy after 1993, for both the maximum and core range of *T. vulpecula* declined by more than double that of *P. ariel*. Mean annual rainfall was strongly correlated with the extent of geographic range contraction for both species (Table 2.3), with the geographic range of both *T. vulpecula* and *P. ariel* contracting to areas of higher rainfall (Fig. 2.1). The coastal areas of our study region are also where human population densities are highest, thus urban development is not considered as an explanation for these range contractions.

Table 2.2: The modelled geographic range changes for *Trichosurus vulpecula* and *Petaurus ariel*. The maximum range was where predicted occupancy (of 50 × 50 km cells) was ≥5 %, and the core range was where predicted occupancy was ≥50 %. Predictions are given for historical and current periods (before and after 1993, respectively), within the defined study area in northwestern Australia. Predictions are based on the best single-season occupancy model in Table 2.3.

	Proportion of study area occupied before 1993	Proportion of study area occupied after 1993	Proportional change in area occupied
Trichosurus vulpecula			
Maximum geographic range	100 %	28 %	↓ 72 %
Core geographic range	34 %	6 %	↓ 84 %
Petaurus ariel			
Maximum geographic range	75 %	49 %	↓ 35 %
Core geographic range	44 %	29 %	↓ 34 %

Table 2.3: Model selection results for the best three single-season occupancy models (lowest AIC by >2AIC units) to assess change in area and extent of occupancy for *Trichosurus vulpecula* and *Petaurus ariel*. w_i is the Akaike weight; ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion) value and that of the top-ranking model. Ψ denotes the occupancy component of the model and ϱ denotes the detectability component. Bold text indicates most supported models (ΔAIC ≤2).

Model	ΔAIC	w_i
(a) *Trichosurus vulpecula*		
ψ (Sampling effort + Rainfall + Time period) ρ (Rainfall * Time period)	**0.0**	**1.00**
ψ (Sampling effort + Rainfall + Time period) ρ (Rainfall + Time period)	13.9	0.00
ψ (Sampling effort + Rainfall * Time period) ρ (Rainfall * Time period)	13.9	0.00
(b) *Petaurus ariel*		
ψ (Sampling effort) ϱ (Rainfall * Time period)	**0.0**	**0.65**
ψ (Sampling effort) ϱ (Rainfall + Time period)	**1.3**	**0.34**
ψ (Sampling effort + Rainfall + Time period) ϱ (Rainfall * Time period)	9.9	0.00

Correlates of current abundance

Rainfall was the only significant geographic (broad-scale) predictor of abundance common to both species (Table 2.4). Model averaging demonstrated that both *T. vulpecula* and *P. ariel* abundance increased with increasing rainfall (Fig. 2.3). For *T. vulpecula*, model averaging indicated that shrub density (≥100 cm height) was an important predictor variable, with *T. vulpecula* abundance increasing with greater shrub density (Fig. 2.3). For both *T. vulpecula* and *P. ariel*, abundance was correlated positively with canopy cover. Predicted abundances for both *T. vulpecula* and *P. ariel* were greatest in the northern, mesic parts of their range (Fig. 2.2), which coincided with the core parts of their contemporary geographic range. No other site-based predictor variable was a significant correlate of either *T. vulpecula* or *P. ariel* abundance.

Table 2.4: Relative variable importance (RVI) of geographic (broad-scale) and site-based (fine-scale) variables on *Trichosurus vulpecula* and *Petaurus ariel* abundance ; calculated from Akaike weight's using negative binomial generalised linear models. Variables with a RVI ≥ 0.73 (indicated in bold) are considered significant predictor variables and were included in the top model.

RVI	*Trichosurus vulpecula*	*Petaurus ariel*
(a) Geographic variables		
Rainfall	**0.92**	**0.99**
Topographic Wetness Index	0.32	0.22
(b) Site-based variables		
Canopy cover	**0.77**	**0.97**
Shrubs (≥100 cm height)	**0.95**	0.29
Late fire frequency	0.27	0.46

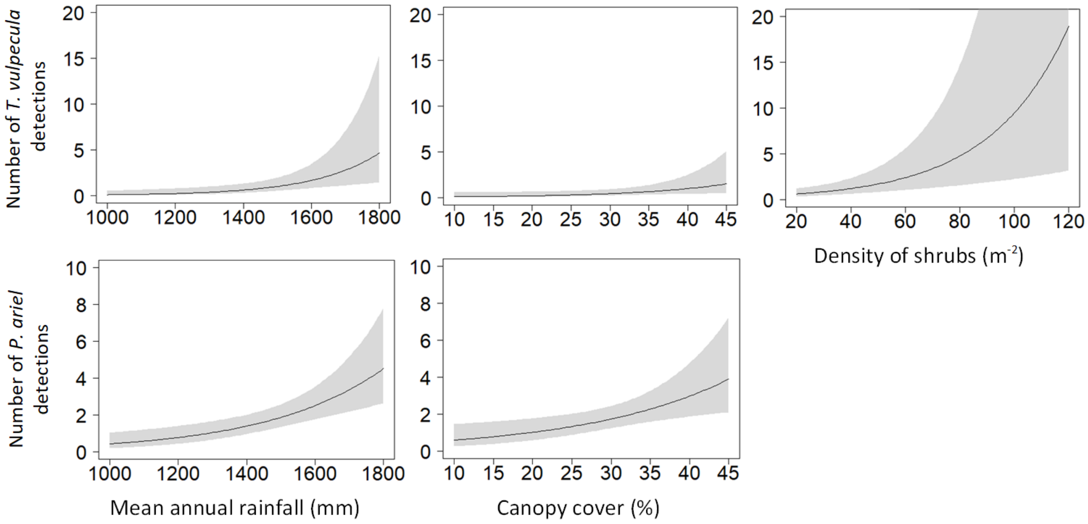

Figure 2.3: Modelled relationship for mean annual rainfall, canopy cover and shrub density (>100 cm height) on *Trichosurus vulpecula* abundance and mean annual rainfall and canopy cover on *Petaurus ariel* abundancebased on total count of individuals from three spotlight surveys, holding all other variables at fixed median level derived from the best negative binomial generalised linear model using geographic and site-based variables. Abundance is the total number of detections from the three spotlight transects per site. Black solid line is model fit and grey band indicates 95% confidence interval.

Discussion

Due to limited historical survey effort, our inability to model change in the geographic range of species has hamstrung our efforts to understand patterns of species decline globally. Here, our analysis of historical and contemporary records using an occupancy–detection model framework (MacKenzie *et al.*, 2002; Royle *et al.*, 2005), has demonstrated that *T. vulpecula* – once Australia's most widespread marsupial (Burbidge *et al.*, 2009) – has dramatically contracted to the mesic areas of its distribution within northwestern Australia, becoming almost extinct in arid areas. Our findings are in addition to documented declines throughout southern and western regions of Australia (Woinarski *et al.*, 2014) and support prior evidence of *T. vulpecula* decline in northern Australia (Woinarski *et al.*, 2010; Ziembicki *et al.*, 2013b).

A decline in *T. vulpecula* contrasts markedly with *P. ariel,* where while we noted some apparent contraction, we found a less severe range reduction. Thus, only *T.* vulpecula showed a marked decline in distribution corresponding to the pattern of decline in other small- to medium-sized mammals. As such identifying the ecological processes – particularly changed resource availability versus increased predation pressure – that are impacting *T. vulpecula* but not *P.* ariel, will help us to identify key drivers of mammal decline in northern Australia. At a local scale, we found *T. vulpecula* to be more prevalent in areas of higher shrub abundance (≥ 100 cm height), but established no such relationship between *P. ariel* abundance and shrub abundance. We suggest the contrasting patterns of decline between *T. vulpecula* (dramatic contraction to mesic areas) and *P. ariel* (relative stability, with limited contraction to mesic areas) is linked to the greater reliance of *T. vulpecula* on a shrubby understorey.

The apparent dependence of *T. vulpecula* on a shrubby understorey relative to *P. ariel* may be explained by the different degrees of arboreality between the two species in terms of foraging behaviour and movement between trees. While little is known of the foraging behaviour of *P. ariel,* during our spotlight surveys *P. ariel* was only occasionally observed foraging on low shrubs and grasses, and was more often observed within the tree canopy or the branches just below. *Petaurus ariel* foraging behaviour is consistent with other well-studied marsupial gliders within Australia which are predominantly arboreal foragers, known to spend a larger proportion of time foraging within the canopy, with only a small proportion of time spent in low shrubs (Goldingay, 1990; Sharpe & Goldingay, 1998; Jackson, 2001). This contrasts with *T. vulpecula,* which was frequently observed on the ground and is easily detected with ground-based camera surveys (Davies *et al.*, 2018). In other studies, *T. vulpecula* has been found to feed extensively on the leaves, flowers and fruits of understorey shrubs in northern Australia (Kerle & Burgman, 1984), often coming to ground while foraging and to move between trees (which are typically not overlapping in savannas). Thus, relative to *P. ariel* which has the unique ability to glide between trees rather than traversing along the ground, *T. vulpecula* is likely more dependent on shrubs as a food source and more exposed to predation by ground-based predators.

Habitat patches that have a high abundance of shrubs have previously been found to facilitate the persistence of *T. vulpecula* and other small- to medium-sized mammals, by providing an important food source as well as shelter from predators (Kerle & Burgman, 1984; Kerle, 1998; Leahy *et al.*, 2016; Davies *et al.*, 2017b; Davies *et al.*, 2018). However, the mechanism underlying the relationship between shrub density and mammal persistence in northern Australia is yet to be identified. We offer two (not mutually exclusive) explanations for why *T. vulpecula* has remained more common in areas with high shrub abundance. Firstly, we hypothesise the loss of shrubs within the region has resulted in the subsequent loss of critical food sources and/or refuges (i.e. lower resource availability). Secondly, predation by the feral cat, a ground-based predator, has resulted in greater dependence of *T. vulpecula* on areas containing shrubs for shelter from predation.

An overall reduction in shrub density in northern Australia since European settlement may have led to the loss of a critical source of food and/or refuge for small- to medium-sized mammals. In northern Australia, overgrazing by livestock has been linked to a decline in shrub abundance (Legge *et al.*, 2011), and this is especially evident in the arid zone (Milton *et al.*, 1994; McKenzie *et al.*, 2007). In the mesic savannas of northern Australia, habitat simplification due to altered fire regimes – namely an increase in fire frequency and intensity – is widely believed to have resulted in a decline in the density of shrubs in the understorey and midstorey (Vigilante & Bowman, 2004; Atchison *et al.*, 2005; Russell-Smith *et al.*, 2012). Although shrub loss is evident within northern Australia, *T. vulpecula* distribution historically covered areas of relatively low productivity, for example the central Australian deserts, where shrubs are naturally sparse. As *T. vulpecula* has a patchy distribution (Kerle & Burgman, 1984), it is possible that they only ever persisted in riparian refuges within the arid zone, similar to other arid-zone mammals that depend on access to refuges (Pavey *et al.*, 2014; McDonald *et al.*, 2017). Yet it remains unclear whether a dependence on structurally complex habitat patches and the patchy distribution of *T. vulpecula* and other small- to medium-sized mammals reflects a natural historical or altered contemporary pattern.

An alternative, and complementary explanation to that of a decline in the availability of shrubs for food and shelter, is a contraction of the range of *T. vulpecula* and other small- to medium-sized mammals to more densely vegetated habitat due to predation by feral cats. Feral cats have been linked to the decline of numerous mammal species throughout Australia (Johnson & Isaac, 2009; Fisher *et al.*, 2014; Woinarski *et al.*, 2015; Davies *et al.*, 2017b). There is evidence that cats consume mammals in the size range of *T. vulpecula* and *P. ariel* (Doherty *et al.*, 2015b). A recent study in Kakadu National Park recorded *T. vulpecula* and *P. ariel* remains in 12% and 13%, respectively, of the scats of feral cats (Stokeld *et al.*, 2018). Additionally, feral cats have been shown to prefer hunting in open landscapes, compared to densely vegetated landscapes in northern Australia (McGregor *et al.*, 2014; McGregor *et al.*, 2015; Hohnen *et al.*, 2016). The loss of the brush-tailed rabbit-rat (*Conilurus penicillatus*), a small semi-arboreal rodent, from much of northern Australia has been linked to predation by feral cats, and predation pressure appears to be greater in areas of low shrub abundance (Davies *et al.*, 2017b). Areas with high shrub abundance may provide important contemporary refuges for *T. vulpecula*, despite not necessarily being important prior to the establishment of cats in the region in the early 1900's (Abbott, 2008).

The persistence of *T. vulpecula* in the rugged desert uplands within the arid zone of the Northern Territory (in lieu of dense shrubby habitat), provides further evidence that *T. vulpecula* is not strictly dependent on high shrub abundance where other forms of shelter from predation exist. Indeed, in that region *T. vulpecula* is now only known to occur in these rugged rocky areas, despite the persistence of relatively productive, tree-lined watercourses and alluvial woodlands (McDonald *et al.*, 2015). Thus *T. vulpecula* most likely selects habitat to better evade ground-based predation rather than occupying riparian areas where typical food sources are more abundant (McDonald *et al.*, 2017). Selection for rugged areas to avoid predation has also been shown in the northern quoll (*Dasyurus hallucatus*) (Braithwaite & Scientific, 1985; Hernandez-Santin *et al.*, 2016), another semi-arboreal mammal that has suffered severe declines in northern Australia (Woinarski *et al.*, 2010). Thus, we speculate that in northern Australia, a shrubby understorey provides important refuges from predation by the feral cat, a highly effective ground-based predator (Kutt, 2012; Frank *et al.*, 2014; Doherty *et al.*, 2015a).

Although it is recognised that predation by feral cats is one of the key threatening processes for small- to medium-sized mammals in northern Australia, there is a perception that mammal declines began well after the initial introduction of cats and thus cannot be the ultimate driver of decline (Woinarski *et al.*, 2011). Abbott (2002) suggested the establishment of feral cat populations throughout Australia was likely slow and patchy, with feral cats reaching most of northern Australia at least 60 years after their initial colonization in southeastern Australia. Thus, feral cat abundance and predation pressure may have increased over time. Alternatively, the pattern of recent mammal decline in northern Australia may reflect our limited ability to detect the early stages of mammal decline in the historical record, and that long-term population decline is only now becoming evident (without any recent change in the threatening process).

Our findings link low shrub abundance to mammal declines in northern Australia. Whether the ultimate mechanism is through changes in resource availability (food and/or shelter) and/or increased predation pressure, future conservation management within northern Australia should concentrate efforts on improving or maintaining shrub abundance in tropical savannas. This can be achieved through reductions in fire frequency and/or intensity, and/or reduction in grazing pressure by cattle, as both changed fire regimes and overgrazing have been identified as key drivers of shrub loss in northern Australia. Our conclusions would be strengthened by an improved understanding of the dependence of *T. vulpecula* and *P. ariel* on shrubs for food or shelter from predation. Further research in the region should aim to quantify rates of ground or shrub-based foraging between and within species.

Understanding the patterns and drivers of species decline is essential to developing strategies to mitigate threatening processes. Our comparative methods approach and novel use of presence-only occurrence data allowed us to model changes in the distribution of two species and infer the drivers of their decline. We provide a potentially robust and accessible tool to detect early stages of species decline. While the marked decline of *T. vulpecula* is alarming, evidence of a decline (albeit less marked) in the distribution of *P. ariel* is also concerning. Our findings should be viewed as an indicator of early stages of *P. ariel* decline and prompt further investigation.

Acknowledgements

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(LP150100615) and the generous donations made by supporters of the ‘Unknown Glider’ crowdfunding campaign. We also thank Rebecca Montague-Drake for her observation records of *Petaurus ariel*.

Supplementary information

Table S2.1: Complete model selection results for single-season occupancy models to assess change in area and extent of occupancy for *Trichosurus vulpecula* and Petaurus *ariel*. *K* indicates the number of parameters; w_i is the Akaike weight; ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion) value and that of the top-ranking model. Ψ denotes the occupancy component of the model and ϱ denotes the detectability component. Bold text indicates well-supported models (ΔAIC ≤2).

Model	ΔAIC	w_i
a) *Trichosurus vulpecula*		
ψ (Sampling effort + Rainfall + Time period) *ρ* (Rainfall * Time period)	**0.0**	**1.00**
ψ (Sampling effort + Rainfall + Time period) *ρ* (Rainfall + Time period)	13.9	0.00
ψ (Sampling effort + Rainfall * Time period) *ρ* (Rainfall * Time period)	13.9	0.00
ψ (Sampling effort + Rainfall) *ρ* (Rainfall)	68.5	0.00
ψ (Sampling effort + Rainfall) *ρ* (Rainfall + Time period)	73.5	0.00
ψ (Sampling effort + Rainfall) *ρ* (Rainfall * Time period)	77.5	0.00
ψ (Sampling effort) *ρ* (Rainfall * Time period)	195.9	0.00
ψ (Sampling effort) *ρ* (Rainfall)	205.6	0.00
ψ (Sampling effort) *ρ* (Rainfall + Time period)	207.9	0.00
ψ (Sampling effort) *ρ* (~1)	320.7	0.00
b) *Petaurus ariel*		
ψ (Sampling effort) ρ (Rainfall * Time period)	**0.0**	**0.65**
ψ (Sampling effort) ρ (Rainfall + Time period)	**1.3**	**0.34**
ψ (Sampling effort + Rainfall + Time period) ρ (Rainfall * Time period)	9.9	0.00
ψ (Sampling effort) ρ (Rainfall)	12.0	0.00
ψ (Sampling effort + Rainfall) ρ (Rainfall * Time period)	42.3	0.00
ψ (Sampling effort + Rainfall) ρ (Rainfall)	43.3	0.00
ψ (Sampling effort + Rainfall) ρ (Rainfall + Time period)	46.4	0.00
ψ (Sampling effort + Rainfall * Time period) ρ (Rainfall * Time period)	49.4	0.00
ψ (Sampling effort + Rainfall + Time period) ρ (Rainfall + Time period)	60.4	0.00
ψ (Sampling effort) ρ (~1)	192.5	0.00

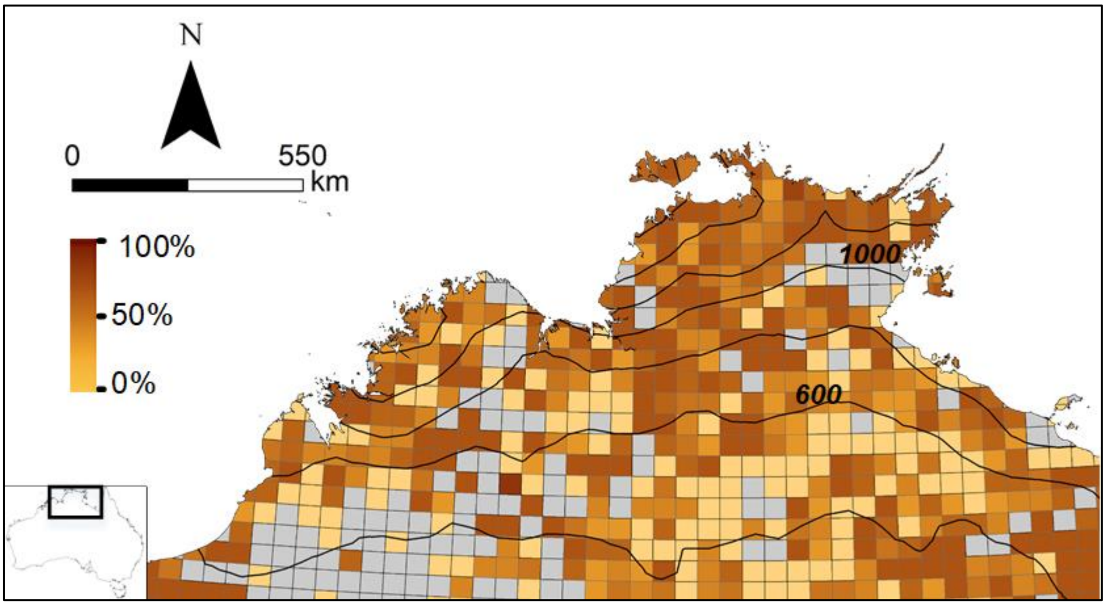

Figure S2.1. Proportion of mammal occurrence records post-1993 used to measure sampling effort for occupancy analysis. Darker shaded cells indicate a greater proportion of sampling effort post-1993, and light-yellow cells indicate areas only sampled pre-1993. Grey cells indicate areas that included no occurrence records and were therefore considered unsurveyed.

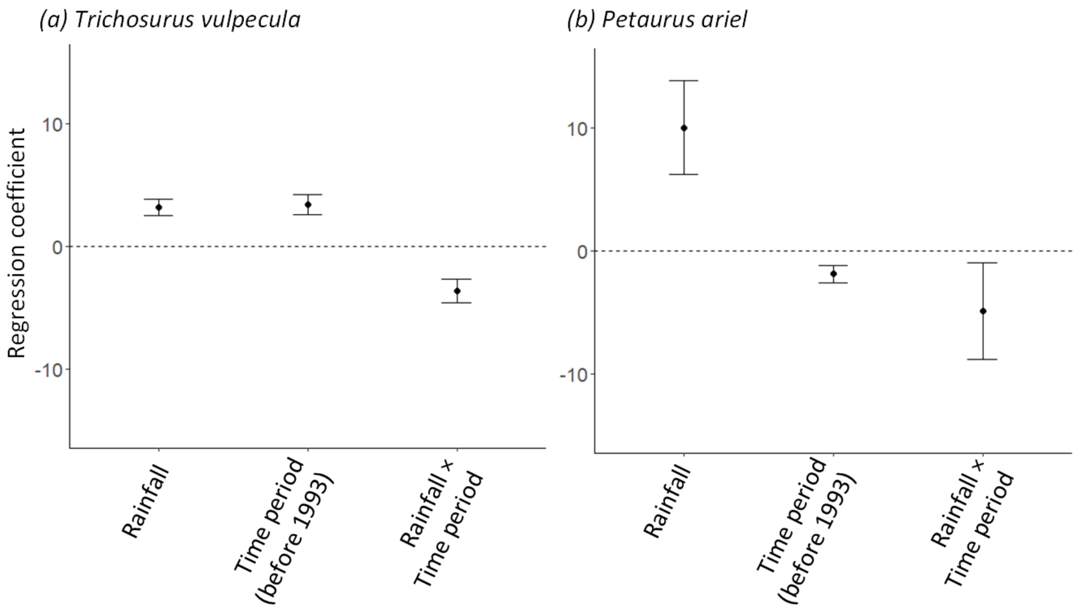

Figure S2.2. Estimated regression coefficients for (a) *Trichosurus vulpecula* and (b) *Petaurus ariel* occupancy derived from single-species occupancy models (Table 2.3). Error bars indicate 95% confidence intervals; error bars that do not overlap zero are significant.

Chapter 3 :

Geographic variation in body size of Australian marsupials supports Bergmann's thermoregulation hypothesis

Measuring live gliders in the field (above left and right) and preserved gliders in the museum (below).

Chapter Three cover page photo credit Teigan Cremona, Aline Gibson Vega and Robert Brandle

Abstract

Aim What drives geographic variation in body size is a key unresolved question in biogeography. Despite a plethora of research, little agreement has been reached on the ultimate driver/s. The primary hypotheses surrounding geographic variation in body size identify ambient temperature, productivity and seasonality as the drivers of variation. Here we test these hypotheses on five Australian marsupials using a revised articulation of Bergmann's rule, wherein evidence for thermoregulation (*heat dissipation* or *heat conservation*) is considered supportive of Bergmann's rule.

Location Australia

Taxon Marsupial suborder Phalangeroidea; *Petaurus ariel, Petaurus breviceps, Petaurus norfolcensis, Petaurus notatus, Trichosurus vulpecula.*

Methods To determine drivers of geographic variation in body size, we modelled the skull lengths (as a surrogate for body size) of four *Petaurus* species and the brushtail possum (*Trichosurus vulpecula*) as a function of indices of ambient temperature, productivity and seasonality.

Results The body size of *Petaurus ariel*, *P. notatus* and the squirrel glider (*P. norfolcensis*) increased with increasing winter minimum temperature, while that of *T. vulpecula* decreased with increasing summer maximum temperature. *Petaurus ariel* body size decreased with indices of productivity, contradicting the productivity hypothesis. Only *P. ariel* met the hypothesis of seasonality, as body size increased with increasing seasonality.

Main conclusions Thermoregulation was the most consistently supported driver of geographic variation in body size. This was either through evidence of heat conservation or heat dissipation for almost all species. We found the geographic range of the individual species and the climate space in which the species occurred was integral to understanding the species response to climate variables, especially ambient temperature. We argue that future studies should use specimens that are representative of the species entire geographic range, encompass a variety of climatic regions and use consistent methodologies and terminology when testing drivers of geographic variation in body size.

Keywords

Bergmann's rule, biogeography, heat conservation, heat dissipation, intraspecific variation, Mammalia, size clines, thermoregulation.

Introduction

What drives geographic variation in body size, is a key unresolved question in biogeography. The question is important because body size is linked to a species' life history, physiology, behaviour, density and extinction risk (Lindstedt & Calder, 1976; Johnson, 1999; Cardillo *et al.*, 2005; McCain & King, 2014; Tucker *et al.*, 2014). Despite a plethora of research focussed on intraspecific geographic variation in body size, little agreement has been reached on a definitive driver/s (Geist, 1987; Ashton *et al.*, 2000; Meiri & Dayan, 2003; Watt *et al.*, 2010; Clauss *et al.*, 2013). 'Bergmann's rule' was one of the earliest ecogeographic hypotheses explaining geographic variation in body size (Bergmann, 1847). It is typically stated as "races of warm-blooded vertebrates from cooler climates tend to be larger than races of the same species from warmer climates" (Mayr, 1956; Thomas, 2009; Olalla-Tárraga, 2011). This interpretation of the rule suggests ambient temperature is the primary driver of geographic variation in body size, as a larger body size has a smaller surface area to volume ratio, and *heat conservation* is the underlying mechanism (Mayr, 1956; Thomas, 2009; Olalla-Tárraga, 2011).

Alternative hypotheses have been proposed to explain intraspecific geographic variation in body size, each linking a different environmental driver with an underlying mechanism. James (1970) also hypothesised ambient temperature as a driver of geographic variation in body size, but in contrast to Bergmann's rule, identifies *heat dissipation* as the mechanism, with individuals decreasing in size in warmer environments due to a greater need to dissipate heat, which occurs more effectively in smaller individuals. Other commonly cited hypotheses relate to spatial and/or temporal variability in resource availability (i.e. food availability), describing a positive relationship between body size and primary productivity (Rosenzweig, 1968; McNab, 2010; Huston & Wolverton, 2011), and/or environmental seasonality (Boyce, 1978). These hypotheses suggest that unproductive environments will favour smaller body sizes because there are too few resources to maintain viable populations of larger bodied animals. Additionally, highly seasonal environments will select for larger body sizes as they have greater ability to cope with lack of food during periods of resource shortage. However, of these various hypotheses, Bergmann's rule remains the most widely recognised explanation of intraspecific geographic variation in body size.

The literature surrounding Bergmann's rule and other ecogeographic hypotheses of body size variation has been described as reaching "a near-chaotic intellectual state" (McNab, 2010; p. 13), and that the problem is plagued with "obvious analytical flaws" (Ashton *et al.*, 2000; p. 391). Issues that are cited include inconsistencies in relation to spatial scale, statistical methods that do not account for spatial autocorrelation and the different indices of body size used for analyses (Ashton *et al.*, 2000). Interpretation of the published literature is further confused by the multitude of highly correlated environmental variables used to support various hypotheses (i.e. ambient temperature, rainfall, primary productivity) (Yom-Tov & Nix, 1986; Yom-Tov & Geffen, 2006). However, arguably the most critical issue throughout the literature is the inconsistencies in the interpretation of Bergmann's rule (Watt *et al.*, 2010). Specifically, this includes whether Bergmann's rule relates to intra- or inter- species variation, or both (Clauss *et al.*, 2013; Gohli & Voje, 2016), and whether it was established to explain body size variation in endotherms, homeotherms or mammals only (Ashton, 2002; Olalla-Tárraga, 2011).

A recent translation and review of Bergmann's original (German) paper clarified Bergmann's rule to be "within species and amongst closely related species of homoeothermic animals, a larger size is often achieved in colder climates than in warmer ones, which is linked to the temperature budget of these animals" (Salewski

& Watt, 2017; p. 170). Salewski and Watt (2017) emphasise Bergmann's use of the term *warmth economy* throughout the paper (otherwise known as thermoregulation), and not *heat conservation*, which is more commonly referenced when referring to Bergmann's rule (Mayr, 1956; Huston & Wolverton, 2011; Meiri, 2011; Olalla-Tárraga, 2011). This renewed interpretation of Bergmann's rule highlights ambient temperature as the driver and thermoregulation as the mechanism for geographic variation in body size. Thus, alternative ecogeographic hypotheses, specifically the reformulation of Bergmann's rule by James (1970); "small size is associated with hot humid conditions, larger size with cooler or drier conditions" (p. 387), are not distinctly different from - and in fact support - Bergmann's original hypothesis of thermoregulation. Without consistency in the analytical methods, interpretation of results and a consistent articulation of Bergmann's rule, a large body of research may have inappropriately rejected Bergmann's rule (Huston & Wolverton, 2011; Terada *et al.*, 2012; Gohli & Voje, 2016), or failed to correctly test for the rule (Ashton *et al.*, 2000; Correll *et al.*, 2016).

Most of the research focussed on geographic variation in body size has been confined to the high latitudes of the Northern Hemisphere, with a noticeable deficiency of studies in tropical and sub-tropical regions, especially in the Southern Hemisphere. This geographic imbalance is important, because the effects of ambient temperature (and an animal's imperative to conserve vs. dissipate heat) varies dramatically between the high and low latitudes. The Australian continent is an excellent model system to help address this geographic imbalance in the study of ecogeographic rules. Australia spans tropical to alpine climate zones, with many groups of endemic marsupials occurring over large biogeographic gradients, from the tropical forests and neighbouring savannas of northern Australia, to the deserts of central Australia and/or the temperate forests and alpine areas of southern Australia.

Of the limited studies from Australia, most support Bergmann's rule (Yom-Tov & Nix, 1986; Quin *et al.*, 1996; Briscoe *et al.*, 2015), while a recent comprehensive study found productivity to be a stronger correlate of body size than ambient temperature (Correll *et al.*, 2016). Correll *et al.* (2016) found a strong, positive relationship between the skull size of the common brushtail possum (*Trichosurus vulpecula*) and primary productivity in the least productive season. In contrast to Yom-Tov and Nix (1986), Correll *et al.* (2016) concluded that there was only weak evidence of Bergmann's rule. However, all of these studies are based on the earlier interpretation of Bergmann's rule, which incorrectly assumes that *heat conservation* is the sole hypothesised mechanism of geographic variation in body size. Correll *et al.* (2016) concluded that there was strong support for James' (1970) *heat dissipation* hypothesis. Their findings are therefore consistent with the refined interpretation of Bergmann's rule referring to thermoregulation (Salewski & Watt, 2017) and may be an example of where the hypothesis has been mistakenly rejected.

We aim to build on existing studies of geographic variation in body size of Australian mammals (Yom-Tov & Nix, 1986; Quin *et al.*, 1996; Correll *et al.*, 2016) by incorporating multiple species that occur across a diverse range of habitats, using robust models that deal explicitly with the issue of spatial autocorrelation. Here, we examine the extent to which intraspecific variation in the body size of four *Petaurus* (marsupial glider) species and *T. vulpecula* is consistent with prominent hypotheses of geographic variation in body size, specifically Bergmann's rule of thermoregulation (Salewski & Watt, 2017). Like Correll *et al.* (2016), we evaluate the influence of climate variables reflecting ambient temperature, productivity and seasonality. However, unlike Correll *et al.* (2016) we use the revised articulation of Bergmann's rule (Salewski & Watt, 2017), wherein evidence for either *heat dissipation* or *heat conservation* was considered supportive of Bergmann's rule. The findings of this study will improve global understanding of environmental drivers of intraspecific variation in body size, which is fundamental information due to the significant influence body size has on a species' ecology and consequently conservation (McCain & King, 2014; Tucker *et al.*, 2014).

Materials and methods

Study species

We examined geographic variation in body size of four Petaurid gliders and *Trichosurus vulpecula*; all of which belong to the marsupial suborder Phalangeroidea. The Petaurid gliders studied here included the sugar glider *Petaurus breviceps* and squirrel glider *P. norfolcensis*, and two recently distinguished Petaurid species *P. notatus* and the savanna glider *P. ariel* (T. Cremona and S. Carthew, unpublished data), previously considered subspecies of *P. breviceps*. The combined distribution of the four Petaurid gliders covers five of the six climate zones recognised by the Köppen classification system (Kottek *et al.*, 2006), while the distribution of *T. vulpecula* encompasses all six climate zones (Fig. 3.1). As all study species are nocturnal, arboreal, hollow-dwellers, any variation in response to environmental variables between our study species is unlikely to be explained by general habitat use. *Petaurus* species are typically exudivorous and opportunistically insectivorous, while *T. vulpecula* has a relatively folivorous diet (Jackson & Johnson, 2002). *Trichosurus vulpecula* is noticeably larger than the Petaurid gliders (Table 3.1). Variation between the *Petaurus* species is primarily in head shape, pelage colour, body size and social-structure, with species ranging from being monogamous to a colonial social structure (Goldingay & Jackson, 2004; Jackson, 2012). Despite the varied body sizes and feeding ecology between study species, for any ecogeographic hypothesis (thermoregulation, primary productivity or seasonality) to be supported in this study, the body size of all species should vary predictably with at least one climate variable consistent with that hypothesis.

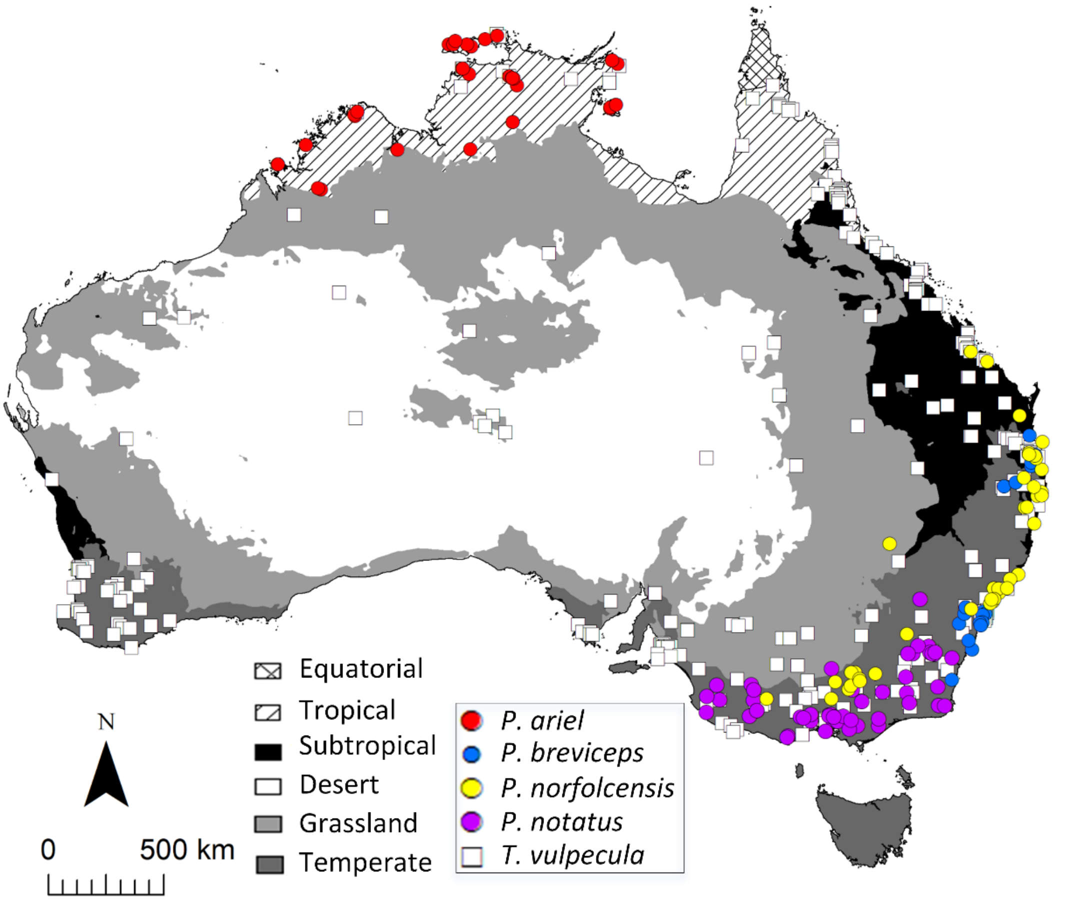

Figure 3.1: Source locations of four Petaurid gliders and *Trichosurus vulpecula* skulls used for body size analyses, overlaying the major Köppen climate zones.

Table 3.1: Number of skulls measured to assess variation in body size, and the mean, minimum and maximum skull length for the four *Petaurus* species and *Trichosurus vulpecula* specimens used in this study.

Species	Number of skulls	Body mass range (g)	Mean skull length (mm) (minimum–maximum)
Petaurus ariel	41	50 - 150*	41.6 (33.6 - 48.5)
Petaurus breviceps	23	60 - 150#	38.2 (35.1 - 44.1)
Petaurus norfolcensis	44	150 - 300#	45.7 (40.1 - 48.5)
Petaurus notatus	61	60 - 150#	38.3 (35.1 - 44.1)
Trichosurus vulpecula	436	1400 - 3600#	78.3 (63.2 - 91.5)

*based on the authors field measurements
#taken from Goldingay and Jackson (2004). As *P. breviceps* and *P. notatus* were conflated at that time, we have used the body mass range indicated for *P. breviceps* for both species

Data collection

Petaurus skull measurements

As in other studies (Correll *et al.*, 2016), we used skull length as a proxy for body size. We measured 305 adult skulls of known sex and origin, sourced from the Northern Territory Museum and Art Gallery (n = 8), Australian Museum (n = 88), Queensland Museum (n = 46), Museum of Victoria (n = 62), Western Australia Museum (n = 18), South Australia Museum (n = 21), Commonwealth Scientific and Industrial Research Organisation Australian National Wildlife Collection (n = 43) and the British Natural History Museum (n = 19). Skulls were deemed to be from adult specimens if there was evidence of erupted permanent teeth. Given that *P. breviceps* has been introduced to Tasmania (Campbell *et al.*, 2018), we excluded skulls of this species that were collected in Tasmania. Using digital callipers, two cranial variables, maximum skull length (MSL; greatest distance between the most prominent point at the root of the nose, to the most prominent point on the occipital bone) and zygomatic breadth (ZB; greatest distance between arches of the cranium, at right angle to the longest axis of the skull), were measured (to the nearest 0.01 mm) on each skull specimen of *P. ariel*, *P. norfolcensis*, *P. notatus* and *P. breviceps*.

Trichosurus vulpecula skull measurements

For *T. vulpecula* skull measurements, we used data for Australian mainland animals (n=436) from Correll *et al.* (2016), available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.gq264>. As a proxy for body size, we used the condylobasal length (CBL; greatest distance from the anterior point of the premaxilla to the posterior surface of the occipital condyles) measurements from adult specimens. Unfortunately, sex was not provided in their dataset, so we were unable to distinguish between males and females in the *T. vulpecula* analysis. However, Correll *et al.* (2016) found no significant difference between male and female CBL for *T. vulpecula*. Given that Correll *et al.* (2016) found a positive effect of island isolation on *T. vulpecula* body size, we excluded observations that originated from any islands off the Australian mainland, including Tasmania.

Data analyses

All analyses were conducted in the program R (R development Core Team, 2017). Environmental covariate values were sourced from datasets obtained from the Australian Bureau of Meteorology (BoM) (2016; <www.bom.gov.au>) and NASA Earth Observing System MODIS Land Algorithm (2017; <https://neo.sci.gsfc.nasa.gov>) (Table 3.2). The year in which skull specimens were collected was not available for all skulls, however majority of specimens were collected between 1940 and 2000 (97% of samples). As such, we used environmental covariates averaged over a 30yr time-period (1960-1990) to best overlap when the specimens were collected. We argue that although we have not encompassed the complete time-period in which specimens were collected, the environmental variables used in this study have remained relatively constant.

We used MSL as a proxy for body size for all *Petaurus* spp. and CBL as a proxy for body size for *T. vulpecula*. As CBL was the only measure of body size available in the Correll *et al.* (2016) data set, we chose to use MSL as a proxy for *Petaurus* spp. body size as it is the most comparable measure to CBL. Additionally, due to damage to the available skull specimens, MSL was the most consistently available proxy for body size across all *Petaurus* spp. Both measures of skull length have been found to strongly correlate with body mass in mammals (Damuth *et al.*, 1990; Bertrand *et al.*, 2016). Both CBL and MSL are hereon referred to as skull length.

As all specimens for this study were sourced from museums we cannot know whether skulls of the same species were collected from the same population. To account for possible dependencies we instead use analysis methods that accommodate spatial autocorrelation. To model the body size of each species as a function of climate, we used either an ordinary least-squares linear (OLS) model or from the 'nlme' package a generalised least-squares linear (GLS) model. In cases where there was significant autocorrelation of model residuals, we used a GLS model. Otherwise we used an OLS model. We evaluated the significance of spatial autocorrelation using Moran's I (Cliff & Ord, 1972), where $p \leq 0.05$ indicates strong evidence of spatial autocorrelation. For the GLS models, we specified a rational quadratic spatial correlation structure (Crawley, 2012). We used Akaike's Information Criterion (AIC) to rank the models, balancing both model fit and model simplicity (Burnham & Anderson, 2003).

To ensure a climate variable could be linked to a corresponding hypothesis and not an opposing hypothesis, we assessed the level of correlation between climate variables of alternative hypothesis. We used all measures of ambient temperature as indicators of the thermoregulation hypothesis, the coefficient of variance of effective rainfall as an indicator of the seasonality hypothesis, and net primary productivity as an indicator of the productivity hypothesis (Table 3.2). All other variables were excluded as they strongly correlated ($r > 0.7$) with indices of thermoregulation (temperature) and as they were not direct measures of productivity or seasonality they could not be exclusively linked to those hypotheses.

Before identifying correlates of body size for *Petaurus* skulls, we first included 'sex' (male/female) as a non-climate variable in our models of skull length. If 'sex' improved model fit, we then added climate predictor variables. 'Sex' was retained in the simplest model if it improved the null model by ≥2 AIC units (Burnham & Anderson, 2003). We then deemed a climate variable to be significant if it improved the simplest or null model by ≥2 AIC units.

Table 3.2: Climate predictor variables used for hypothesis testing of geographic variation in body size of four *Petaurus* species and *Trichosurus vulpecula*. Predictor variables were each associated with a hypothesis and each hypothesis has a proposed mechanism and a predicted relationship between body size and the variable

Hypothesis	Predictor variable	Description
Hypothesis 1: Thermoregulation (Bergmann's Rule). Low surface area to volume ratios of large individuals increases heat conservation in cold environments; high surface area to volume ratios of small individuals increases heat dissipation in warm humid environments (Bergmann, 1847; James, 1970; Salewski & Watt, 2017). **Predicted pattern:** Body size decreases with increasing temperature.	Mean annual temperature	Mean annual temperature, based on a 30-year climatology (1961-1990); 5 km resolution (BoM, 2016)
	Winter minimum temperature	Mean minimum temperature for June, July and August, based on a 30-year climatology (1961-1990); 5 km resolution (BoM, 2016)
	Summer maximum temperature	Mean maximum temperature for December, January and February, based on a 30-year climatology (1961-1990); 5 km resolution (BoM, 2016)
Hypothesis 2: Net primary productivity. Body size is limited by the availability of food (net primary productivity) (Rosenzweig, 1968; McNab, 2010; Huston & Wolverton, 2011). **Predicted pattern:** Body size increases with net primary productivity.	Actual evapotranspiration	Mean areal actual evapotranspiration based on a 30-year climatology (1961-1990); 10 km resolution (BoM, 2016)
	Rainfall	Mean annual rainfall based on a 30-year climatology (1961-1990); 5 km resolution (BoM, 2016)
	Effective rainfall	A measure of climatic water balance, calculated from mean annual rainfall minus mean annual areal potential evapotranspiration; 10 km resolution (1961-1990) (BoM, 2016)
	NPP	Mean annual net primary productivity; 1 km resolution (product of NASA Earth Observing System MODIS Land Algorithm, 2017)
	Lean season effective rainfall	Effective rainfall (as above) averaged over the three consecutive months with the lowest total. (BoM, 2016)
Hypothesis 3: Seasonality. Large individuals are better able to cope with food shortage in more seasonal environments because of their greater relative and absolute capacity for fat storage (Boyce, 1978). **Predicted pattern:** Body size increases with seasonality.	Effective rainfall CV	Coefficient of variance for effective rainfall, calculated from monthly indices of mean rainfall minus average areal potential evapotranspiration (1961-1990); 10 km resolution (BoM, 2016)
	Rainfall CV	Coefficient of variance for mean rainfall calculated from monthly indices of mean rainfall (1961-1990); 5 km resolution (BoM, 2016)

Results

Climate variables consistent with the thermoregulation hypothesis were important predictors of body size (skull length) for all species except *P. breviceps* (Table 3.3). *Trichosurus vulpecula* body size decreased with increasing summer maximum temperature and *P. ariel, P. norfolcensis* and *P. notatus* body size decreased with increasing winter minimum temperature (Fig. 3.2). All of this is consistent with the thermoregulation hypothesis. Additionally, *P. norfolcensis* body size decreased with increasing mean annual temperature (Fig. 3.3).

There was no single indicator of thermoregulation in which the body size of all species responded uniformly. However, when reviewing the full suite of indices of thermoregulation, the body size of *T. vulpecula, P. norfolcensis* and *P. notatus* responded consistently with the thermoregulation hypothesis for at least one indicator of thermoregulation (evidence of *heat conservation* and/or *heat dissipation*) and provided no evidence to reject the thermoregulation hypothesis.

The response of *P. ariel* body size to indices of thermoregulation was less intuitive. Summer maximum temperature was the best predictor of *P. ariel* body size; body size increased with increasing maximum summer temperature (Table 3.3, Fig. 3.2). Increasing body size with increasing maximum temperature is inconsistent with *heat dissipation* and seemingly rejects the thermoregulation hypothesis. However, *P. ariel* body size also increased with decreasing winter minimum temperature, potentially supporting *heat conservation* as a driver of *P. ariel* body size. Within the geographic range of *P. ariel,* winter minimum temperature correlates strongly with maximum summer temperature (r = 0.7), such that areas with colder minimum temperatures also have higher maximum temperatures. Furthermore, based on the location of the specimens used in this study, the range in summer maximum temperature that *P. ariel* is exposed to (31 – 36°C) is significantly less than the range in winter minimum temperature (12 – 22°C) (Fig. 3.2). This may explain the seemingly contradicting support for the thermoregulation hypothesis. Therefore, based on variation in *P. ariel, T. vulpecula, P. norfolcensis* and *P. notatus* body size, we found support for the thermoregulation hypothesis through evidence of *heat conservation* and/or *heat dissipation*.

Models that included indices of productivity were supported by evidence of variation in both *T. vulpecula* and *P. notatus* body size (Table 3.3), as body size for both species increased with increasing values of productivity (Fig. 3.3). *P. ariel* body size also responded significantly to both indices of productivity. However, *P. ariel* body size decreased with increasing values of productivity, thus rejecting the productivity hypothesis as a definitive driver of geographic variation in body size. *P. ariel* body size varied significantly with the one indicator for seasonality, as body size increased with increasing values of seasonality. Thus, although no other species' body size varied significantly with seasonality, we found some evidence to support the seasonality hypothesis and could not reject the hypothesis.

Neither non-climatic nor climatic predictor variables significantly predicted variation in body size for *P. breviceps* (Table 3.3). This may simply reflect the relatively small sample size for *P. breviceps* (n=23 compared with >40 for other species), and/or the more limited climatic variation encompassed within the geographic range of these samples (Fig. 3.1).

Table 3.3: Model selection results for single-species modelling of skull length of four *Petaurus* species and *Trichosurus vulpecula*. w_i indicates the Akaike weight; ΔAIC represents the difference between the model's Akaike Information Criterion (AIC) value and that of the top-ranking model; R^2 indicates the conditional goodness-of-fit (not supported for generalised least-square models so values have been generated from ordinary least-square models). Bold text indicates well-supported models (ΔAIC ≤2) of skull length. Grey highlighted models indicate the simplest model in the candidate set.

Hypothesis	Model	ΔAIC	w_i	R^2
a) Petaurus ariel				
Thermoregulation	**Summer max temp**	**0.0**	**0.40**	**0.39**
Productivity	NPP	7.7	0.24	0.31
Seasonality	Effective rainfall CV	8.0	0.15	0.28
Thermoregulation	Winter min temp	13.5	0.09	0.21
Productivity	Lean season effective rainfall	19.5	0.05	0.11
	Sex	23.3	0.03	0.06
Thermoregulation	Mean annual temp	22.2	0.02	0.05
b) Petaurus norfolcensis				
Thermoregulation	**Sex + Winter min temp**	**0.0**	**0.55**	**0.37**
Thermoregulation	**Sex + Mean annual temp**	**0.4**	**0.45**	**0.36**
Productivity	Sex + NPP	12.2	<0.01	0.16
Seasonality	Sex + Effective rainfall CV	13.3	<0.01	0.14
	Sex	14.0	<0.01	0.09
Productivity	Sex + Lean season effective rainfall	14.2	<0.01	0.12
Thermoregulation	Sex + Summer max temp	15.6	<0.01	0.10
c) Petaurus notatus				
Thermoregulation	**Sex + Winter min temp**	**0.0**	**0.41**	**0.19**
Productivity	**Sex + Lean season effective rainfall**	**0.7**	**0.29**	**0.19**
Seasonality	Sex + Effective rainfall CV	2.3	0.13	0.16
	Sex	3.7	0.06	0.11
Thermoregulation	Sex + Mean annual temp	4.3	0.05	0.14
Productivity	Sex + NPP	5.0	0.03	0.13
Thermoregulation	Sex + Summer max temp	5.6	0.02	0.12
d) Petaurus breviceps				
Thermoregulation	**Mean annual temp**	**0.0**	**0.27**	**0.14**
Thermoregulation	**Summer max temp**	**0.7**	**0.19**	**0.11**

Thermoregulation	**Winter min temp**	**1.4**	**0.14**	**0.09**
	Null	**1.5**	**0.13**	
Productivity	NPP	2.4	0.08	0.04
Productivity	Lean season effective rainfall	2.7	0.07	0.03
	Sex	3.0	0.06	0.02
Seasonality	Effective rainfall CV	3.4	0.05	<0.01
e) Trichosurus vulpecula				
Thermoregulation	**Summer max temp**	**0.0**	**0.49**	**0.21**
Productivity	**Lean season effective rainfall**	**1.5**	**0.23**	**0.31**
Productivity	NPP	3.0	0.11	0.14
Seasonality	Effective rainfall CV	4.0	0.07	0.05
Thermoregulation	Mean annual temp	5.2	0.04	0.10
	Null	5.4	0.03	
Thermoregulation	Winter min temp	5.7	0.03	0.06

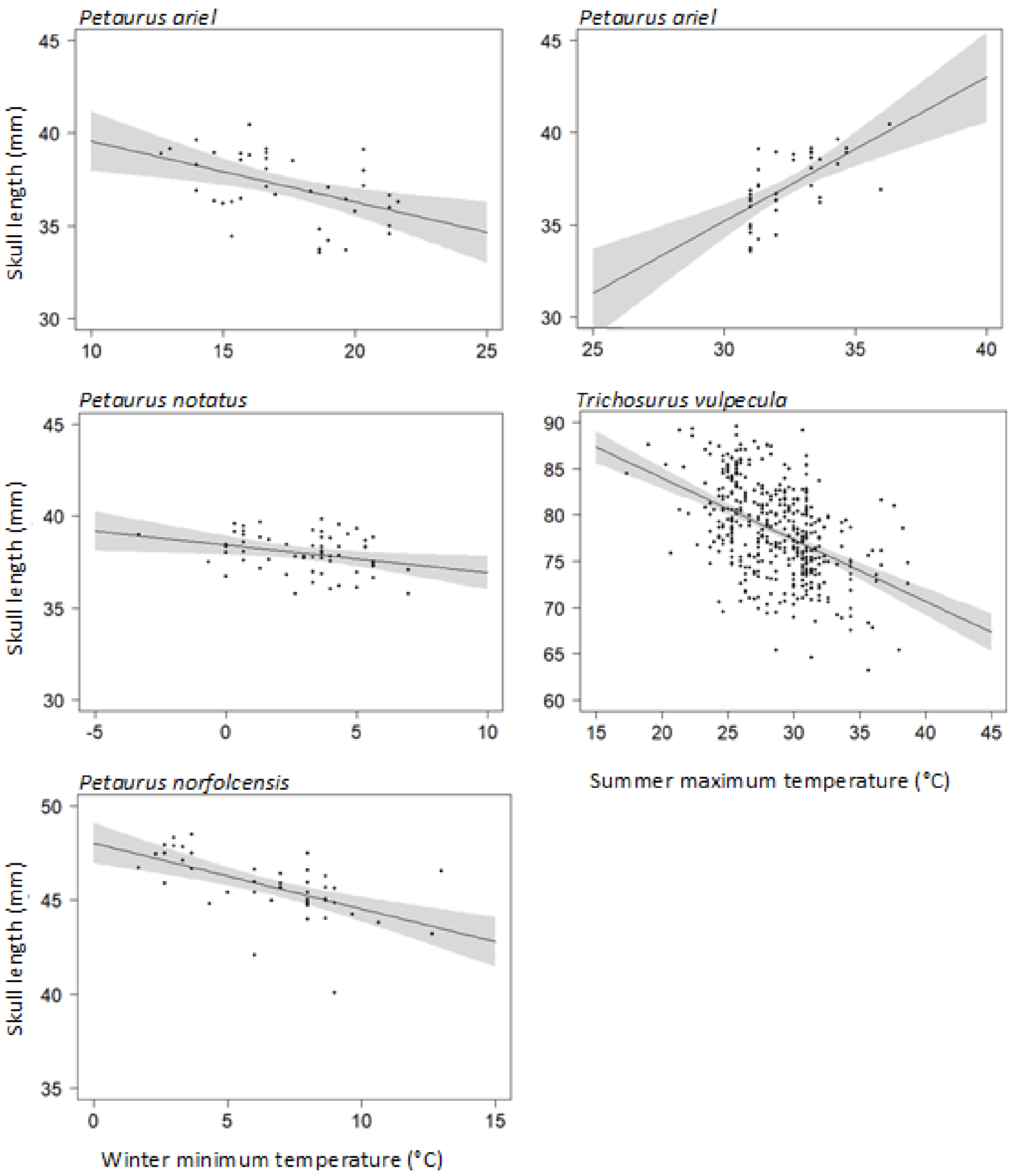

Figure 3.2: Modelled relationship for winter (June-August) minimum temperature (°C) and summer (December-February) maximum temperature (°C) on *Petaurus ariel*, *P. notatus*, *P. norfolcensis* and *Trichosurus vulpecula* body size (skull length; mm) derived from ordinary least-squares linear models. Black dots are the collected data points, black solid lines show model fit and grey bands indicate 95% confidence intervals.

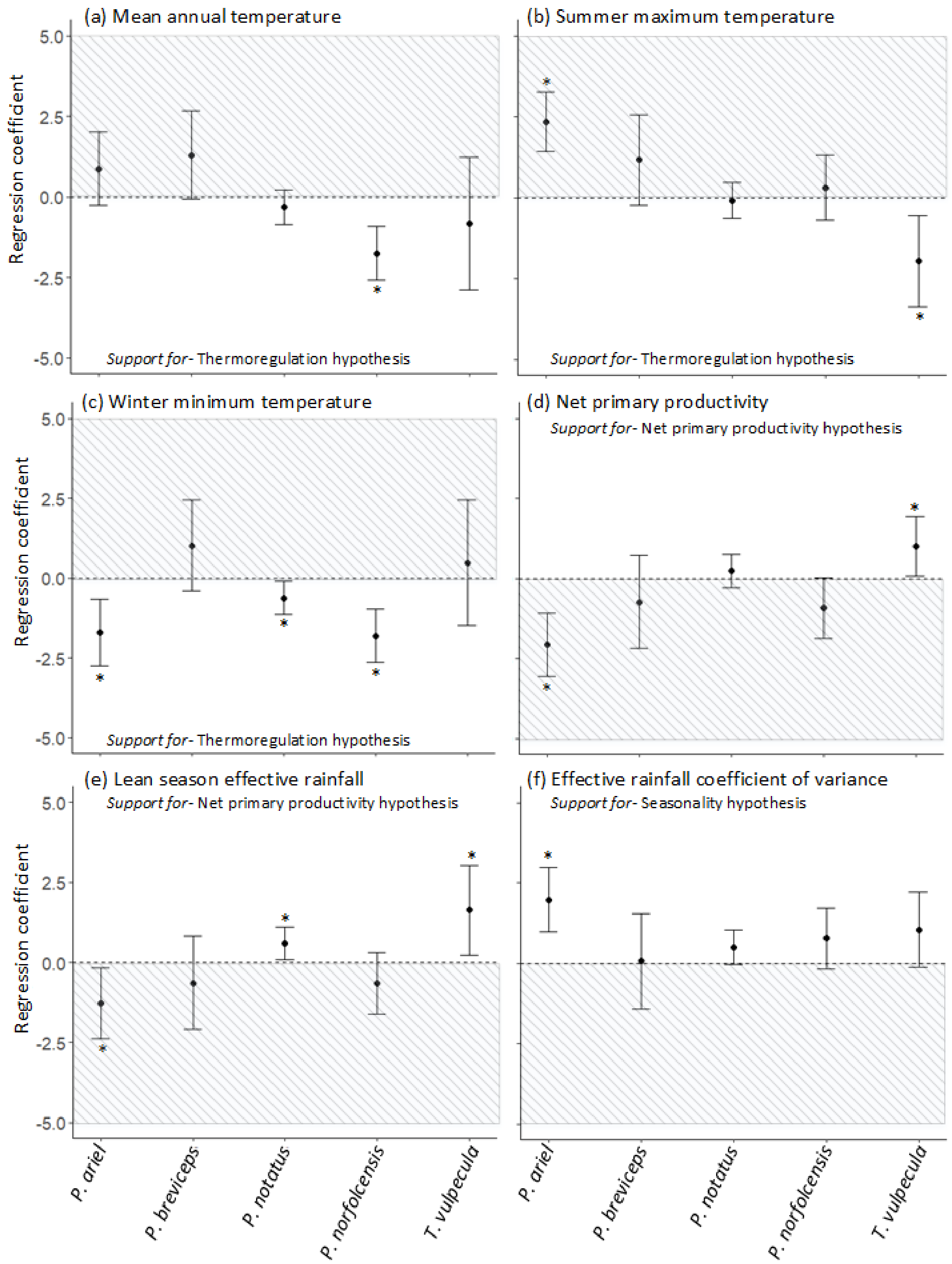

Figure 3.3: Estimated regression coefficients for the four Petaurid gliders and *Trichosurus vulpecula* derived from single-species models (Table 3.3). Error bars indicate 95% confidence intervals; asterisks indicate where an effect is statistically significant, i.e. 95% confidence intervals don't overlap zero. Values that fall within cross-hatched zones represent responses that are contradictory to the tested hypothesis.

Discussion

Here we modelled environmental drivers of geographic variation in body size of five Australian mammals (four *Petaurus* species and *T. vulpecula*). We found thermoregulation (through evidence of either *heat conservation* or *heat dissipation*) to be the most consistently supported driver of intraspecific geographic variation in body size. We found evidence to reject the productivity hypothesis (based on contrasting variation in *P. ariel* body size) and only minimal evidence to support the seasonality hypothesis. Therefore, our findings most strongly support Bergmann's thermoregulation hypothesis, as articulated by Salewski and Watt (2017), that geographic variation in body size in these five species is primarily driven by ambient temperature and the need to thermoregulate.

One apparent contradiction of thermoregulation as a driver for variation in body size was that *P. ariel* body size increased with increasing values of maximum temperature. This is contrary to what we would expect if the pattern was driven by the need to dissipate heat, and at face value provides evidence against the thermoregulation hypothesis. However, it is likely that this response reflects the geographic range of *P. ariel,* which is confined to the tropics of northern Australia, where summer maximum temperatures are consistently high (31 – 36°C), while summer relative humidity (58 – 76%) and winter minimum temperature vary more substantially (13 – 22 °C). In this region, areas with the highest temperatures have the lowest humidity and the lowest winter minimum temperatures, so there is a strong correlation between dry heat and lower minimum temperatures. Thus, we suggest maximum summer temperature may not accurately reflect the apparent temperature within the region as humidity is not accounted for. As *P. ariel* are smaller where relative humidity is greater, *heat dissipation* through evaporative heat loss in response to greater atmospheric water vapour, may also be driving variation in *P. ariel* body size. Further research on how body size varies with heat in humid environments would help clarify our findings. Indeed, the unique climate envelope of the tropics may shed light on the relative lack of evidence for Bergmann's rule in the tropics in earlier studies (Rodríguez *et al.*, 2008; Huston & Wolverton, 2011; Freeman, 2017).

Trichosurus vulpecula was the only species to show evidence of *heat dissipation* rather than *heat conservation*. *Trichosurus vulpecula* body size decreased with increasing values of summer maximum temperature (*heat dissipation*) but did not increase with decreasing values of minimum temperature (*heat conservation*). This may reflect the wide range of climate zones in which *T. vulpecula* occurs, and the larger body size of *T. vulpecula* relative to the other study species. *Trichosurus vulpecula* is the only study species that occurs in Australia's arid zone, where *T. vulpecula* body size is consistently small. The arid zone has the highest summer maximum temperatures on the Australian continent. In contrast, the region has much lower winter minimum temperatures (7 – 11°C) relative to the tropics (12 – 22°C), but higher winter minimum temperatures relative to the temperate zone (-3°C was the lowest winter minimum temperature recorded in the temperate zone in this study, taken from locations for both *P. notatus* and *T. vulpecula*). Thus, *heat dissipation* may be a better predictor of *T. vulpecula* body size, as unlike the other focal species, the geographic range of *T. vulpecula* encompasses areas of more extreme, dry heat. Additionally, since *T. vulpecula* has a larger body size than any of the *Petaurus* species studied here, *T.*

vulpecula can more easily conserve heat than dissipate heat. The smaller body size of the *Petaurus* species means that *heat conservation* is more likely a driver of geographic variation in body size than *heat dissipation*.

Our study supports the original findings of Correll *et al.* (2016) that summer maximum temperature and lean season effective rainfall are significant drivers of *T. vulpecula* body size. However, since Correll *et al.* (2016) did not find evidence for *heat conservation* by *T. vulpecula* they rejected Bergmann's hypothesis. Based on the refined articulation of Bergmann's rule by Salewski and Watt (2017), we argue that both our study and that of Correll *et al.* (2016) support Bergmann's thermoregulation hypothesis, as both studies provide evidence of *heat dissipation* by *T. vulpecula* (as well as in the additional species in this study). In contrast, our study rejects Correll et al.'s (2016) finding of productivity as a significant driver of variation in body size. Although lean season effective rainfall was an important driver of *T. vulpecula* in both studies, our study rejected the productivity hypothesis (which it corresponds to) as *P. ariel* body size significantly decreased with increasing values of productivity, the opposite response to that predicted by the productivity hypothesis.

We suggest support for the productivity hypothesis in previous studies of geographic variation in Australian mammal body size (Yom-Tov & Nix, 1986; Yom-Tov & Geffen, 2006; Correll *et al.*, 2016) may be an artefact of decreasing primary productivity with increasing maximum temperatures. In this study, there was a moderate negative relationship (r = 0.4) between net primary productivity and summer maximum temperature. Therefore, if thermoregulation is the driver of geographic variation in body size, larger body sizes should occur in areas of low summer maximum temperatures, which coincides with areas of greater net primary productivity. However, in the tropical north, there is also a strong correlation between summer maximum temperature and winter minimum temperature which is not typical for the rest of Australia ($r = 0.3$, compared to $r = 0.7$ in tropics). As *P. ariel* body size increases with increasing winter minimum temperatures (which coincides with increasing summer maximum temperature), *P. ariel* body size is smaller where net primary productivity is greater, therefore rejecting the primary productivity hypothesis, at least for this species.

Within Australia, evidence for Bergmann's thermoregulation hypothesis has previously been found in studies on the short-beaked echidna (*Tachyglossus aculeatus*), kangaroos (*Macropus gigantus, M. fuliginosus, M. rufus*), the koala (*Phascolarctos cinereus*), and in earlier studies of *P. breviceps*, *P. norfolcensis* and *T. vulpecula* (Yom-Tov & Nix, 1986; Quin *et al.*, 1996; Agnarsson *et al.*, 2011; Briscoe *et al.*, 2015). In contrast to Yom-Tov and Nix (1986), we found no support for Bergmann's rule or any other competing hypotheses relating to variation in body size for *P. breviceps*. Yom-Tov and Nix (1986) would not have made a distinction between *P. breviceps* and *P. notatus*, likely including skulls from both species within what they classified as *P. breviceps*. We believe the disparity in our findings likely reflects the restricted climatic range over which those skulls occurred, and our smaller sample size of *P. breviceps* skulls (23). Regardless, based on the consistent evidence to support Bergmann's thermoregulation hypothesis and lack of evidence to reject the hypothesis, we conclude that thermoregulation is a significant driver of variation in the body size of Australia's marsupials.

Although this study has found consistent evidence to support thermoregulation as a significant driver of variation in body size, our findings are complex and not easily interpretable. This is a fundamental issue with many studies pertaining to ecogeographic rules and likely reflects the unaccounted influence of other species traits such as habitat use, population density and fur thickness, in mediating the response of individuals to their external environment. For example, Briscoe *et al.* (2015) found a stronger relationship between fur properties of *Ph. cinereus* and climate, than with body size and climate. Additionally, *P. breviceps* is known to employ torpor daily and reduce activity time during adverse weather conditions as a potential alternative to thermoregulation which is more energetically expensive (Körtner & Geiser, 2000)(Körtner and Geiser 2000). Further work into how species traits, in addition to body size, vary with climate would greatly facilitate our understanding of the mechanisms behind Bergmann's rule and should be a priority for future research.

More generally, future studies on the drivers of geographic variation in body size should critically evaluate the geographical context from which specimens of their study species have been collected. In this study, both winter minimum temperature and summer maximum temperature better explained variation in body size than average annual temperature. Thus, our findings suggest the extremes of temperature likely have a stronger influence on variation in body size than average annual temperature. Further understanding on how the extremes of temperature drive variation in body size and the point at which *heat conservation* becomes more important than *heat dissipation* would yield a better understanding of how ambient temperature drives variation in body size. Future studies should subsequently seek to encompass specimens from a species' entire geographic range to capture the full suite of climatic variation that occurs within it. Without this, we can only capture part of the story and are unlikely to resolve the debate surrounding geographic variation in body size.

Furthermore, there is a need for more consistent methodologies and terminology within the literature surrounding geographic variation in body size. Our study provides a model example for future studies of geographic variation in body size, as our approach includes: (1) multiple species that occur over different climatic regions; (2) rigorous models that explicitly account for spatial autocorrelation; and (3) the use of uncorrelated climate predictor variables that are linked to hypotheses of geographic variation in body size. Importantly, we have made use of the recent articulation of Bergmann's hypothesis by Salewski and Watt (2017). Using this approach, our study has provided evidence to support Bergmann's hypothesis that thermoregulation drives intraspecific geographic variation in body size. Support for this ecogeographic hypothesis highlights ambient temperature (due to an individual's need to thermoregulate), as a significant evolutionary force on fauna species globally and should not be underestimated in the wake of climate change, especially considering the subsequent influence body size has on a species' ecology, (McCain & King, 2014; Tucker *et al.*, 2014).

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Chapter 4 :

Resource availability drives variation in a marsupial glider's home range

Moments captured by my volunteers of me capturing the savanna glider. A smiling face shows a successful night of trapping at Nitmiluk National Park (left), my first tagged and collared savanna glider 'Phife' from Nitmiluk NP (above) and locating den trees at Melville Island (above left).

Chapter Four cover page photo credit Clementine Menz, Emily Burton and Amanda McLean

Abstract

Numerous studies have detailed the home range size of a variety of species, yet the relative contributions of species' traits (i.e. body mass and diet) and the external environment (i.e. resource availability) to variation in home range size is not fully understood. We investigated the importance of species' traits and resource availability on the home range size of a marsupial glider, the savanna glider (*Petaurus ariel*), in the tropical savannas of northern Australia. *Petaurus ariel* is a newly described species and the only Petaurid glider to occur only in the tropical savannas of northern Australia. A strong rainfall gradient occurs over the region, resulting in significant variation in resource availability throughout the geographic range of *P. ariel*. To determine *P. ariel* home range size, we radio-tracked individuals from two populations at the climatic extremes of the species' geographic range, representing areas of high and low rainfall (mean annual rainfall: 1695 mm and 1074 mm, respectively). Additionally, we conducted spotlight surveys at each site to determine population density and collated live-trapping data to model the body mass of *P. ariel* over its geographic range. Movement behaviour of *P. ariel* varied significantly over its geographic range, with an almost 10-fold increase in home range size between the two study areas (high rainfall: 2.5 ha vs. low rainfall: 23.0 ha). Body mass (67.5 to 101.1 g) and density (1.1 to 0.2 glider ha^{-1}) varied significantly between the high and low rainfall populations, respectively. Mean *P. ariel* home range was larger than any other similar-sized Australian Petaurid and was in the top 6% of home range size relative to body mass of terrestrial, omnivorous mammals globally. The disproportionately large home range of *P. ariel* is most likely driven by low resource availability within the species' geographic range. Our findings highlight that when resources are limiting, home range size can exceed what is predicted by body mass and diet alone.

Keywords

Arboreal marsupial, Australia, ecology, movement behaviour, Petauridae, omnivore.

Introduction

Knowledge of home range and patterns of movement is fundamental to understanding the ecology and conservation requirements of species (Holbrook et al., 2017). A home range is the area inhabited by an individual that contains the resources necessary to ensure its survival and reproduction (Burt, 1943). Considerable (spatial and temporal) variation in home range size has been found to occur within and between species at both the population and individual level (Herfindal et al., 2004; Pérez-Solano et al., 2016). Both endogenous (i.e. species traits) and exogenous factors (i.e. the external environment) can be important drivers of variation in home range size. Species traits include body mass, social structure and diet (e.g. carnivory, herbivory or omnivory) (Carbone et al., 1999; Williams et al., 2002; Ferguson et al., 2009; Tucker et al., 2014; Duncan et al., 2015), and external environment incorporate a species' physical environment (e.g. marine versus terrestrial), spatial and temporal resource availability and competition (Trewhella et al., 1988; Zabel et al., 1995; Herfindal et al., 2004). While numerous studies have detailed home range size for a variety of species, the relative contributions of species' traits and external environment, to variation in home range size are not yet fully understood.

Two recent meta-analyses of mammalian home range size identified species' traits as the primary driver of home range size (Tucker et al., 2014; Duncan et al., 2015). The authors found body mass had the most significant impact on home range size, with an additive, but less significant, influence of diet (Tucker et al., 2014; Duncan et al., 2015). Body mass has an overarching influence on home range size due to a trade-off between the higher cost of locomotion for smaller-bodied animals and an increase in energetic requirements for larger-bodied animals (McNab, 1963). Similarly, carnivores have larger home ranges relative to omnivores and herbivores, as they must gather food over larger areas due to variable prey availability, low hunting success and often migratory patterns of their prey (McNab, 1963; Gittleman & Harvey, 1982). In contrast, Tucker et al. (2014) and Duncan et al. (2015) found the external environment to have a significantly less important influence on home range size compared to species' traits. Both the physical environment (i.e. terrestrial vs. marine) (Tucker et al., 2014) and resource availability (Duncan et al., 2015) had some influence on home range size, as home range size was typically larger for marine species' and in areas of low resource availability. Interestingly, the extent to which home range size varied with resource availability was not predictable based on a species' body mass or diet (Duncan *et al.*, 2015). Suggesting a species external environment, specifically through resource availability, can have an underlying influence on home range size irrespective of species' traits such as body size and diet.

Home range size is typically found to increase with decreasing resource availability, as individuals are required to move further to meet their resource needs (Nilsen et al., 2005; Bengsen et al., 2016). This has been well demonstrated in many studies where an increase in home range size has occurred in response to localised habitat loss due to the associated loss of food or shelter (Taulman & Smith, 2004; Walton et al., 2017). Controlled experiments have shown that home range size increases as individuals are removed from a population, effectively reducing the level of competition between individuals and increasing resource availability for those remaining (Schoepf et al., 2015). However, the influence of resource availability as a driver of variation in home range size can be difficult to ascertain definitively, as the relationship can vary both spatially and temporarily. For example, home range size may vary temporally due to seasonal variation in resource availability (Kjellander et al., 2004), or spatially due to variation in resource availability over a species' geographic range (Walton et al., 2017). This illustrates a complex and dynamic interaction between resource availability, home range size and a species ecology.

Few home range studies incorporate estimates of home range size that encompass the spatial variability of resources that occurs over a species' geographic range. This may explain inconsistencies in the literature regarding the impact of resource availability on home range size. To investigate resource availability as a driver of home range size here, we measured the home range size of an omnivorous marsupial glider, the savanna glider (*Petaurus ariel*), at the climatic extremes of its geographic range in the tropical savannas of northern Australia. The tropical savannas of northern Australia are generally considered to have relatively low productivity compared to other forested regions in Australia (Hutley et al., 2011). However, productivity across the tropical savannas is not uniform due to the strong rainfall gradient that occurs over northern Australia. This rainfall gradient creates a transition of relatively high productivity in the wetter northern regions, to low productivity in the drier southern end of the savanna. The range in productivity has been directly linked to a gradient in basal area, tree-hollow abundance and canopy cover (Williams *et al.*, 1996; Cook *et al.*, 2002; Cook *et al.*, 2015; Woolley *et al.*, 2018) throughout the savannas. As such, a gradient in productivity arguably results in a gradient in critical resources for arboreal mammals that are hollow-dependent and reliant on forested ecosystems (Goldingay & Jackson, 2004; Firth *et al.*, 2006b; Goldingay, 2011; Lindenmayer *et al.*, 2014). Northern Australia is therefore a good model system for studying the influence of resource availability on home range size, especially that of an arboreal mammal.

Petaurus ariel is the only Petaurid glider to occur exclusively in the tropical savannas of northern Australia. Research on the ecology of Petaurid gliders, including home range assessment, has been largely concentrated in south-east Australia where most species occur (Goldingay & Jackson, 2004). Petaurid gliders are nocturnal arboreal marsupials that are primarily exudivorous feeders (Jackson, 2012). Previous research has found Petaurid gliders to exhibit considerable flexibility in ecology, body mass and home range size both between and within species (Goldingay & Jackson, 2004; Jackson, 2012). Studies on variation in glider home range size have found that within a species, home range size varies with season due to variation in food resources (Jackson, 2000a), and spatially due to localised structural changes in habitat (van der Ree & Bennett, 2003). Between species, home range size has also been found to increase with body size (Goldingay & Jackson, 2004). However, to date, no studies have characterised the influence of species' traits versus external environment on the home range size of Petaurid gliders.

Our objective here was to investigate whether resource availability becomes a stronger driver of home range size when resources are limiting, relative to the influence of species' traits, namely body size and diet. To understand the role of resource availability on *P. ariel* home range size, we first investigated intra-specific variation in *P. ariel* home range size from two population monitoring sites over which productivity, and subsequently fine-scale resource availability, vary substantially. Fine-scale habitat use by *P. ariel* was used to identify critical resources for *P. ariel* and determine resource availability at either end of the species geographic range. We then calculated mean *P. ariel* home range size to make a comparison between *P. ariel* and other similar-sized Petaurid gliders and omnivorous mammals globally. If *P. ariel* home range size is found to be significantly larger than these other species, we propose that resource availability becomes an important influence on home range size when resources are low or limiting. This is due to the relatively low productivity of the tropical savannas, compared to other forested regions in Australia. Alternatively, if resource availability is not an important driver of *P. ariel* home range size, we expect *P. ariel* home range size can be predicted by body size and diet alone.

Materials and methods

Study species

Petaurus ariel has only recently been taxonomically elevated to species level (T. Cremona and S. Carthew, unpublished data), thus making ours the first study to describe the species' ecology. However, museum specimens have provided some evidence of variation in *P. ariel* body mass throughout the species' geographic range.

Petaurus ariel is one of few arboreal mammals in northern Australia that has apparently not experienced dramatic declines in its geographic range in recent decades (Woinarski *et al.*, 2010; Woinarski *et al.*, 2014), although a recent analysis of the species' contemporary distribution has found some evidence of decline (Chapter Two).

Study region

The fire-prone tropical savannas of northern Australia occur above the 600 mm isohyet and are typically dominated by eucalypts (*Eucalyptus* and *Corymbia* spp.) (Williams *et al.*, 1996). They comprise the world's largest remaining expanse of tropical savanna woodland (Bradshaw, 2012). The region is characterised by a distinct wet season (December-April) which encompasses a large part of the years' rainfall, and an almost rainless dry season (May-November), which coincides with the regions' fire season. A strong rainfall gradient occurs across the region (Fig. 4.1), with areas of higher rainfall in the north having higher productivity and vegetation structural complexity (Woinarski *et al.*, 1992; Woinarski *et al.*, 1999). To capture likely variability in *P. ariel* ecology, we established two population monitoring sites; one site at the northern end of the species' range where rainfall is high (mean annual rainfall: 1695 mm) and one at the southern end of the species' range where rainfall is relatively low (mean annual rainfall: 1074 mm) (Fig. 4.1).

It is important to acknowledge that our high rainfall site is an island site. However, for the following reasons we do not consider the results from this site to be in some way confounded by this: the island (Melville Island) is the largest island off the northern Australian coast (5788 km^2) and is less likely to be subjected to density-dependent dynamics which essentially underpins island biogeography; the island has only recently separated from the mainland (between 12000 and 8000 years ago; Woodrofffe *et al.,* 1992) and has a similar mammal assemblage to that of the mainland; there is substantial evidence that mammal decline has occurred on Melville Island (Davies *et al.*, 2018) thus the mammal assemblage on the island is likely subjected to the same key threats as areas on the mainland; and lastly, patterns of *P. ariel* body size on Melville Island are consistent with areas with the same latitude on the mainland (this is evident in the body mass results of this study). A comparison of the environmental characteristics between the two study sites which are likely associated with *P. ariel* resource availability is given in Table 4.1. We note that we have not controlled for variation in fire regime between our study sites, however within the tropical savannas, areas of higher rainfall typically have greater fire frequency but lower fire intensity, relative to areas of low rainfall (Murphy *et al.*, 2019).

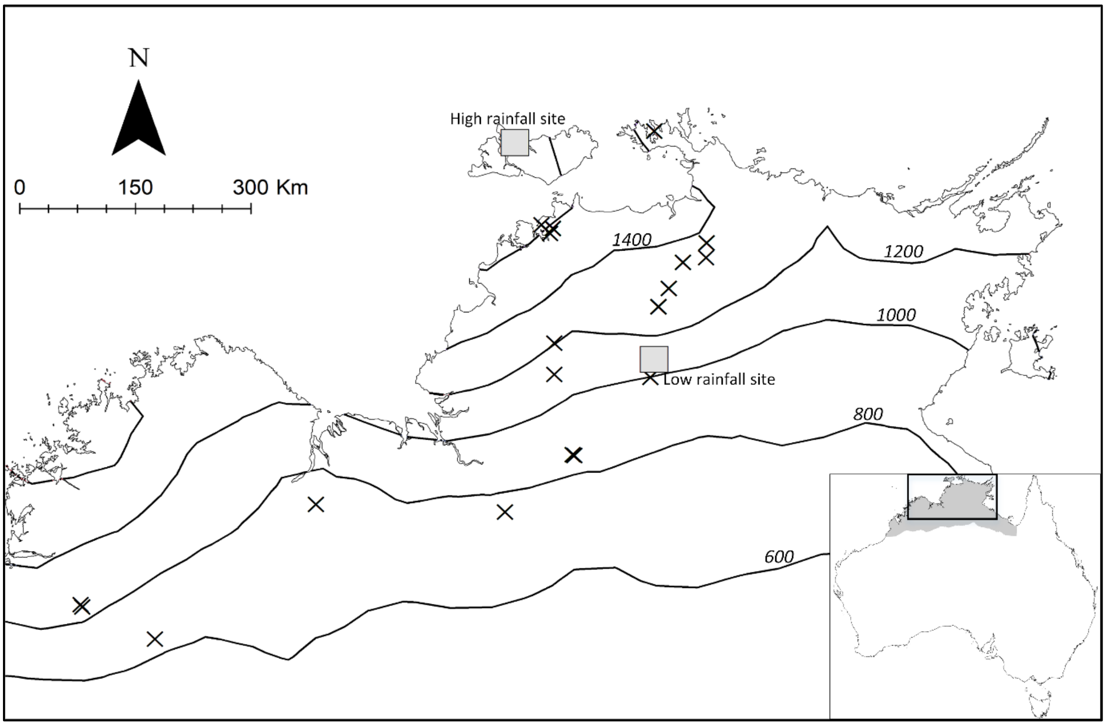

Figure 4.1: Location of study site in northern Australia ; grey squares mark the location of the two study sites used to represent areas of high and low rainfall, and crosses represent additional sites where gliders were live-trapped and weighed. Solid black lines indicate 200 mm rainfall contours, according to mean annual rainfall. Inset shows location of study area relative to Australia, with the contemporary distribution of *Petaurus ariel* in grey.

Table 4.1: Environmental characteristics for the two study sites within the tropical savannas of the Northern Territory where *Petaurus ariel* populations were radio-tracked between 2016-2017.

Location (Latitude; Longitude)	Min. daily temperature (°C)	Max. daily temperature (°C)	No. years burnt (2000-2017)	Mean annual rainfall (mm)	Mean tree density (ha^{-1})*	Mean hollow abundance (ha^{-1})*	Basal area (m^{2} ha^{-1})*	Canopy cover (%)	Net primary productivity (t C ha^{-1} year^{-1})
High rainfall site									
Melville Island -11.40°; 130.58°	22	31	5	1695	883.3	100	16.5	75	11.5
Low rainfall site									
Nitmiluk National Park -14.15°; 132.20°	20	33	8	1074	466.7	300	10.5	21	3.4

*Based on trees with a diameter at breast height >5 cm

Data collection

Body mass - Between 2013 and 2017 we collected live measurements from 118 adult *P. ariel* individuals live-captured from various locations in northern Australia (Fig. 4.1). Individuals were weighed, and sex and age determined upon capture. The reproductive condition for both sexes was used to discriminate adults from sub-adults and juveniles. Males with a developed head scent gland were classified as adults (Jackson, 2003). Females that showed signs of being reproductively active, i.e. pouch with loose skin, elongated or lactating teats, or had pouch young, were classified as adults (Jackson, 2003).

Spotlight surveys - To estimate the densities of *P. ariel*, we surveyed six transects at both the low rainfall and high rainfall study sites (Fig. 4.1). All transects were initially surveyed between May and July 2016, then two transects within each site were surveyed again twice between October and November 2016 and June and August 2017. To detect *P. ariel*, we undertook surveys on foot at night, using spotlights (1000 lumens output; Ledlenser, Solingen, Germany). We walked 700 m transects over 45 min, scanning all vegetation on either side of the transect. Up to three transects were surveyed within a night, with no single site surveyed more than once in a night. Each transect was surveyed at 0.5, 2.5 and 4 h after sunset (a total of three surveys per transect). We recorded locations of animals sighted using a handheld global positioning system and marked all trees in which a glider was detected. We measured the distance from the spotlight transect to each tree in which a glider was detected using a laser rangefinder (TruPulse 200, Laser Technology Inc, Colorado, USA), to enable estimation of density using distance sampling (McDonald *et al.*, 2018).

Radio-tracking - During the dry seasons (May-November) of 2016 and 2017, we installed 40-50 Elliot (aluminium box) traps each night for up to 20 nights at each site, over an area of about 0.05 km^2 at the high rainfall site and 0.40 km^2 at the low rainfall site. Trapping area varied between sites due to apparent differences in population density. Traps were placed at 20-50 m intervals, 4-5 m above ground level. Traps were attached to brackets with tape and were secured to trees with three galvanised nails. Traps were placed so that the entry faced the tree with a gap of 10 cm between the entrance of the trap and the base of the tree to act as a landing platform. We baited traps with a mixture of peanut butter, honey and rolled oats. We sprayed a solution of honey and water (ratio 1:5) on the tree from the base of the trap to the canopy of the tree. Animals were removed from traps at first light each morning, then held and processed in calico bags until release. We fitted gliders with a single-stage brass-loop radio-transmitter weighing 3.2 g (Sirtrack, Hawkes Bay, New Zealand); ensuring collars weighed less than 5% of any individual gliders body. Animals were released at the point of capture, either within an hour of capture or at last light in the evening. Handling of live mammals was in accordance with guidelines of the American Society of Mammalogists (Sikes *et al.*, 2016).

We used a Yagi Antenna and Ultra Receiver (Sirtrack, Hawkes Bay, New Zealand) to track and locate gliders. Den locations were recorded daily for all individuals, from the day after release until collars were removed (14–44 days after capture). Additionally, we tracked each glider three to five times throughout a given night, with all fixes for an individual >2 hrs apart to maximise the independence of the fixes.

Gliders were tracked to their exact location (tree), the position of which was recorded using a handheld GPS. We recorded the date, time, animal ID and any behavioural observations (including feeding behaviour) for each fixture, aided by a spotlight (1000 lumens output; Ledlenser, Solingen, Germany) and high-powered binoculars. If the glider was not visible in the tree or were moving away from the observer, the fixture was recorded for home range analysis but not included as a nocturnal foraging observation. For each marked tree, we recorded the diameter at breast height (DBH: 130 cm), height (using a laser rangefinder/clinometer), species, number of visible hollows and estimated proportion of the canopy that was flowering. Additionally, at each site, we recorded the species, DBH, height and number of visible hollows (entrance diameter ≥5 cm) of all trees (>5 cm DBH) within 12 randomly distributed quadrats (10 × 10 m), encompassing the area in which radio-locations were recorded.

Data analysis

All analyses were conducted in the program R (R Core Team, 2017).

Body mass - We used ordinary least-squares linear models to describe variation in *P. ariel* body mass. We used Akaike Information Criterion (AIC) to rank the models, balancing both model fit and model simplicity (Burnham & Anderson, 2003). We included the explanatory variables 'sex' (female/male), 'latitude' (taken from the location in which the individual was trapped) and 'rainfall' (mean annual rainfall; Bureau of Meteorology, www.bom.gov.au). We also included 'Julian day' (day of the calendar year the individual was trapped) in all models to account for seasonal body size variation.

Density estimate - We estimated the density of *P. ariel* at the two study sites with distance sampling using the package 'Rdistance' (McDonald *et al.*, 2018). Rdistance estimates a distance-based detection function (sightability curve) and abundance based on line-transect observations. The analysis compensates for present but undetected animals. The package uses the detectability at the site to calculate the density, providing 95% confidence intervals. We used AIC corrected for small sample size (AICc) (Hurvich & Tsai, 1989) to determine the best-fitting detection function (lowest AICc) for each site. A half-normal detection function was appropriate for the high rainfall site and a negative-exponential likelihood detection function for the low rainfall site.

Home range - We estimated both the 50% and 95% kernel utilisation distribution from the nocturnal and den fixes collected for each glider, using the function 'kernelUD' in package 'adehabitatHR' (Calenge, 2006). For calculating kernel utilisation distribution, we used the reference bandwidth for estimation of the smoothing parameter (h=href) and held this term constant for animals within each study site. The parameter grid (grid=200) was held constant for all individuals. We used home range area curves to estimate the number of fixes needed to accurately estimate home range size for *P. ariel*. We generated a daily trajectory for individual gliders for each night of radio-tracking where there was >1 fix, using function 'as.traj' in package 'adehabitat' (Calenge, 2006). We then calculated the distance of each trajectory to get the average and maximum distance moved for each glider. We used a generalised linear model (GLM) with a gamma distribution to model the 50% and 95% kernel utilisation distribution and both the maximum distance and average daily distance for each glider, with 'site' (low/high rainfall) and 'sex' (female/male) as predictor variables.

For each glider, we calculated the number of dens used, the average distance between dens and the number of consecutive days per den. We used a GLM with a Poisson distribution to model the number of dens used. As each glider was tracked for a different number of days we included 'log effort' (the natural logarithm of the number days each glider was tracked to its den) as an offset in the model. We used a GLM with a gamma distribution to model the distance between dens and the number of consecutive days a glider used the same den. We modelled 'site' and 'sex' as predictor variables for number of dens used, the average distance between dens and the number of consecutive days per den.

To compare broad-scale resource availability within the geographic range of *P. ariel* relative to that of other Australian Petaurid gliders, we used values of net primary productivity (average annual net primary productivity; product of NASA Earth Observing System MODIS Land Algorithm, 2017) and persistent green fraction as a proxy for canopy cover (derived from Landsat data as an index of woody cover; TERN AusCover, www.auscover.org.au) to indicate relative resource availability. We used ArcMap to extract values from observation record locations downloaded from the online database Atlas of Living Australia (http://www.ala.org.au), for the sugar glider (*P. breviceps*), squirrel glider (*P. norfolcensis*) and the yellow-bellied glider (*P. australis*). *Petaurus ariel* observation records were sourced from our own trapping and spotlighting surveys throughout northern Australia (Chapter Two).

To determine whether broad-scale resource availability had a significant influence on *P. ariel* home range size relative to species traits, namely body mass and diet, we compared the home range size of *P. ariel* against that of similar sized terrestrial, omnivorous mammals. To do this we used the phylogenetic regression of terrestrial, omnivorous mammals calculated by Tucker *et al.* (2014) ($\log Y = 1.19 \log X - 0.91$), comparing the home range size of *P. ariel* as predicted by Tucker *et al.* (2014) against the mean home range size of *P. ariel* recorded in this study.

Results

Body mass

Mean *P. ariel* body mass was 97.8 g for males (n = 60) and 91.0 g for females (n = 58). However, there was significant variation in *P. ariel* body mass throughout the species geographic range (48–151 g). *P. ariel* body mass significantly increased with decreasing rainfall (Table 4.2; Fig. 4.2). In areas of high rainfall there was also significant sexual dimorphism in *P. ariel* body mass, with males larger in size than females (maximum body mass at the highest rainfall site was 85 g and 75 g for males and females respectively; mean annual rainfall: 1695 mm). There was no significant difference in body mass between sex in areas of low rainfall (maximum body mass at lowest rainfall was 150 g and 151 g for males and females respectively; mean annual rainfall: 637 mm and 760 mm).

Table 4.2: Model selection results based on Akaike Information Criterion (AIC) to test the effects of predictor variables 'Julian day', 'Sex', 'Latitude' and 'Mean annual rainfall' on *Petaurus ariel* weight; based on 118 adults *Petaurus ariel* gliders live-trapped over 2013-2017.

Model	Δ AIC	w_i
Julian day + Sex * Rainfall	**0.0**	**0.83**
Julian day + Sex + Rainfall	3.2	0.17
Julian day + Sex * Latitude	14.6	0.00
Julian day + Sex + Latitude	16.0	0.00
Julian day + Rainfall	18.3	0.00
Julian day + Latitude	28.2	0.00
Julian day + Sex	129.6	0.00
Julian day	129.7	0.00
Sex	137.8	0.00
Null	138.0	0.00

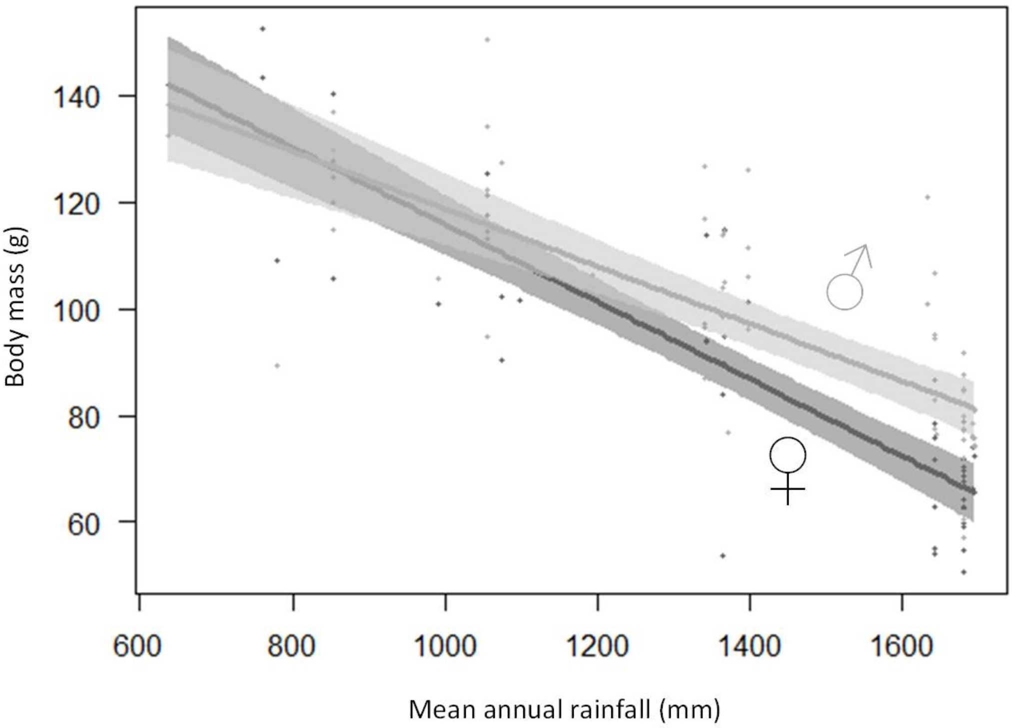

Figure 4.2: Fitted relationship for mean annual rainfall against body mass for male (light grey) and female (dark grey) *Petaurus ariel* , derived from the best linear model (Table 4.2). Solid lines represent models best fit and shaded bands represent 95% confidence intervals.

Density estimate

We recorded a greater number of sightings from standardised spotlight surveys at the high rainfall site (54 gliders sightings) than the low rainfall site (6 gliders sightings). The overall density estimate for the high rainfall site was significantly higher than the low rainfall site, with 1.1 individuals ha^{-1} (95% CI: 1.0–1.2) versus 0.2 individuals ha^{-1} (95% CI: 0.1–0.3).

Population ecology

During 2016 and 2017, we captured a greater number of gliders at the high rainfall site (96 captures over 1712 trap nights; 5.6% trap success) than the low rainfall site (22 captures over 1513 trap nights; 1.5% trap success). We radio-collared 17 gliders (11 male; 7 female) at the high rainfall site (8 in 2016; 10 in 2017) and 8 gliders (4 male; 4 female) at the low rainfall site (3 in 2016; 5 in 2017). We recorded 457 den and 748 nocturnal fixes from gliders at the high rainfall site and 147 den and 269 nocturnal fixes from gliders at the low rainfall site. Overall, mean number of fixes for each glider at the high rainfall site was 67 (95% CI: 57–77) over 37 days and at the low rainfall site, 52 fixes (95% CI: 32–72) over 22 days. Based on home range area curves, only 40% of individual home ranges from either site were stable (>70% fixes), thus the following home range estimates are likely conservative estimates for home range of *P. ariel*.

Home range and nightly distances moved were calculated for all collared gliders, except for one female glider from the low rainfall site with < 10 fixes. There was a tenfold difference for both the 50% and 95% home range size estimates between the low rainfall site (50% home range: 4.0 ha, 95% CI: 2.8–5.2; 95% home range: 23.0 ha, 95% CI: 15.7–30.3) and the high rainfall site (50% home range: 0.4 ha, 95% CI: 0.3–0.5; 95% home range: 2.5 ha, 95% CI: 1.7–3.2) (Table 4.3; Fig. 4.3a). The nightly distance and maximum distance moved per glider was also greater for gliders at the low rainfall site (nightly distance: 670 m, 95% CI: 490–850; maximum distance: 1540 m, 95% CI: 1090–1990) than the high rainfall site (nightly distance: 270 m, 95% CI: 220–320; maximum distance: 690 m, 95% CI: 550–840). The maximum distance moved by a glider in a single night was 2131 m and 1368 m at the low and high rainfall site, respectively; both records were from male gliders. Regardless, sex was not found to improve model fit for either home range size or nightly distance moved (Table 4.3). Based on habitat surveys and the mean home range of *P. ariel* at each site, we estimate there to be greater basal area, tree abundance and hollow availability within an average home range at the low rainfall site relative to the high rainfall site (Table 4.4).

The number of consecutive days an animal used a den varied significantly with sex but not site, as males at both sites changed dens more frequently (every 3 days, 95% CI: 2–4) than females (every 9 days, 95% CI: 5–14) (Table 4.3). There was no significant difference in the total number of dens used by gliders (4 dens, 95% CI: 3–5) at either site or by sex. However, the mean distance between the nearest neighbouring den tree used by an individual glider was significantly larger at the low rainfall site (118.9 m, 95% CI: 84.0–153.8) than at the high rainfall site (35.9 m, 95% CI: 26.7–45.2) (Table 4.3).

Table 4.3: Model selection results based on Akaike Information Criterion (AIC) to test the effects of predictor variables 'Site' and 'Sex' on the den use, distance moved and home range characteristics of *Petaurus ariel* generated from radio-tracking data collected in the 2016-2017 field season.

Response variable	Model dist.	Predictor	ΔAICc	w_i	R^2
Number of dens used	Poisson	Sex + Offset (effort)	0	0.3	0.09
	Poisson	Offset (effort)	0.2	0.2	0.00
	Poisson	Sex + Site + Offset (effort)	0.3	0.2	0.18
	Poisson	Site + Offset (effort)	0.7	0.2	0.07
	Poisson	Sex*Site + Offset (effort)	2.7	0.1	0.19
	Poisson	Null	5.3	0.0	0.00
Number of days per den	Gamma	**Sex**	**0**	**0.6**	**0.43**
	Gamma	Sex*Site	2.2	0.2	0.50
	Gamma	Sex + Site	2.7	0.2	0.43
	Gamma	Null	12.6	0.0	0.00
	Gamma	Site	14.2	0.0	0.03
Glider weight (g)	Gamma	**Sex*Site**	**0**	**0.5**	**0.75**
	Gamma	**Site**	**1.5**	**0.2**	**0.66**
	Gamma	**Sex + Site**	**1.7**	**0.2**	**0.69**
	Gamma	Null	25.9	0.0	0.00
	Gamma	Sex	28.2	0.0	0.01
Avg. nightly distance	Gamma	**Site**	**0**	**0.6**	**0.55**
	Gamma	**Sex + Site**	**1.3**	**0.3**	**0.58**
	Gamma	Sex*Site	4.5	0.1	0.58
	Gamma	Null	17.3	0.0	0.00
	Gamma	Sex	18.9	0.0	0.04
Max. nightly distance	Gamma	**Site**	**0**	**0.6**	**0.45**
	Gamma	Sex + Site	2.3	0.2	0.47
	Gamma	Sex*Site	2.4	0.2	0.47
	Gamma	Null	12.7	0.0	0.00
	Gamma	Sex	14.6	0.0	0.03
95% KUD	Gamma	**Site**	**0**	**0.5**	**0.81**
	Gamma	**Sex + Site**	**0.4**	**0.4**	**0.83**
	Gamma	Sex*Site	3.5	0.1	0.83
	Gamma	Null	42.7	0.0	0.00
	Gamma	Sex	44.0	0.0	0.04
50% KUD	Gamma	**Sex + Site**	**0**	**0.5**	**0.84**
	Gamma	**Site**	**0.8**	**0.4**	**0.81**
	Gamma	Sex*Site	3.1	0.1	0.84
	Gamma	Null	43.1	0.0	0.00
	Gamma	Sex	44.9	0.0	0.03
Distance between dens	Gamma	**Site**	**0.0**	**0.7**	**0.67**
	Gamma	Sex + Site	3.0	0.2	0.67
	Gamma	Sex*Site	3.7	0.1	0.71
	Gamma	Null	23.5	0.0	0.00
	Gamma	Sex	26.2	0.0	0.00

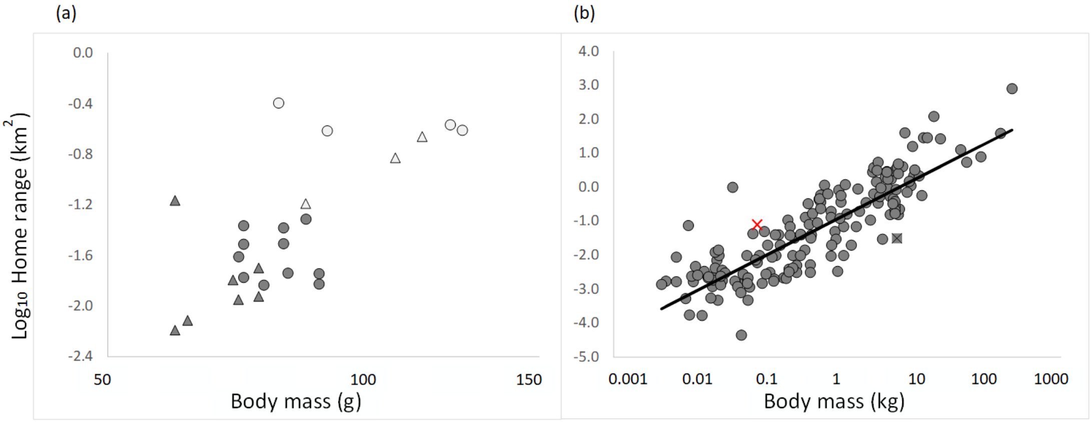

Figure 4.3: Relationship between body mass (Log_{10}) and home range for (a) *Petaurus ariel* data collected from this study (dark grey points are individuals radio tracked at the high rainfall site and light grey points are individuals radio tracked at the low rainfall site; triangles represent female gliders and circles represent male gliders) and (b) mean body mass (Log_{10}) and home range of *P. ariel* (red cross) collected from this study compared to mean values of body mass and home range of other terrestrial omnivorous mammals (dark grey points) (Tucker *et al.*, 2014); solid black line is the phylogenetic regression of terrestrial omnivorous mammals: $\log Y = 1.12 \log X - 0.94$, generated by Tucker *et al.* (2014)

Table 4.4: Comparison of mean *Petaurus ariel* home range size, nightly distance moved, body mass, numbers of dens per individual glider and distance between dens at the two study sites (± standard error), and estimated basal area and number of trees within an average home range. Estimates are calculated from the environmental characteristics recorded in Table 4.1, and home ranges generated from radio-tracking results.

Mean home range (ha; ± SE)	Mean nightly distance (km; ± SE)	Mean body mass (g; ± SE)	Mean dens per glider (± SE)	Mean distance between dens (m) per glider (± SE)	Estimated basal area (m^2) per home range (± SE)	Estimated number of trees per home range (± SE)	Estimated number of hollows per home range (± SE)
High rainfall site							
2.5 ± 0.4	0.27 ± 0.0	67.4 ± 0.2	4.2 ± 0.5	35.9 ± 4.7	41.4 ± 5.0	2208.3 ± 201.6	250 ± 106.2
Low rainfall site							
23.0 ± 3.7	0.67 ± 0.1	101.1 ± 7.0	4.3 ± 0.7	118.9 ± 17.8	242.5 ± 42.9	10733.3 ± 1222.3	6900 ± 1756.6

We recorded nocturnal foraging observations for *P. ariel* in 10 tree species at the high rainfall site (420 fixes from the total of 748) and 12 tree species at the low rainfall site (151 fixes from a total of 269). At the high rainfall site, there were two tree species that each made up ≥10% of all nocturnal observations (Fig. 4.4); *Eucalyptus miniata* (63% of observations; 32% of trees observed in habitat surveys) and *Eu. tetrodonta* (18% of observations, 35% of trees observed in habitat surveys). Although detailed feeding observations were not collected for the study, *P. ariel* was only observed feeding on flowers in these tree species. At the low rainfall site, there were three tree species that each made up ≥10% of all nocturnal observations; *Eu. tintinnans* (33% of observations, 0% of trees observed in habitat surveys), *Erythrophleum chlorostachys* (22% of observations, 36% of trees observed in habitat surveys) and *Eu. tectifica* (10% of observations, 20% of trees observed in habitat surveys). *Petaurus ariel* foraging behaviours in the low rainfall site were seemingly more varied. Of the 48 confirmed foraging observations (as opposed to nocturnal observations where feeding could not be confirmed), 42% of observations were of gliders foraging on flowers (15 observations in *Eu. tintinnans*, 3 observations in *Eu. confertiflora*, 1 observation in *Grevillia pteridifolia* and 1 observation in *Eu. tectifica*), 38% of observations were gliders sap feeding (10 observations in *Er. chlorostachys*, 3 observations in *Eu. confertiflora*, 2 observations in *Terminalia ferdinandiana*, 1 observation in *Eu. tintinnans*, 1 observation in *Eu. tectifica*, and 1 observation in *Corymbia* spp.), 15% of observations were gliders on fungi (all observations in *Cochlospermum fraseri*) and 6% of observations were gliders feeding on insects or geckoes. In total, we recorded relatively equal tree species richness at each study (8 and 10 unique species at the high and low rainfall respectively), and observed *P. ariel* in most species.

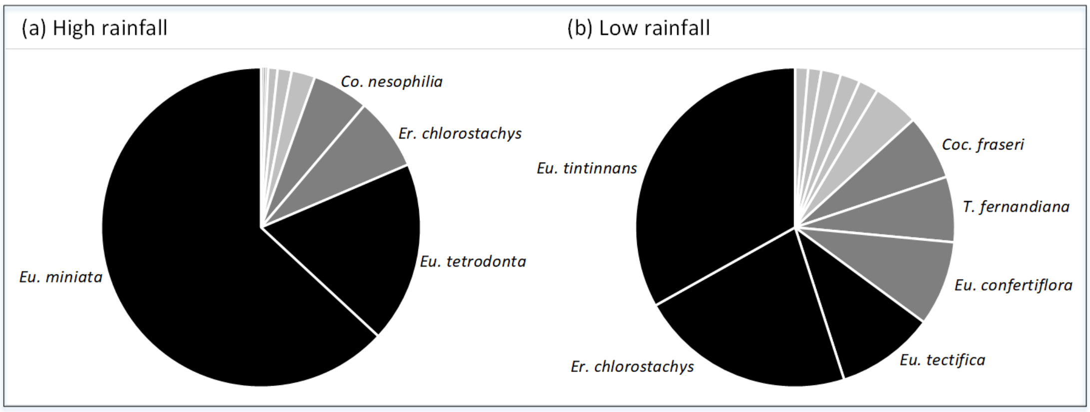

Figure 4.4: Proportion of nocturnal fixes recorded for each different tree species *Petaurus ariel* was detected in at the high and low rainfall site. Black indicates tree species that made up ≥10 % of the observation records (two tree species at the high rainfall site and three tree species at the low rainfall site); dark grey indicates tree species that made up 5 - 9.9 % of the observation records (two tree species at the high rainfall site and three tree species at the low rainfall site); light grey indicates all other tree species making up < 5 % of observations (six tree species at each site).

The estimates of home range size for *P. ariel* obtained here were considerably larger than similarly sized *P. breviceps* (Table 4.5; Fig. 4.5), and at the upper end was within the range of the considerably larger-bodied *P. australis*. The ratio between the maximum and minimum home range size of *P. ariel* was also the largest of all Australian Petaurids, highlighting greater intra-species variability in *P. ariel* home range size relative to other Petaurids. Additionally, we found the geographic range of *P. ariel* exhibited the lowest median values of resource availability (as measured by net primary productivity and canopy cover), relative to *P. breviceps*, *P. norfolcensis*, and *P. australis* (Table 4.6). Compared to other omnivorous terrestrial species globally (Tucker *et al.*, 2014), mean *P. ariel* home range size falls within the top 6% of species relative to body size (Fig. 4.3b). Furthermore, the mean home range size of *P. ariel* at the low rainfall site falls within the top 2.5% of species relative to body size.

Table 4.5: Comparison of mean home range area, mean body mass and density known for other gliding Petauridae species (Goldingay & Jackson, 2004) against findings from this study for *Petaurus ariel* (in bold); with the range for the entire species and the mean for two separate study sites high rainfall and low rainfall.

Home range area (range)	Home range ratio (maximum/minimum)	Body mass (range)	Density (range)
Petaurus breviceps			
0.2 – 10 ha	50.0	60 – 150 g	0.23 – 6.10 per ha^{-1}
Petaurus norfolcensis			
0.7 – 10.5 ha	15.0	150 – 300 g	0.35 – 1.54 per ha^{-1}
Petaurus gracilis			
10.0 – 34.0 ha	3.4	310 – 500 g	0.15 – 0.24 per ha^{-1}
Petaurus australis			
25.0 – 120.0 ha	4.5	435 – 727 g	0.04 – 0.16 per ha^{-1}
Petaurus ariel			
0.6 – 40.8 ha	**63.4**	**48 – 151 g***	**0.22 – 1.13 per ha**$^{-1}$
High rainfall *P. ariel*			
2.5 ha	**-**	**67 g**	**1.13 per ha**$^{-1}$
Low rainfall *P. ariel*			
23.0 ha	**-**	**101 g**	**0.22 per ha**$^{-1}$

**P. ariel* body mass range taken from all live-trapped adult measurements collected throughout the species geographic range (see Fig. 4.1)

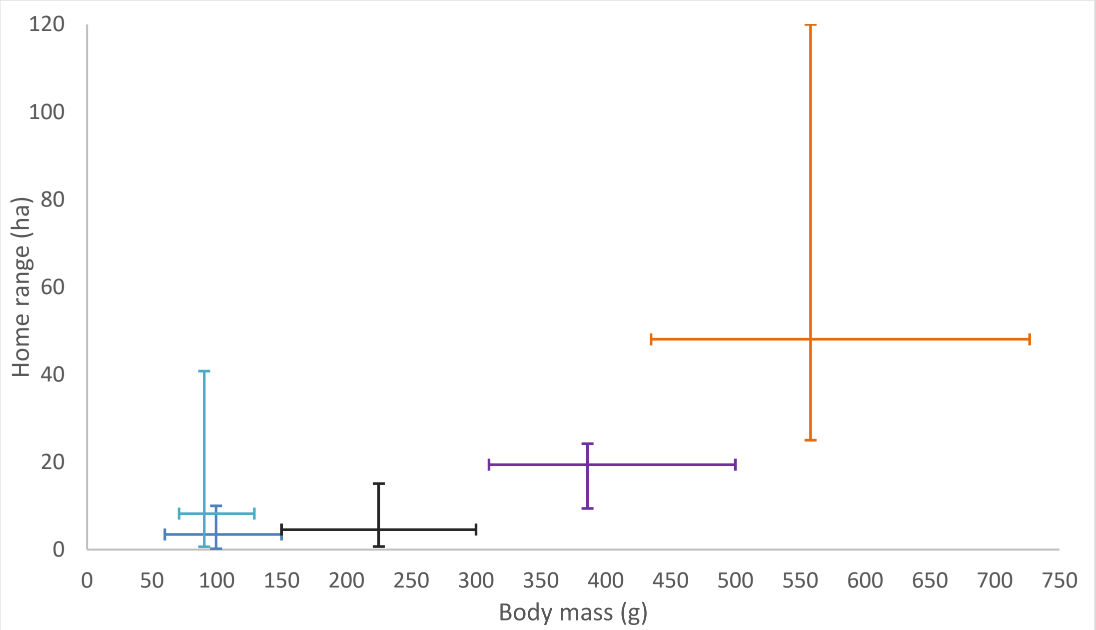

Figure 4.5: Relationship between the body mass and home range of *Petaurus breviceps* (dark blue), *P. norfolcensis* (black), *P. gracilis* (purple), *P. australis* (orange) and the findings from this study of *P. ariel* (light blue). Vertical confidence intervals are the known range of the species home range and horizontal confidence intervals are the known range of the species body weight. The point at where the lines intersect represents the mean value for both home range and body mass.

Table 4.6: Comparison of net primary productivity and canopy cover (ranked in order of decreasing values) based on the geographic range for other Australian Petaurids' (excluding *Petaurus gracilis*) against *P. ariel* (in bold). Observation records were sourced from the online database Atlas of Living Australia (http://www.ala.org.au) and A. Stobo-Wilson (Chapter Two). Values of net primary productivity and canopy cover were extracted from the location of observation records.

	Net primary productivity (median; range) (t C ha^{-1} year^{-1})	Canopy cover (median; range) (%)
Petaurus australis	18.6; 7.7 – 19.4	75.2; 10.5 - 83.3
Petaurus breviceps	15.4; 1.1 – 19.6	65.7; 10 - 84.1
Petaurus norfolcensis	10.9; 1.1 – 19.2	29.8; 10 - 78.9
Petaurus ariel	**4.6; 1.1 – 10.1**	**16.4; 10 - 40.4**

Discussion

The degree to which home range size is driven by the external environment through resource availability is unresolved. Here we found dramatic variation in the home range size of *P. ariel* over the species' geographic range. Over the relatively short distance of 350 km, there was a ten-fold increase in mean *P. ariel* home range size from the high rainfall site (1695 mm) to the low rainfall site (1074 mm). Relative to body size, mean *P. ariel* home range size was found to be larger than any other Australian Petaurid, and in the top 6% of terrestrial, omnivorous mammals globally. Our findings suggest that the disproportionately large home range of *P. ariel* is driven by naturally low resource availability within the species' geographic range. Our study highlights that when resources are limiting, resource availability can have a greater influence on home range size than what is typically predicted by species' traits such as body mass and diet.

We did not find body mass to be the primary driver of variation in *P. ariel* home range size. Both the home range size and body mass of *P. ariel* were greater at the low rainfall site than at the high rainfall site. However, the magnitude of change in *P. ariel* home range size between the two study sites far exceeded the change in *P. ariel* body mass (50% larger at the low rainfall site). Furthermore, the mean and maximum home range of *P. ariel* was considerably larger than that of closely related and similar sized *P. breviceps,* and was instead more comparable with that of *P. gracilis* (that is more than twice the body mass of *P. ariel*). Although the area encompassed by the geographic range of *P. ariel* had similar minimum values of net primary productivity compared to *P. breviceps* and *P. notatus*, *P. ariel* by far had the lowest median and maximum values of net primary productivity and canopy cover, compared to the ranges of all other Australian Petaurids. Thus, the discrepancy in home range size between these species is more likely explained by low resource availability in northern Australia, than differences in body size. This is further supported a by ten-fold decrease in *P. ariel* density at the low rainfall site where home range size was largest. Globally, the population density of mammalian species has been found to decrease with decreasing resource availability (Santini *et al.*, 2018). Thus, variation in *P. ariel* home range size and population density is more likely in response to variation in resource availability between the two study sites rather than variation in *P. ariel* body mass.

The substantial variation in *P. ariel* body mass throughout the study region is in and of itself an interesting finding. An earlier study looking at body size variation from skull measurements of Petauridae across Australia (Chapter Three) found thermoregulation explained variation in *P. ariel* body size throughout the species geographic range. *Petaurus ariel* body size increased with decreasing winter minimum temperature and decreased with increasing relative humidity (Chapter Three). This finding supports heat conservation and/or heat dissipation as the driving mechanism for *P. ariel* body size. Consistent with the findings of this study, *P. ariel* body size decreased with increasing primary productivity (Chapter Three), which rejects the ecogeographic hypothesis that productivity (through resource availability) is a primary driver of mammalian body size (body size should increase with increasing productivity; Rozenzweig,1968; McNab, 2010; Huston & Wolverton, 2011). The increase in *P. ariel* home range size with decreasing resource availability may provide some insight as to why productivity is not a driver of *P. ariel* body size. For example, if species' traits, such as home range size, can facilitate an individual/species to cope with variation in resource availability, there would no subsequent selective pressure for variation in body size. Future research should aim to explore this pattern further to better understand these competing ecogeographic hypotheses.

Intraspecific variation in *P. ariel* home range size is likely a response to both lower quality and quantity of denning and food resources with declining rainfall. Within a given night at the low rainfall site, *P. ariel* moves twice the distance and therefore expends more than twice the energy to access both den and food resources relative to gliders at the high rainfall site. This is despite similar diversity in tree species at the sites and greater tree and hollow abundance within an average home range at the low rainfall site. For example, we found the distance between *P. ariel* den trees at the low rainfall site was more than three-times greater than the distance between den trees at the high rainfall site. Furthermore, *P. ariel* foraged on a greater variety of trees at the low rainfall site relative to the high rainfall site. Over 80% of foraging observations at the high rainfall site occurred within only two tree species, where *P. ariel* foraged solely on flowers. In contrast, at the low rainfall site, 80% of foraging observations occurred within five tree species, and gliders were observed foraging on flowers, insects and sap. Both sites were surveyed in the same season, therefore the timing of flowering (and access to flowering trees) was similar at both sites and cannot explain the difference in *P. ariel* foraging behaviour. Although variation in den use and foraging behaviour is common both within - and between - species of other Australian Petaurids (Goldingay & Jackson, 2004), in this instance we believe the contrasting behaviour of *P. ariel* between the two study sites is indicative of relatively lower resource availability at the low rainfall site. Consequently, low resource availability in northern Australia, especially in areas of low rainfall, has effectively increased the area requirements of *P. ariel* to the extremes of known home range size (relative to body size) for both Australian Petaurids and other gliding mammals globally (Jackson, 2012).

It has previously been suggested that gliding mammals are able to maintain larger home ranges than other mammal's due to their unique gliding locomotion (Hanski *et al.*, 2000; Sharpe & Goldingay, 2007). Globally, there are some similar sized gliding mammals that have a mean home range size as large as *P. ariel.* For example, in one study of the Siberian flying squirrel (*Pteromys volans*) (95-200 g; Jackson (2012)), the mean male home range size was 60 ha ± SE 41.1 (Hanski *et al.*, 2000), compared to 3.7-9.9 ha in other locations (Fridell & Litvaitis, 1991; Witt, 1992)). Similarly, for one population of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) (110g-185 g; Jackson (2012)) the mean male home range was 60 ha ± SE 24 (Menzel *et al.*, 2006). The large home range size (reported as within 3-15 ha previously; Weigl (2007)) of *G. s. fuscus* was attributed to a 90% reduction in suitable habitat within the region due to habitat destruction (Menzel *et al.*, 2006). No single explanation was provided for the increased home range size of *Pt. volans*. However, low food availability, the patchy distribution and low abundance of females throughout the landscape and selection for high canopy cover were all suggested as contributing factors (Hanski *et al.*, 2000). In addition to having a large home range size, the population density of *Pt. volans* was also regionally low (0.04-0.08 ha^{-1}), similarly to *P. ariel* in the low rainfall site.

These examples illustrate that gliding mammals can exhibit large intraspecific variation in home range size, with instances of home range size far exceeding what is anticipated based on body size and diet alone. However, unlike *P. ariel*, in these studies the home range size for populations of *Pt. volans* and *G. s. fuscus* were atypical for those species and most likely a response to human-altered landscapes. Of Australian Petaurids, Goldingay and Kavanagh (1993) found the home range size of *P. australis* throughout the species' geographic range was consistently larger than expected based on the body size of an omnivorous species. As previously suggested, the large home range of gliders may be linked to the lower locomotor costs of gliding (Scheibe *et al.*, 2006). However, the ability to glide cannot explain the large home range size of *P. ariel*, as no other gliding mammals (in which home range estimates are reported) had a mean home range size relative to body size within the top 6% of terrestrial omnivorous mammals globally (Tucker *et al.*, 2014).

Low resource availability within the geographic range of *P. ariel* most likely explains the species' disproportionately large home range size relative to both Australian Petaurids and other omnivorous species globally. Our findings illustrate that when resources become limiting, home range size can exceed what is predicted by body mass and diet alone. To build on our findings, further research should investigate temporal variation in *P. ariel* home range size. Indeed, it seems likely that the timing of our study would have meant an underestimate of home range size for *P. ariel*, as our study took place during a seasonal peak in resource availability (i.e. a time when home ranges are expected to be smaller). Furthermore, this study would have benefitted by collecting measurements of *P. ariel* home range size from a greater number of sites throughout the species geographic range. To attain greater insight into the relationship between resource availability and home range size, future research could explore the point at which resources become limiting for *P. ariel* and the way in which home range size increases throughout the species' geographic range.

Our study exemplifies why researchers should seek to account for the variation in home range size that occurs within a species' geographic range as opposed to relying on one spatial reference. Although *P. ariel* was in the top 6% of home range size relative to body mass, our estimates did fall within the limits of other omnivorous mammals globally (Tucker *et al.*, 2014). Thus, body mass and diet are clearly also important drivers of mean *P. ariel* home range size. In this instance, low resource availability pushes home range size to the upper limits typical for omnivores of equivalent size globally. Our study illustrates how a species-specific ecological study can be used to explain broad geographic trends.

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Chapter 5 :

Illuminating den-tree selection by an arboreal mammal using terrestrial laser scanning in northern Australia

Savanna glider 'Hagrid' during a night of radiotracking at Nitmiluk National Park field site

Chapter Five cover page photo credit Aline Gibson Vega

Abstract

There has been a significant decline of numerous arboreal mammals in northern Australia, especially in areas of low rainfall. We aimed to better understand the habitat requirements of these mammals by investigating how variation in habitat structure and associated hollow abundance influence den-tree selection by the savanna glider (*Petaurus ariel*). We compared den-tree selection by *P. ariel* in two populations at the climatic extremes of the species' geographic range, representing areas of high and low rainfall (mean annual rainfall: 1695 mm and 1074 mm, respectively). We used traditional habitat surveys complemented by advanced terrestrial Light Detection And Ranging (LiDAR) technology to compare site habitat structure and subsequent den-tree selection by *P. ariel*. Height of the canopy and total canopy cover increased significantly with rainfall. At the high rainfall site, the size of *P. ariel* den trees was greater than that of neighbouring trees. Mean trunk diameter at breast height was 53.4 and 33.8 cm, and mean canopy diameter was 14.0 m and 10.4 m, for den and neighbouring trees, respectively. In contrast, *P. ariel* den trees at the low rainfall site were no larger than neighbouring trees but were more likely to be a specific tree species. At both sites, *P. ariel* selected den trees that were more likely to be hollow bearing (through either larger tree size or specific tree species). We conclude that hollow availability is likely to be a key limiting resource for arboreal mammals in northern Australia and emphasise the importance of land management practices that maximise the persistence of large eucalypt trees to support hollow-dwelling arboreal mammals.

Keywords:

Habitat use, hollow availability, LiDAR, movement ecology, *Petaurus ariel*, tree structure

Introduction

Habitat modification (e.g. logging and vegetation clearing) and alteration of ecosystem processes (e.g. intensification of disturbance regimes) by humans have resulted in substantial declines in biodiversity globally (Ceballos *et al.*, 2015). Human-driven declines in the abundance of large, hollow-bearing trees (Cockle *et al.*, 2011; Lindenmayer *et al.*, 2012; Lindenmayer *et al.*, 2013) has been particularly detrimental to hollow-dependent fauna, including many arboreal mammals (Lindenmayer, 2000; Wayne *et al.*, 2006; Lampila *et al.*, 2009). Due to the long-time periods required for tree hollows to form, conservation efforts are best targeted at identifying and protecting these critical resources (Fisher & Wilkinson, 2005; Lindenmayer *et al.*, 2014). Thus, considerable research effort has been spent determining the fine-scale habitat requirements of arboreal mammals, particularly den-tree requirements (Hanski *et al.*, 2000; Goldingay, 2011; Lindenmayer *et al.*, 2017). Without this knowledge, land managers are unable to identify and subsequently protect this critical resource for arboreal mammals and other hollow-dependent species.

The last 200 years has seen an exceptionally high rate of extinction of Australia's native mammal fauna (Short & Smith, 1994; McKenzie *et al.*, 2007; Woinarski *et al.*, 2015). Mammal declines in northern Australia's tropical savannas are the most recently recorded declines on the continent (Woinarski *et al.*, 2010). For many species, declines first occurred in more southerly areas of lower rainfall, with a gradual and continuing contraction to the northern mesic ends of the species' former distribution (Firth *et al.*, 2010; Start *et al.*, 2012; Ziembicki *et al.*, 2013a; Chapter Two). Of those mammals that have experienced marked declines in northern Australia, the majority are semi-arboreal and arboreal (Fitzsimons *et al.*, 2010). Thus, arboreal mammals may be more susceptible to decline than exclusively terrestrial mammals, particularly in areas of relatively low rainfall and tree cover. Predation by feral cats (Frank *et al.*, 2014; Davies *et al.*, 2017b; Davies *et al.*, 2018) and altered fire regimes (Kerle & Burgman, 1984; Firth *et al.*, 2006a; Firth *et al.*, 2010) have been linked to the decline of several small mammal species in northern Australia. However, to date, no studies have explicitly identified how these threats explain the increased vulnerability of arboreal mammals in northern Australia and why declines have first occurred in areas of lower rainfall.

The continuing decline of arboreal mammals in northern Australia has highlighted significant gaps in our knowledge of fine-scale habitat requirements of arboreal mammals in the tropical savannas. Most research on habitat use by arboreal mammals and drivers of hollow availability in Australia, has thus far been confined to the temperate zone and localised areas in the Wet Tropics bioregion of northern Queensland (Goldingay, 2011; Lindenmayer *et al.*, 2017). A review on tree-hollow use by Australian arboreal mammals showed a strong link between species abundance and hollow availability (Goldingay, 2011). Recently, the first study on hollow availability in the tropical savannas of northern Australia established that hollow abundance decreases with decreasing rainfall and is likely to be declining under current fire regimes (more frequent, high-intensity fires) (Woolley *et al.*, 2018). Thus, it is plausible that declines of arboreal mammals in the tropical savannas of northern Australia may in part be the result of reduced hollow availability throughout the region due to altered fire regimes.

Considerable research effort has been spent detailing fine-scale attributes of trees selected as dens by arboreal mammals in southeastern Australia (Lindenmayer & Meggs, 1996; Rowston, 1998; Jackson, 2000a). However, only two studies have described use and selection of den trees by arboreal mammals in the tropical savannas of northern Australia (Griffiths *et al.*, 2001; Firth *et al.*, 2006a). Both studies highlighted a preference for larger eucalypt species as den trees. However, these studies were confined to the more northerly, mesic areas of Australia's tropical savannas, where there is greater productivity and structural complexity relative to more southerly areas with lower rainfall (Woinarski *et al.*, 1992; Woinarski *et al.*, 1999). Therefore, these studies provide little insight into how den selection varies throughout the tropical savannas or why arboreal mammals in the drier, southern parts of the tropical savannas declined before, and more severely than, those in areas of higher rainfall.

There has been a recent increase in cross-disciplinary studies that combine remote-sensing technologies (which characterise fine-scale habitat structure), with behavioural and movement ecology studies to determine patterns of habitat use (Squires *et al.*, 2013; Davies & Asner, 2014; McLean *et al.*, 2016). Light detection and ranging (LiDAR) technology provides a novel and effective method for ecologists to capture variation in habitat structure, especially three-dimensional forest structure, over a large area (Lefsky *et al.*, 2002; Hudak *et al.*, 2009). LiDAR has improved our ability to model fine-scale habitat selection and movement patterns of arboreal mammals (McLean *et al.*, 2016; Blakey *et al.*, 2017; Davies *et al.*, 2017a; Davies *et al.*, 2019) by providing measures of canopy structure that were previously unmeasurable or required considerable effort to capture using traditional field measurement methods (Dial *et al.*, 2004; Davies *et al.*, 2017a). For example, Davies *et al.* (2017a; 2019) found structural attributes of the upper forest canopy (i.e. increased canopy cover and uniform canopy height) were important for movement by the Bornean orangutan (*Pongo pygmaeus*). Furthermore, Blakey *et al.* (2017) used LiDAR to link elements of lower canopy structure with the foraging strategy of three different bat species. Despite the importance of den-trees for a range of arboreal mammals, LiDAR has not yet been used to determine fine-scale den-tree selection by a hollow-dependent arboreal mammal.

To improve our knowledge of the habitat requirements of arboreal mammals in the tropical savannas of northern Australia, we investigated den-tree selection by a little known arboreal marsupial, the savanna glider (*Petaurus ariel*). Recent work has shown that *P. ariel* has declined in the lower-rainfall parts of its range, although not as severely as other arboreal mammals (Chapter Two). We aimed to quantify how variation in habitat structure and hollow abundance influence den-tree selection by *P. ariel* in areas of high and low rainfall. Here, we focused on characteristics that would most likely influence movement and habitat-use by an arboreal mammal, such as canopy dimensions and tree size. To accurately capture structural variation, we used contemporary terrestrial (ground-based) LiDAR technology to complement field-based habitat surveys. This study will provide new information on the plausibility of hollow abundance, i.e. hollow availability, as a contributing factor to arboreal mammal decline in northern Australia.

Materials and methods

Study species

Petaurus ariel is an obligate hollow-denning arboreal marsupial, recently elevated to species level (T. Cremona and S. Carthew, unpublished data), formerly known as *P. breviceps ariel*. Until recently, *P. ariel* was anecdotally believed to be the only widespread savanna mammal within the so-called 'critical weight range' that had not declined within northern Australia (Woinarski *et al.*, 2010; Woinarski *et al.*, 2014). The 'critical weight range' refers to Australian native mammals with body mass 35–5500 g, that are highly susceptible to decline and extinction (Burbidge & McKenzie, 1989). However, analysis of the contemporary distribution of *P. ariel* has found evidence of moderate decline in the southern (lower rainfall) end of its distribution (Chapter Two).

Study region

The fire-prone tropical savannas of northern Australia occur above the 500 mm isohyet and are typically dominated by eucalypts (*Eucalyptus* and *Corymbia* spp.) (Williams *et al.*, 1996). They comprise one of the world's largest remaining expanses of tropical savanna, covering an estimated 1.9 million km^2 (Bradshaw, 2012). The region is characterised by a distinct wet season (December-April), which encompasses almost all (>90%) of the year's rainfall, and an almost rainless dry season (May-November), which coincides with the region's fire season. To determine vegetation structure and fine-scale habitat preferences by *P. ariel* across the species' geographic range, we established two population monitoring sites, one site at the northern end of the species' range where mean annual rainfall is relatively high (1695 mm) and one at the southern end of the species' range where rainfall is relatively low (1074 mm) (Fig. 5.1).

It is important to acknowledge that our high rainfall site is an island site. However, for the following reasons we do not consider the results from this site to be in some way confounded by this: the island (Melville Island) is the largest island off the northern Australian coast (5788 km^2) and is less likely to be subjected to density-dependent dynamics which essentially underpins island biogeography; the island has only recently separated from the mainland (between 12000 and 8000 years ago; Woodrofffe *et al.*, 1992) and has a similar mammal assemblage to that of the mainland; there is substantial evidence that mammal decline has occurred on Melville Island (Davies *et al.*, 2018) thus the mammal assemblage on the island is likely subjected to the same key threats as areas on the mainland; and lastly, patterns of *P. ariel* body size on Melville Island are consistent with areas with the same latitude on the mainland (Chapter Four). A comparison of broad environmental characteristics between the two study sites is given in Table 5.1. We note that we have not controlled for variation in fire regime between our study sites, however within the tropical savannas, areas of higher rainfall typically have greater fire frequency but lower fire intensity, relative to areas of low rainfall (Murphy *et al.*, 2019).

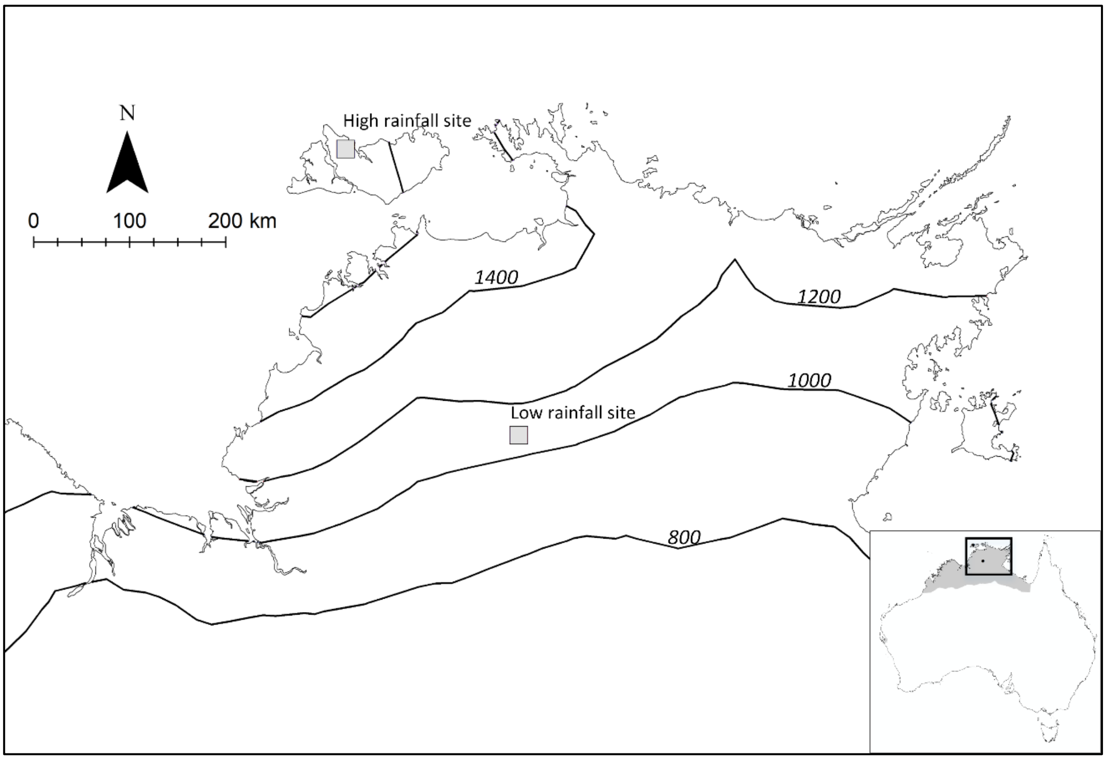

Figure 5.1: Location of study sites in the Northern Territory ; solid black lines indicate mean annual rainfall isohyets. Square inset shows location of study region relative to Australia and the contemporary distribution of *Petaurus ariel* (shaded grey; Chapter Two).

Table 5.1: Environmental characteristics of the two study sites within the tropical savannas of the Northern Territory where *Petaurus ariel* individuals were radio-tracked between 2016 and 2017.

Location (Latitude; Longitude)	Minimum daily temperature (°C)	Maximum daily temperature (°C)	Number years burnt (2000-2017)	Mean annual rainfall (mm)	Mean tree density (ha^{-1})*	Mean hollow abundance (ha^{-1})*	Live tree basal area (m^2 ha^{-1})*	Net primary productivity (t C ha^{-1} $year^{-1}$)
High rainfall site								
Melville Island -11.40°; 130.58°	22	31	5	1695	891.7	100	16.6	11.5
Low rainfall site								
Nitmiluk National Park -14.15°; 132.20°	20	33	8	1074	521.4	300	12.6	3.4

*Based on trees with a diameter at breast height >5cm

Radiotracking

During the dry seasons (May-November) of 2016 and 2017, we set 40-50 Elliot (aluminium box) traps each night for up to 20 nights at each site, over an area of about 0.05 km^2 at the high rainfall site and 0.40 km^2 at the low rainfall site. Traps were placed at 20–50 m intervals, 4–5 m above ground level. Traps were attached to brackets with tape and were secured to trees with three galvanised nails. Traps were placed so that the entry faced the tree with a gap of 10 cm between the entrance of the trap and the base of the tree to act as a landing platform. We baited traps with a mixture of peanut butter, honey and rolled oats. We sprayed a solution of honey and water (ratio 1:5) on the tree from the base of the trap to the canopy of the tree. Animasls were removed from traps at first light each morning, then held and processed in calico bags until release. We fitted gliders with a single-stage brass-loop radio-transmitter collars weighing 3.2 g (Sirtrack, Hawkes Bay, New Zealand). Animals were released at the point of capture, either within an hour of capture or at last light the next evening.

In total, we radio-collared 17 adult gliders (11 male; 7 female) at the high rainfall site (8 in 2016; 10 in 2017) and 8 adult gliders (4 male; 4 female) at the low rainfall site (3 in 2016; 5 in 2017). We used a hand-held antenna and Ultra Receiver (Sirtrack, Hawkes Bay, New Zealand) to track gliders. Den locations were recorded daily for all individuals from the day after release until collars were removed (10–45 days and 8–28 days after capture at the high and low rainfall sites, respectively). We recorded dens being used on 457 occasions at the high rainfall site and 147 occasions at the low rainfall site. For each tree where *P. ariel* was recorded denning, we recorded the diameter at breast height (130 cm; DBH), tree height (using a laser rangefinder with a built-in clinometer), species and number of visible hollows (entrance diameter ≥5 cm) for all den trees. In total, we identified and collected field measurements from 74 den trees; 48 from the high rainfall site and 26 from the low rainfall site. At each site, we recorded the species, DBH, height and number of visible hollows (entrance diameter ≥5 cm) of all trees (>5 cm DBH) within 12 randomly distributed quadrats (10 × 10 m), encompassing the area in which radio-locations were recorded.

Terrestrial LiDAR scanning

Scan of study site

We used a Riegl VZ-2000 terrestrial (ground-based) laser scanner (RIEGL Laser Measurement Systems GmbH) to capture the three-dimensional vegetation structure of both study sites. We completed 45 and 30 scans at the high and low rainfall sites, respectively, with scans spaced 25 m apart along a straight-line transect. The scanner was operated at 550 kHz with an angular sampling step of 0.02 mrad. We integrated a Leica GS16 RTK GNSS system with the laser scanner to obtain high positional accuracy. Individual scans were co-registered using the Multi-station Adjustment Module (ICP based) embedded in Riegl's RiSCAN PRO software. Co-registered scans were merged, filtered for noise, and thinned with a 2 cm octree filter prior to export in .las format in UTM52S for further analysis (Fig. 5.2).

Randomly generated survey plots

To compare structural characteristics of each study site, we used a polygon to clip 20 m-diameter circular plots, evenly-spaced throughout the merged LiDAR point cloud of each study site, giving 80 plots at the high rainfall site and 90 plots at the low rainfall site. We generated LiDAR-derived metrics from the point cloud of each plot using 'lascanopy' within LAStools (rapidlasso GmbH, 2014). To compare the canopy structure of the randomly generated survey plots from each study site, we calculated point density for every 1 m in height from 1–35 m, for the 95th percentile of height and calculated canopy cover for each plot.

Individual den and neighbour trees

We identified den trees in the point cloud of each study site using the GPS locations recorded during radiotracking. Once the den tree was confidently identified, three neighbouring trees were marked. We selected the largest neighbouring trees as they were more likely to be hollow-bearing and therefore more informative for comparison against den trees. We intersected the merged LiDAR points clouds with the den and neighbour tree location data and clipped a 20 m-diameter plot at the location of each den and neighbouring tree. In LAStools, we classified the ground returns and normalised the point clouds to elevation above ground level. We then manually cropped each den and neighbouring tree from the point cloud plots using Quick Terrain Modeler (Applied Imagery, 2017) (Fig. 5.2e, 5.2f).

To compare the canopy height structure of the cropped den and neighbouring tree point clouds, we calculated point density for every 1 m in height from 1–35 m using LAStools. To model den-tree selection by *P. ariel*, we generated a range of LiDAR-derived measures of tree structure using the free online software SAGA GIS (Conrad *et al.*, 2015), 3D Forest (Trochta *et al.*, 2017) and CloudCompare (GPL software, 2018) (Table 5.2). We did this for 25 den trees and 67 neighbouring trees at the high rainfall site, and 25 den trees and 50 neighbouring trees at the low rainfall site. Unfortunately, some of the den trees identified during radio-tracking could not be characterised using LiDAR as they either fell outside of the scanned area or the point clouds of the individual trees were not of high enough quality (due to occlusion artefacts) to generate reliable metrics.

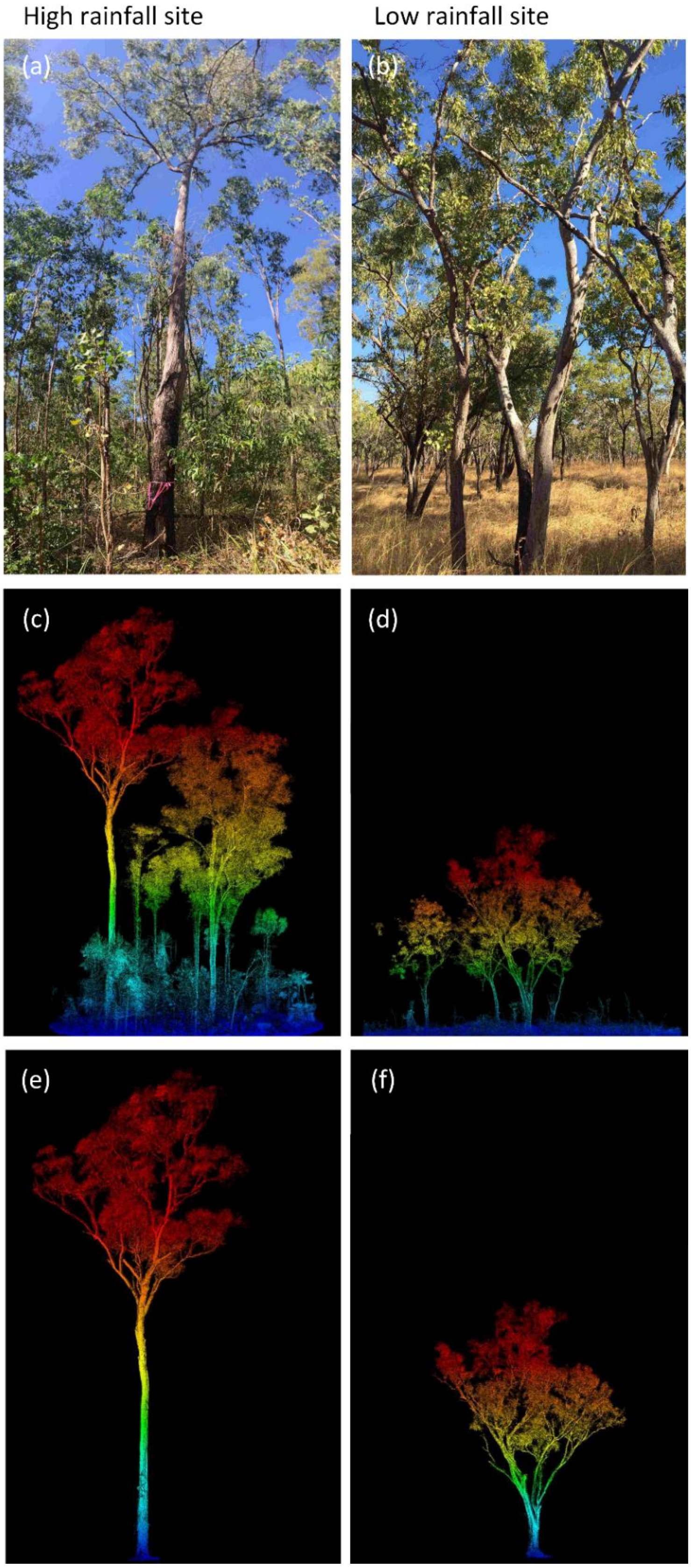

Figure 5.2: Comparison of vegetation structure at the high (a, c and e) and low (b, d and f) rainfall sites, including examples of terrestrial LiDAR scans from each site (c, d) and den trees clipped from LiDAR point clouds (e, f). Note that the trees visible in (a) and (b) differ markedly in height: ≤29.8 m in (a) and ≤14.4 m in (b).

Table 5.2: Terrestrial LiDAR-derived measures of tree structure generated from point clouds of den and neighbouring trees, used for modelling fine-scale den selection by *Petaurus ariel* at the high and low rainfall study sites in northern Australia. All measures were generated using free online software, including SAGA GIS (Conrad *et al.*, 2015), 3D Forest (Trochta *et al.*, 2017) and CloudCompare (GPL software, 2018).

Predictor variable	Description and source
Tree height (m)	3D Forest metric: height of entire tree
Canopy height (m)	3D Forest metric: measure of crown from crown base to top of crown
Canopy surface area (concave hull) (m^2)	3D Forest metric: surface area of 3D concave hull of the crown
Canopy surface area (convex hull) (m^2)	3D Forest metric: surface area of 3D convex hull of the crown
Canopy volume (concave hull) (m^3)	3D Forest metric: volume of 3D concave hull of the crown
Canopy volume (convex hull) (m^3)	3D Forest metric: volume of 3D convex hull of the crown
Diameter at breast height (cm)	Manually generated with Cloud Compare: Diameter of tree at 1.3 m using 'point picking' tool
Canopy area (m^2)	SAGA polygon metric: area of polygon encompassing crown from birds-eye-view
Maximum canopy distance (m)	SAGA polygon metric: maximum distance across polygon encompassing crown from birds-eye-view
Canopy perimeter (m)	SAGA polygon metric: perimeter of polygon encompassing crown from birds-eye-view
Canopy perimeter / area	SAGA polygon metric: perimeter of polygon encompassing crown from birds-eye-view, divided by area of polygon
Canopy shape	SAGA polygon metric: shape index of polygon encompassing crown from birds-eye-view; lower values indicate a more circular shape

Data analysis

All analyses were conducted in R (R Development Core Team, 2017). We used a Kruskal-Wallis test (Breslow, 1970) to determine differences in canopy structure (canopy height and canopy cover) between areas of high and low rainfall, using LiDAR-derived metrics from the randomly generated survey plots.

We also used a Kruskal-Wallis test to determine if tree attributes (DBH, maximum canopy diameter and tree height) varied between areas of high and low rainfall. For this we used LiDAR-derived measures of tree structure generated from den and neighbour trees at each site. Using an ordinary least-squares linear model, we modelled the relationship between tree height and canopy diameter against DBH at both the high and low rainfall study sites. We used Akaike's Information Criterion (AIC) to rank the models, balancing both model fit and model simplicity (Burnham & Anderson, 2003). The model with the lowest AIC score by ≥2 AIC units was deemed the top model for predicting tree structure between the two study sites.

We used Pearson's chi-squared test (Garson & Moser, 1995) to determine if *P. ariel* preferentially selected particular tree species for denning relative to what was available in the area. Within each site, we calculated 'expected' tree species richness from the field-based habitat surveys and compared that against the 'observed' species richness of den trees. For both study sites, we created a separate dataset combining the field-based habitat surveys with den tree measurements (as both datasets identified tree species and hollow abundance). With this, we modelled mean hollow abundance for each den tree species using a generalised linear model (GLM) from the 'MASS' package in R. We selected a Poisson distribution, unless the data were over-dispersed, in which case we used a negative-binomial GLM. We again used AIC to rank models (Burnham & Anderson, 2003). The model with the lowest AIC score by ≥2 AIC units was deemed the top model for predicting hollow abundance.

To model den-tree selection by *P. ariel*, we used a GLM with a binomial distribution. Each model had a binary response of 'den' (1) or 'neighbour' (0). We analysed the dataset from each site separately and then compared model rankings between sites. We used LiDAR-derived measures of tree structure as predictors of den-tree selection. As many predictor variables within each site were strongly correlated ($r > 0.7$), we included each predictor variable in separate univariate models. Prior to analyses, predictor variables were centred and standardised. We used AIC to rank the models. The model with the lowest AIC by ≥2 AIC units was deemed the top model of fine-scale den-tree selection by *P. ariel*.

Results

To assess the accuracy of LiDAR-derived estimates of DBH, we compared them with those collected using field-based measurement of den trees. We found a strong correlation between the values recorded from each method ($R^2 = 0.87$). The slope of the regression of LiDAR-derived DBH against field-derived DBH was very close to 1 (with 95% confidence intervals overlapping 1), and the intercept was very close to 0 (with 95% confidence intervals overlapping 0) (Fig. 5.3). We therefore report only LiDAR-derived values of DBH for both den and neighbour trees here.

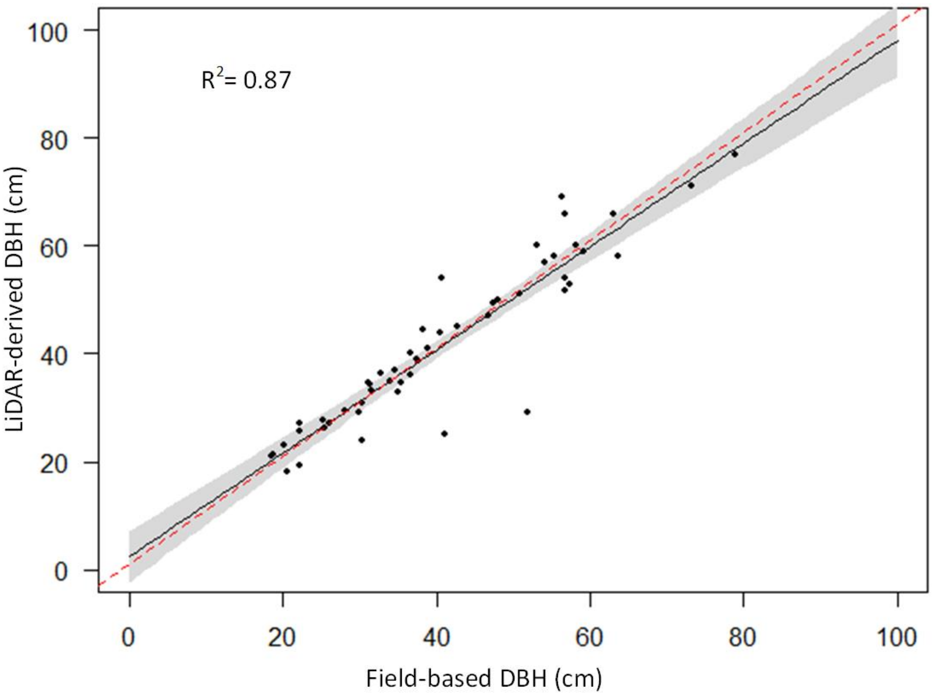

Figure 5.3: Comparison of field-based measures and LiDAR-derived values of diameter at breast height (DBH; cm) collected from den trees across both study sites.Regression line is shown in black, 1:1 line is indicated with a dashed red line shows the accuracy of the regression and grey band represents 95% confidence intervals.

Study site habitat structure

From field-based habitat surveys within the high and low rainfall study sites we recorded similar richness in tree species at both sites, but substantially greater tree abundance (count of trees with DBH ≥5 cm) at the high rainfall site (Table 5.1). Within the 12 surveyed quadrats at the high rainfall site we recorded eight different tree species from a total of 106 trees and at the low rainfall site we recorded ten different tree species from 56 trees. Only three tree species occurred at both sites (*Eucalyptus miniata*, *Erythrophleum chlorostachys* and *T. ferdinandiana*). Eucalypts dominated the high rainfall site (75.5% of trees) but not the low rainfall site (39.9% of trees). At the low rainfall site, *Er. chlorostachys* was the single most abundant species (35.7% of trees; *cf.* 7.6% of trees at the high rainfall site).

Analyses of LiDAR-derived metrics from randomly generated survey plots showed a significantly taller canopy layer and greater canopy cover at the high rainfall site, compared to the low rainfall site (Table 5.3; Fig. 5.4). Trees were substantially larger at the high rainfall site than the low rainfall site (Fig. 5.4). LiDAR-derived measures of DBH, maximum canopy diameter and tree height were all significantly greater at the high rainfall site than the low rainfall site (Table 5.3). There was also greater variability in tree size (DBH, maximum canopy diameter and height) at the high rainfall site than the low rainfall site (Table 5.3; Fig. 5.6). We found trees of a given DBH were substantially taller at the high rainfall site but did not have larger canopies, relative to trees at the low rainfall site (Table 5.4; Fig. 5.5).

Table 5.3: Comparison of the height of the canopy layer and percent of canopy cover taken from randomly generated survey plots at the high and low rainfall site; and tree size (including canopy size) of cropped den and neighbour trees (combined) at the high and low rainfall site. We tested for significant variation between the two sites using a Kruskal-Wallis test and report values here; H is the Kruskal-Wallis statistic and d.f. is degrees of freedom.

	High rainfall study site	Low rainfall study site	Kruskal-Wallis test for significance
Randomly generated survey plots			
Canopy height (m) (Mean; 95% CI)	21.8 (21.2–22.5)	10.4 (10.0–10.7)	H= 126.3, d.f.= 1, p <0.01
Range	16.3–29.8	5.8–14.4	
Canopy cover (%) (Mean; 95% CI)	85.0 (81.4–88.6)	37.3 (33.9–40.6)	H= 109.0, d.f.= 1, p <0.01
Range	24.4–100	3.4–73.3	
Tree size (den and neighbour trees combined)			
DBH (cm) (Mean; 95% CI)	39.1 (35.9–42.3)	27.9 (26.2–29.6)	H= 22.0, d.f.= 1, $p <0.01$
Range	11.0–78.5	13.0–49.5	
Maximum canopy diameter (m) (Mean; 95% CI)	11.3 (10.6–12.0)	9.2 (8.6–9.9)	H= 16.3, d.f.= 1, $p <0.01$
Range	3.4–20.3	4.7–17.8	
Tree height (m) (Mean; 95% CI)	21.1 (20.1–22.0)	11.0 (10.5–11.4)	H= 108.0, d.f.= 1, p <0.01
Range	9.6–30.9	7.2–15.9	

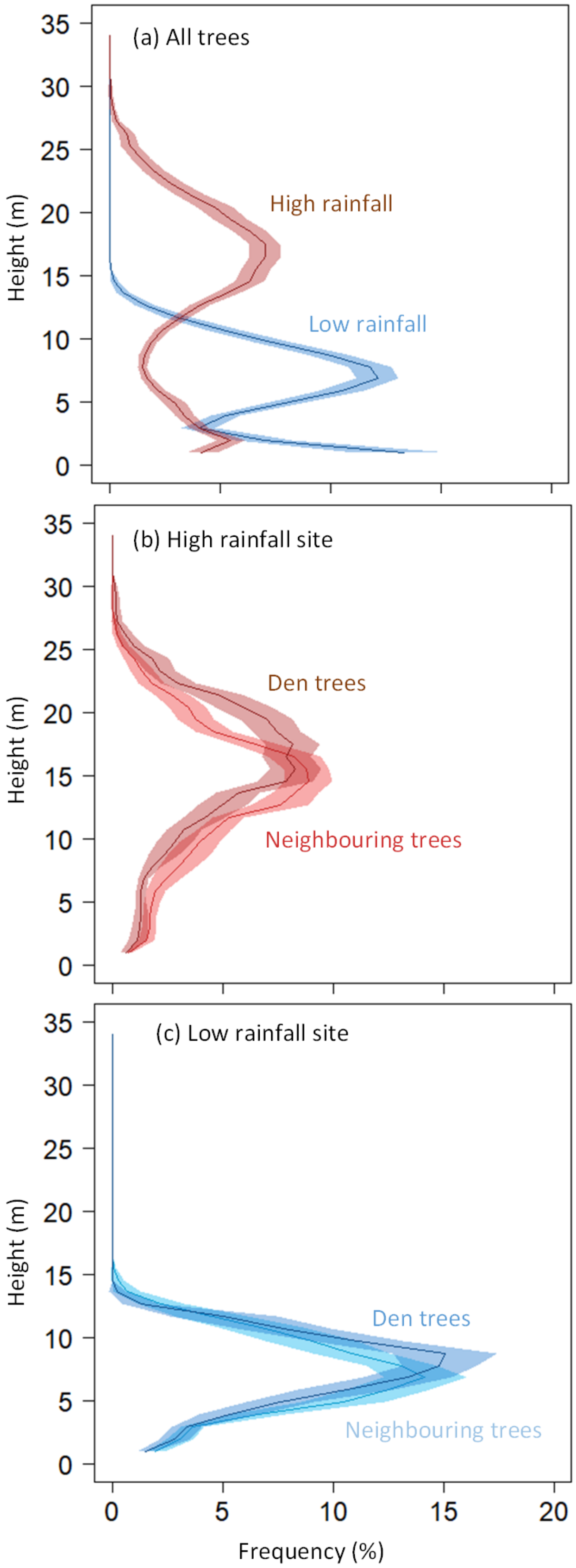

Figure 5.4: Height density plot curves for (a) all trees from randomly generated survey plots at high (dark red) and low (dark blue) rainfall sites, den (darker shade) and neighbour (lighter shade) trees from the (b) high and (c) low rainfall sites, generated from terrestrial LiDAR data. Solid lines indicate mean values and coloured bands represent 95% confidence intervals.

Table 5.4: Model selection results for ordinary least-squares linear models of tree height and maximum canopy diameter, as a function of diameter at breast height (DBH) and site. Data were derived from the combined dataset of den and neighbouring trees at each site. w_i is the Akaike weight; ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion) value and that of the top-ranking model. The grey highlighted model is the null model and bold text indicates the most supported models (ΔAIC ≤2).

Response variable	Model	ΔAIC	w_i
Tree height	**DBH * Site**	**0.0**	**0.84**
Tree height	DBH + Site	3.3	0.16
Tree height	Site	126.8	0.00
Tree height	DBH	188.5	0.00
Tree height	Null	305.5	0.00
Maximum canopy diameter	**DBH**	**0.0**	**0.61**
Maximum canopy diameter	**DBH + Site**	**1.6**	**0.28**
Maximum canopy diameter	DBH * Site	3.5	0.11
Maximum canopy diameter	Site	92.8	0.00
Maximum canopy diameter	Null	107.9	0.00

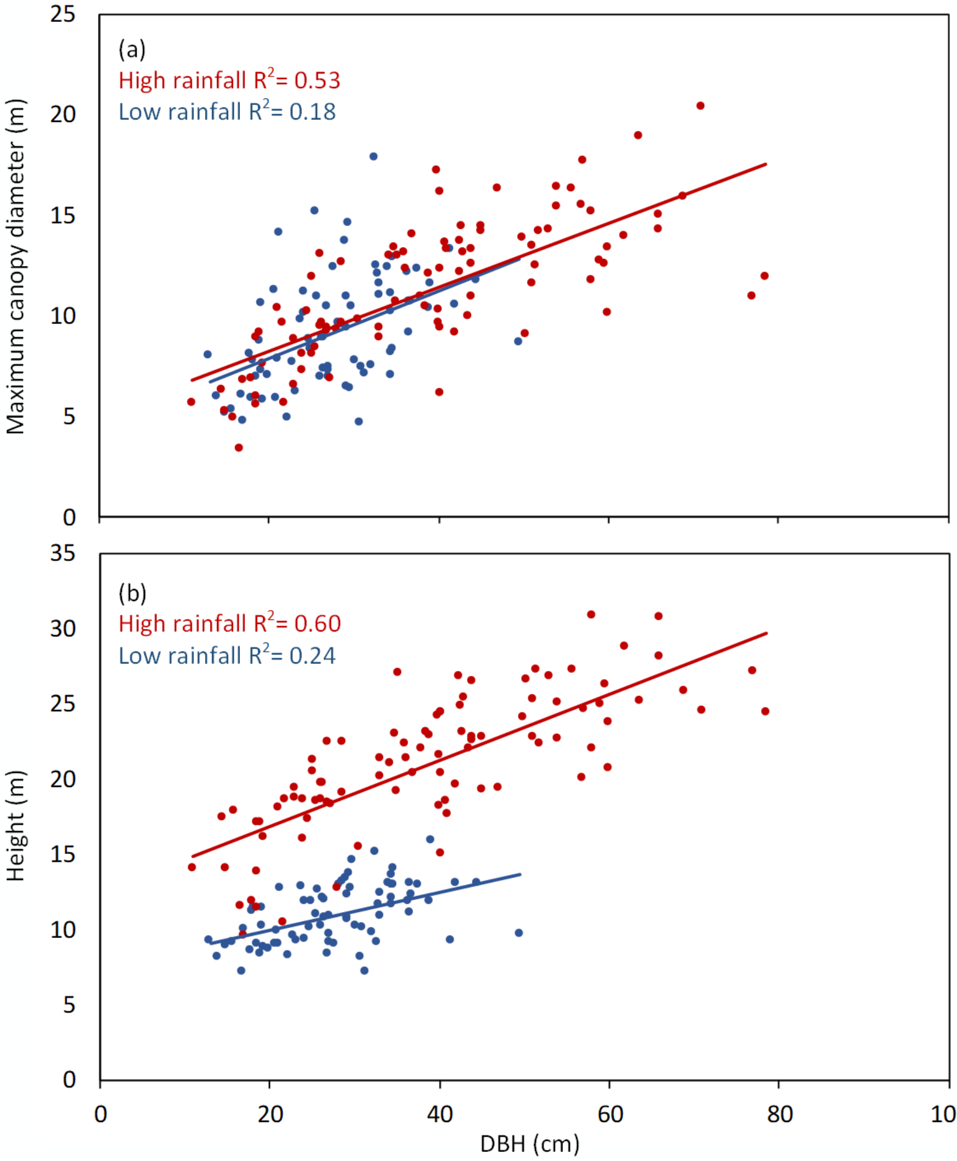

Figure 5.3: Relationships between diameter at breast height (DBH) and: (a) maximum canopy diameter; and (b) tree height, sites based on terrestrial LiDAR-derived measures of tree structure. High rainfall (dark red) and low rainfall (dark blue) sites are shown separately.

Den selection by *P. ariel*

At both study sites, only eucalypt species and *Er. chlorostachys* were used as den-trees by *P. ariel*. At the low rainfall site, the number of tree species used as den trees was significantly less than what was available in the area (p <0.01). Relative to availability, *P. ariel* selected more *Eu. tectifica* (p <0.01), and fewer *Er. chlorostachys* (p <0.05) and dead trees (p <0.05) as den trees. In contrast, at the high rainfall site there was no significant difference in the number of tree species used as den trees and the number of tree species at the site (p >0.05). Based on generalised linear models, hollow abundance varied significantly between tree species at the low rainfall site (tree species model >2 AIC units lower than null model), but not the high rainfall site (null model >2 AIC units lower than tree species model). At the low rainfall site, *Eu. tectifica* had the highest number of hollows per individual tree (mean: 1.5; 95% CI: 1.0–2.0). The mean number of hollows per individual tree for all other tree species combined was 0.7 hollows per tree (95% CI: 0.4–0.9).

Using LiDAR-derived measures of tree size to compare den and neighbouring trees, we only found evidence for den-tree selection by *P. ariel* at the high rainfall site. At that site, all models that included measures of tree size except 'canopy perimeter/area' were better than the null model (≥2AIC units) (Table 5.5; see Supplementary information for full model selection results). At the low rainfall site, there was no evidence of den-tree selection for tree size by *P. ariel*.

At the high rainfall site, DBH was the clearest predictor of den-tree selection by *P. ariel*. Den trees at the high rainfall site had a mean DBH of 53.4 cm (95% CI: 49.6–56.8; minimum DBH 33.0 cm), while neighbouring trees had a much smaller mean DBH of 33.8 cm (95% CI: 30.0–37.6; minimum DBH 11.0 cm). Den trees at the low rainfall site had a mean DBH of 29.9 cm (95% CI: 26.9–32.8; minimum DBH 18.3 cm). Overall, the mean DBH of a den tree used by *P. ariel* at both study sites was 41.7 cm (95% CI: 37.4–45.9).

Table 5.5: Model selection results for the best three generalised linear models to assess den selection by *Petaurus ariel* at the high and low rainfall study sites. w_i is the Akaike weight; ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion) value and that of the top-ranking model. The grey highlighted model is the null model and bold text indicates the most supported model (ΔAIC ≤2).

Model	ΔAIC	w_i
High rainfall site		
Diameter at breast height	**0.0**	**1.0**
Maximum canopy diameter	12.2	0.0
Canopy height	12.3	0.0
Low rainfall site		
Diameter at breast height	0.0	0.2
Null	0.6	0.1
Canopy height	1.4	0.1

All other measures of tree size at the high rainfall site were greater for den trees than neighbouring trees, including both maximum canopy diameter and tree height. The mean value of maximum canopy diameter for den trees at the high rainfall site was 14.0 m (95% CI: 13.1–15.0) *vs.* 10.4 m (95% CI: 9.5–11.3) for neighbouring trees. Mean tree height of den trees was 24.8 m (95% CI: 23.5–26.1) *vs.* 20.1 m (95% CI: 18.9–21.4) for neighbouring trees. In summary, we found substantial variation in tree size between den and neighbouring trees at the high rainfall site, but very little difference at the low rainfall site (Fig. 5.6).

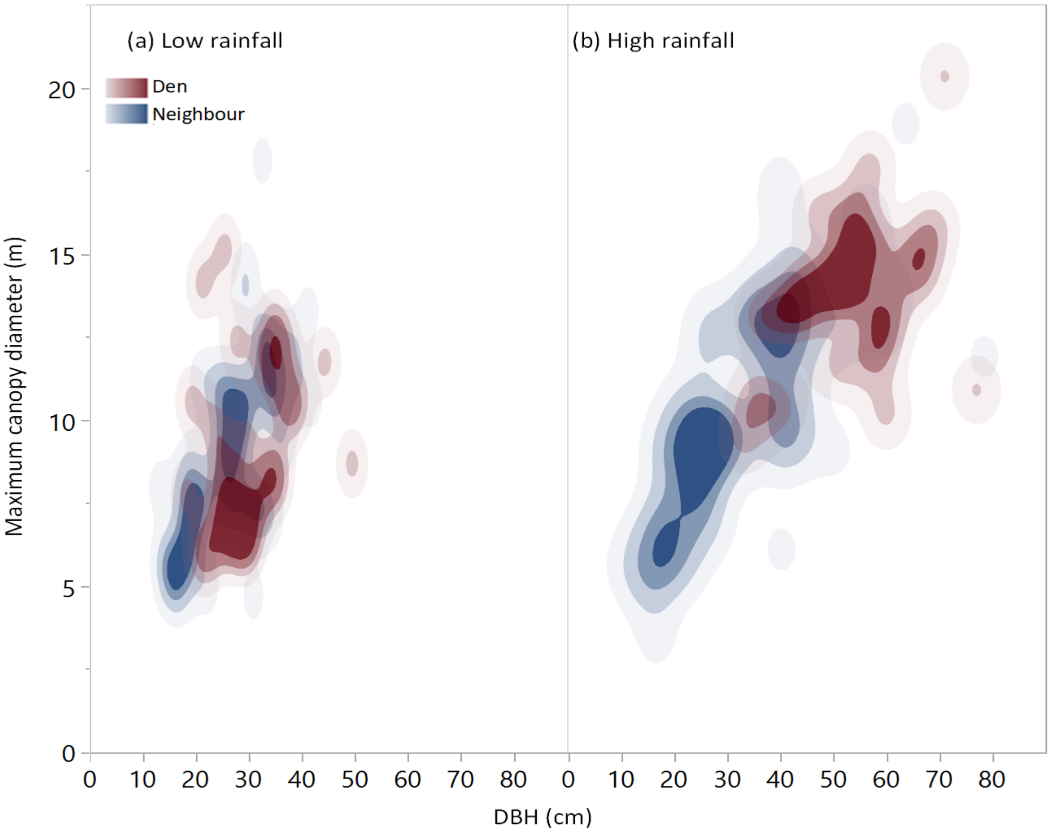

Figure 5.4: Density map of diameter at breast height (DBH) and maximum canopy distance values based on terrestrial LiDAR-derived measures of tree structure from the (a) low and (b) high rainfall study sites, for den (red) and neighbour (blue) trees . Darker shades indicate higher density of values.

Discussion

Here, we uniquely used both field-based surveys and terrestrial LiDAR scanning technology to quantify habitat structure and characterise den-tree selection by an arboreal marsupial, *P. ariel,* in areas of high and low rainfall within northern Australia. The high rainfall site had greater tree abundance, canopy cover and variation in tree size (DBH, height and canopy diameter), relative to the low rainfall site. Den-tree use by *P. ariel* varied significantly between the two study sites. At the high rainfall site, *P. ariel* used den trees with a larger DBH and canopy size than neighbouring trees, presumably because these trees are more likely to contain hollows (Woolley *et al.*, 2018). However, at the low rainfall site, there was no obvious preference for specific tree size (e.g. DBH, canopy size). Rather *P. ariel* selected tree species that were more likely to be hollow-bearing. Our study highlights that large eucalypts – which tend to have abundant hollows –are important resources for hollow-dwelling arboreal mammals in the tropical savannas of northern Australia. This is especially true in areas of lower rainfall where hollow availability is more likely to be limiting because of the smaller proportion of large trees and relatively low tree abundance.

Large hollow-bearing eucalypts are likely to be decreasing in abundance from elevated frequency of high-intensity fires in the region, relative to the historical baseline (Russell-Smith *et al.*, 2007). It was outside the scope of this work to model drivers of hollow availability in the tropical savannas, instead we draw upon existing knowledge to understand variation in hollow availability between our study sites. Previous studies in northern Australia have found old eucalypts are particularly vulnerable to high-intensity fires (Williams *et al.*, 1999), leading to low hollow availability in areas characterised by frequent high-intensity fires (Woolley *et al.*, 2018). The impact of high-intensity fires on older eucalypts is also possibly more pronounced in areas of low rainfall where trees are typically shorter and water-stressed and therefore more likely to be killed and consumed by fire (Midgley *et al.*, 2010; Russell-Smith *et al.*, 2010; Cook *et al.*, 2015). This interaction between altered fire regimes and habitat structure in the tropical savannas may have caused a greater decline in hollow availability in areas of low rainfall. Furthermore, as tree abundance, and consequently hollow abundance, declines with rainfall (Woolley *et al.*, 2018), the loss of older, hollow-bearing eucalypts may be more ecologically significant in areas of low rainfall.

Although tree hollows may be a limiting resource in northern Australian savannas, a decline in tree hollow availability is unlikely to fully explain the disproportionate decline of arboreal mammals throughout the region. When comparing the severity of decline between arboreal mammals in northern Australia, both the brush-tailed rabbit-rat (*Conilurus penicillatus*) and black-footed tree-rat (*Mesembriomys gouldii*) (Firth *et al.*, 2010; Woinarski *et al.*, 2010; Davies *et al.*, 2018) have experienced more marked declines than *P. ariel* (Chapter Two). However, we found that at the high rainfall site, *P. ariel* used den trees that were similar in size to that used by *C. penicillatus* and *M. gouldii* (also at high-rainfall sites). Mean DBH for den trees used by *P. ariel* was 41.7 cm, ranging from 18.3–77 cm, while mean DBH for den trees used by *M. gouldii* was 36 cm (range 12–63 cm; Griffiths *et al.* 2001) and 30.5 cm for *C. penicillatus* (range not specified; Firth *et al.* 2006). All three arboreal mammal species also favoured eucalypts as den trees, presumably because of the high abundance of eucalypts regionally, and their propensity to form hollows. Thus, there is no evidence to suggest that *C. penicillatus* and *M. gouldii* require markedly larger den trees than *P. ariel*. Consequently, tree hollow availability alone unlikely explains why *P. ariel* has persisted in relatively low rainfall areas where other hollow-dwelling arboreal mammals have disappeared. However, the use of dens on the ground (such as fallen logs; Griffiths *et al.* 2001 and Firth *et al.* 2006) and the associated terrestrial behaviour of *C. penicillatus* and *M. gouldii* may have made these species more exposed and vulnerable to predation by the introduced feral cat, compared to *P. ariel* which is dependent on tree hollows and almost strictly arboreal.

Petaurus ariel is unique amongst northern Australian mammals in its ability to glide between trees, and spends very little time on the ground compared to other arboreal mammals. As *P. ariel* is also an obligate hollow-dweller, the species may be more protected from ground-based predation relative to arboreal mammals that sometimes den in fallen logs. In this study, we found canopy structure in areas of low rainfall to be relatively disconnected and significantly lower compared to areas of high rainfall. Arboreal mammals may therefore be more susceptible to ground-based predation in areas of low rainfall, as they are forced to forage and den closer to the ground (in shorter trees) and spend more time on the ground moving between trees. In a related study from the same region (Chapter Two), a range contraction of the common brushtail possum (*Trichosurus vulpecula*) was found to be more pronounced in areas of low shrub density. This was attributed to greater susceptibility of *T. vulpecula* to predation by feral cats in open areas where shrub density was low. Predation pressure by the feral cat on *C. penicillatus* was also found to be greater in areas of low shrub density (Davies *et al.*, 2017b). Variation in terrestrial behaviour between northern Australia's arboreal mammals may therefore explain why some species have declined more severely than others. Unfortunately, recent studies have highlighted that *P. ariel* is also susceptible to predation by ground-based predators, including the feral cat and dingo (*Canis lupus*) (Stokeld *et al.*, 2018). This may provide some explanation as to why they too appear to be declining in areas of low rainfall, albeit less markedly than some other species.

To accurately capture variation in habitat structure in the tropical savannas of northern Australia, our study uniquely complemented conventional field-based habitat surveys with terrestrial LiDAR scanning. By using terrestrial LiDAR scanning, we could quickly capture various structural attributes of the canopy that would have otherwise been too laborious, such as maximum canopy diameter, canopy height and canopy surface area. However, DBH was still the single best predictor of den-tree selection by *P. ariel*. This is consistent with previous studies on den-tree selection by arboreal mammals (Meyer *et al.*, 2005; Goldingay, 2011; Lindenmayer *et al.*, 2017). Incorporating LiDAR in this study allowed us to model (and subsequently eliminate) canopy structural elements previously poorly represented in den-tree selection studies. However, essential features such as tree species and hollow counts could not be confidently identified from our LiDAR analyses, so field-based habitat surveys were still necessary. Further investigation of the relationship between DBH, canopy size and hollow abundance might provide future pathways for large-scale mapping of den availability using terrestrial or air-borne LiDAR. Indeed, LiDAR has already been found to be a promising tool for modelling pathways of movement by arboreal mammals (Blakey *et al.*, 2017; Davies *et al.*, 2017a; Davies *et al.*, 2019). Another unique advantage of terrestrial LiDAR in future studies of den-tree selection will be to monitor and quantify den tree attrition over time, and in response to individual or repeated disturbances, such as high-intensity fire. Our current poor understanding of drivers of den tree attrition severely limits our ability to predict future hollow availability for arboreal mammals (Goldingay, 2011).

Significant variation in the habitat structure of high and low rainfall areas within the tropical savanna of northern Australia has a substantial influence on den-tree selection by the arboreal marsupial, *P. ariel*. At our high-rainfall study site, *P. ariel* had access to a greater number of trees and a more diverse range of tree sizes than at our low-rainfall site. At both sites, *P. ariel* used den trees that were more likely to be hollow-bearing by selecting either larger trees or specific tree species. Due to logistical constraints, this study identified den-tree selection by *P. ariel* from two sites at either extent of the species geographic range. Our study would have been strengthened by monitoring *P. ariel* den-tree selection at a greater number of sites throughout the species geographic range. This would have provided valuable insight on the point at which hollow availability becomes a limiting resource for *P. ariel* and could be explored further in future research.

Due to a decline in hollow-bearing trees with altered fire regimes, hollow availability is likely to be a limiting resource for arboreal mammals in northern Australia, emphasising the importance of retaining large eucalypts that are hollow-bearing. Regardless, similarity of den-trees used by *P. ariel* and other arboreal mammals that have suffered severe decline in northern Australia suggests reduction in hollow availability cannot fully explain the disproportionate decline of arboreal mammals in northern Australia's tropical savannas. Instead, it is possible that there is an increased susceptibility of arboreal mammals to ground-based predation in areas of low rainfall, because of the more open and simplified habitat structure and the expected increase in time spent on or near the ground. The higher degree of arboreality of *P. ariel* may have (somewhat) reduced this species susceptibility to ground-based predation relative to other arboreal mammals.

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Supplementary information

Table S5.1: Full model selection results for generalised linear models to assess den selection by *Petaurus ariel* at the high and low rainfall study sites. *K* indicates the number of parameters; w_i is the Akaike weight; ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion) value and that of the top-ranking model. The grey highlighted models are the Null models and bold text indicates the best-supported model (ΔAIC ≤2).

Model	ΔAIC	w_i
High rainfall site		
Diameter at breast height	**0.0**	**1.0**
Maximum canopy diameter	12.2	0.0
Canopy height	12.3	0.0
Canopy perimeter	15.2	0.0
Canopy width	16.7	0.0
Canopy volume (convex hull)	17.0	0.0
Canopy shape	17.0	0.0
Canopy area (concave hull)	17.6	0.0
Canopy area (convex hull)	19.2	0.0
Tree height	19.6	0.0
Canopy volume (concave hull)	19.7	0.0
Canopy area	21.9	0.0
Null	29.5	0.0
Canopy perimeter/area	30.0	0.0
Low rainfall site		
Diameter at breast height	0.0	0.2
Null	0.6	0.1
Canopy height	1.4	0.1
Tree height	1.6	0.1
Canopy volume (concave hull)	2.2	0.1
Canopy area (convex hull)	2.3	0.1
Canopy volume (convex hull)	2.4	0.1
Canopy area (concave hull)	2.5	0.1
Maximum canopy diameter	2.5	0.1
Canopy perimeter	2.5	0.1
Canopy width	2.6	0.0
Canopy shape	2.6	0.0
Canopy perimeter/area	2.6	0.0
Canopy area	2.6	0.0

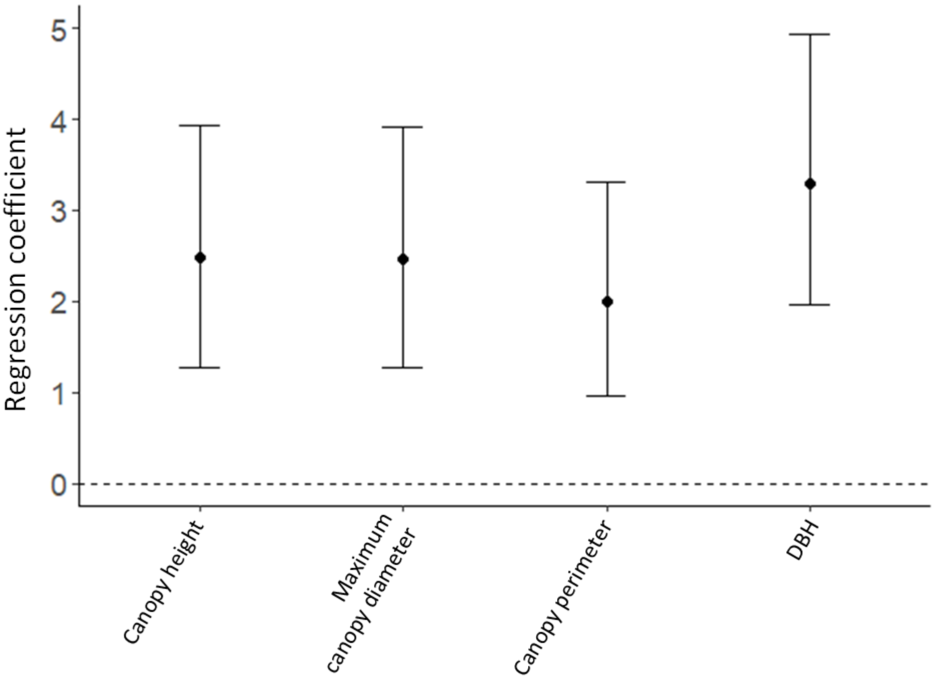


Figure S5.1: Estimated regression coefficients for the top four predictor variables for den trees used by *Petaurus ariel* in the high rainfall study site, derived from generalised linear models (Table 5.4). Error bars indicate 95% confidence intervals. Coefficients further from zero (dashed line) had greater influence on den selection.

Chapter 6 :

General Discussion

Chapter Six cover page is a sunset over Nitmiluk National Park field site

Discussion

Declines in biodiversity can result in the loss of ecosystem function and associated ecosystem services (Ostfeld & LoGiudice, 2003; Sweeney *et al.*, 2004; Potts *et al.*, 2010). Without an adequate knowledge of biodiversity patterns and processes conservationists are limited in their ability to prevent biodiversity declines. The severity of widespread declines of small mammals in the tropical savannas of northern Australia is of global concern (Woinarski *et al.*, 2011; Woinarski *et al.*, 2015; Davies *et al.*, 2018). These declines have been variously and inconclusively attributed to either disruption of available resources through altered fire regimes (Pardon *et al.*, 2003; Firth *et al.*, 2010; Lawes *et al.*, 2015a) or increased predation pressure by the feral cat (Frank *et al.*, 2014; Leahy *et al.*, 2016; Davies *et al.*, 2017b). However, there has been little synthesis of research to explain two significant patterns of decline: firstly, that there has been a disproportionate decline of arboreal mammals in northern Australia, relative to ground-dwelling species (Fitzsimons *et al.*, 2010); and secondly, that declines have first occurred in the southern, drier parts of the tropical savannas (Firth *et al.*, 2010; Start *et al.*, 2012; Ziembicki *et al.*, 2013b). Our poor understanding of the underlying drivers of these patterns of mammal decline has hampered our ability to mitigate further declines in northern Australia; addressing these knowledge gaps has been a core aim of my thesis. My research was conducted at a range of different spatial scales (from individual trees to macroclimatic gradients across a whole region), to provide fundamental knowledge of the ecology of an arboreal marsupial, the savanna glider (*Petaurus ariel*). This taxon has only recently been elevated to the species level, from *P. breviceps ariel* (T. Cremona and S. Carthew, unpublished data), and is one of the savanna mammals we know least about.

In this thesis, I have investigated the abundance and distribution of *P. ariel* in the tropical savannas of northern Australia (Chapter Two), and described key aspects of the species' ecology including body size (Chapter Three and Chapter Four), density (Chapter Four), home range (Chapter Four), foraging behaviour (Chapter Four) and den choice (Chapter Five) (summarised in Box 6.1). I found significant variation in *P. ariel* body mass, abundance, foraging behaviour and movement ecology over the tropical savannas of northern Australia, which was primarily attributed to variation in temperature, resource availability and habitat structure over the region's environmental gradient. This study has provided information essential for future conservation of *P. ariel*, but also addresses some of the fundamental gaps in our knowledge of arboreal mammals in the tropical savannas. More broadly this research has highlighted how gliding as a form of locomotion may have slowed the rate of decline of *P. ariel*. This is through the combined benefit of predator avoidance and better access to resources, relative to less arboreal species such as the common brushtail possum (*Trichosurus vulpecula*) (Chapter Two). Below, I summarise the key findings of this research, discuss how this work improves our capacity to respond to arboreal mammal decline in northern Australia and suggest future research directions.

The distribution, abundance and ecology of *Petaurus ariel*

Despite no targeted studies on *P. ariel* and a disproportionate decline of arboreal mammals in northern Australia, this species is generally not considered to be in decline (Woinarski *et al.*, 2014). However, in Chapter Two, I presented concerning evidence of decline in the southern end of the species' historical range. I found that *P. ariel* still occurs in areas where other arboreal mammals have been lost, and the extent of the decline of *P. ariel* was less substantial than that of *T. vulpecula*, another wide-spread arboreal mammal which has been previously identified as declining in northern Australia (Woinarski *et al.*, 2010; Ziembicki *et al.*, 2013b). There was a noticeable pattern of decline in the southern extent of each species' geographic range, which corresponds to previously established patterns of small mammal decline, i.e. greatest decline in more arid areas (McKenzie *et al.*, 2007). Both species were also found to be more abundant in areas of higher rainfall and canopy cover. However, *T. vulpecula* was also more abundant in areas of greater shrub density. The potential divergence in resource use between *P. ariel* and *T. vulpecula*, namely the increased abundance of *T. vulpecula* in areas of high shrub density, may explain at least in part, the variation in the severity of decline between the two species.

In Chapters Three to Five, I sought to understand how the pervasive environmental gradients in the tropical savannas of northern Australia influence the ecology of *P. ariel*. It was immediately apparent when inspecting morphological measurements of *P. ariel* that the species' body mass changed substantially with latitude, being significantly larger at the southern end of its range. Since body size is closely linked to a species' ecology (through life history, behaviour and physiology) and subsequently its conservation requirements (through density and extinction risk) (Lindstedt & Calder, 1976; Johnson, 1999; Cardillo *et al.*, 2005; McCain & King, 2014; Tucker *et al.*, 2014), I sought to determine the underlying drivers of this variation in body size. Specifically, I sought to determine if geographic variation in *P. ariel* body size corresponded to patterns in resource availability throughout the tropical savannas, or whether it was in response to other underlying climatic drivers. I found that ambient temperature, due to its influence on an animal's need to thermoregulate, was the most likely driver of geographic variation in body size for this species (along with three other Petaurid gliders and *T. vulpecula*), with body size increasing with decreasing winter minimum temperature. Notably, my research identified that geographic variation in *P. ariel* body size was unlikely to be driven primarily by a gradient in resource availability throughout the tropical savannas of northern Australia.

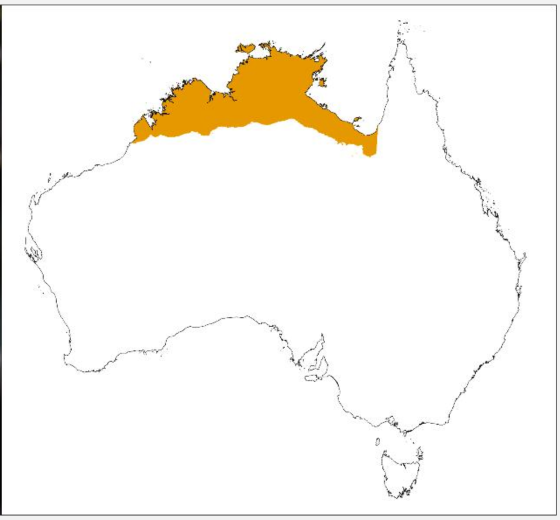
Chapter Four and Chapter Five further highlight significant differences in the ecology of *P. ariel* between areas of high and low rainfall; in this case due to variation in resource availability and fine-scale habitat structure. Of note in Chapter Four is the disproportionately large home range of *P. ariel* relative to body size. This research showed that not only is *P. ariel* home range substantially larger than any other similar sized Petaurid glider, but their home range is in the top 2.5% of terrestrial, omnivorous mammals globally, relative to body size. In the discussion of this chapter I suggest the large variation in *P. ariel* home range size may provide some insight as to why productivity is not a driver of *P. ariel* body size. If home range size can facilitate an individual/species to cope with variation in resource availability, it could potentially eliminate any subsequent selective pressure for variation in body size. This is an unexpected and exciting finding that could provide valuable insight into the multiple interacting ways in which species are able to respond to their external environment. Furthermore, in Chapter Five I showed that den-tree selection by *P. ariel* varied with fine-scale habitat structure, notably due to the substantial difference in habitat complexity, including variation in tree abundance, canopy cover and the height of the canopy layer. Additionally, my findings highlight that hollow availability is likely a limiting resource in northern Australia, especially in areas of low rainfall. Collectively, these findings suggest that the flexible ecology of *P. ariel* has enabled the species to adapt to variable resource availability. This includes relatively lower productivity and a more simplified habitat structure throughout the species geographic range relative to other Australian Petaurids, and substantially low resource availability at the southern, drier margins of the species distribution.

Box 6.1: General species description of *Petaurus ariel* , following the style of Jackson (2012), using data collected during this research project.

Savanna Glider

Petaurus ariel (flying rope-dancer)

FAMILY: PETAURIDAE



Description: The savanna glider is highly variable in body size and colour throughout its distribution. Its underparts range from pale grey to creamy, with noticeable orange–yellow tinges in populations on Melville Island and apricot tinges in populations on Groote Eylandt. Its face is often a lighter grey with some variation to medium grey. A well-defined black band runs from between its eyes along its back; this becomes more prominent in the species' southern populations. The savanna glider is similar in appearance to a squirrel glider (having a longer, pointed nose) but is considerably smaller in body size, and is instead more similar in size to a sugar glider. The savanna glider's tail is evenly furred along its length, coloured dusky-grey, darkening to black distally; some individuals have a white tail-end. Typically, the savanna glider is shorter furred than other Petaurid gliders with the fur gradually becoming thicker in southern populations.

Box 6.1: Continued.

Distribution: This species occurs in the eucalypt-dominated tropical savannas of northern Australia through Western Australia, the Northern Territory and western Queensland. It is found in a variety of vegetation types including eucalypt open forests and woodlands with either a shrubby or grassy understorey. It is occasionally found in *Melaleuca* forests in riparian areas adjacent to eucalypt woodland.

Reproduction: The timing of breeding for the savanna glider is variable, with pouch young recorded between February and September, peaking between June and September. One or two young are born at a time. There is evidence of sexual dimorphism in areas of high rainfall but no significant difference between sexes in areas of low rainfall. The savanna glider's social structure likely varies from socially monogamous groups to polygynous, but this remains unconfirmed. The savanna glider dens in leaf-lined tree hollows, primarily within live eucalypts, but has been found to occasionally den in live ironwood (*Erythrophleum chlorostachys*) and dead trees.

Diet: The savanna glider feeds on plant exudates, including gum of species of *Eucalyptus*, *Acacia*, *Terminalia* and *Er. chlorostachyum* and nectar and pollen of species of *Eucalyptus*, *Corymbia* and *Banksia*. It has also been recorded feeding on *Sorghum* grass seeds, invertebrates, geckoes and fungi found on kapok bush (*Cochospermum fraseri*).

Ecology: Both population density and home range vary significantly throughout the savanna glider's distribution. Population density estimates range from 1.1 to 0.2 ha^{-1} and home range varies from 1 to 104 ha. The savanna glider has been recorded making a variety of calls including monosyllabic or polysyllabic nasal grunts.

Status: The savanna glider is currently classified as 'Least Concern' throughout its geographic range (under *P. b. ariel*) (Woinarski *et al.*, 2014). However, since 1993 its geographic range has contracted by around a third, with the range contraction concentrated in low-rainfall areas.

Box 6.1: Continued.

Morphology measures:

Head–body length: 120–215 mm

Tail length: 150–270 mm

Hind-foot length: 15–27 mm

Mass: 48–151 g

Subspecies: Further investigation is required to clarify a potential subspecies recorded in the Kimberley region of Western Australia.

Other names: Also known as 'Riinga' and 'Rijingini (male and female glider, respectively; Tiwi language: Tiwi Islands), 'Lambalk' (Dalabon language, Arnhem Land), 'Gardbug' and/or 'Ngalmul' (Wardaman language, Victoria River region) and 'Junggaluda' (Wunambul language: North Kimberley).

Gliding past small mammal decline in northern Australia

In this thesis, I have suggested that the unique ability to glide from tree to tree, with little need to travel on the ground, has enabled *P. ariel* to persist in drier areas of the tropical savannas where other arboreal mammals have been lost. I propose two hypotheses, not mutually exclusive, as to how gliding has better enabled *P. ariel* to survive in the changing environment of northern Australia's tropical savannas. The first hypothesis is that the ability to glide reduces the need for *P. ariel* to come to the ground, relative to other arboreal mammals, reducing the species' exposure to predation by exotic predators such as the feral cat, which primarily hunts on the ground. This hypothesis is supported by findings in both Chapters Two and Five, where I compared habitat use by *P. ariel* with other arboreal mammals that have experienced more significant declines in northern Australia. In Chapter Two, I suggest that the more severe decline of *T. vulpecula* is due to its higher susceptibility to feral cat predation. This is based on the higher abundance of *T. vulpecula* in areas with a shrubby understorey which likely acts as shelter from predation by feral cats. My conclusions here are supported by earlier studies that have shown feral cats preferentially hunting in open landscapes in northern Australia (McGregor *et al.*, 2014; McGregor *et al.*, 2015; Hohnen *et al.*, 2016). Additionally, in Chapter Five I argue that there is no significant difference in the den-trees used by *P. ariel* compared to that of the co-occurring brush-tailed rabbit-rat (*Conilurus penicillatus*) and black-footed tree-rat (*Mesembriomys gouldii*), two native arboreal rodents that have suffered marked declines throughout the region. As den-tree selection cannot explain disparities in decline between these species, I argue that the greater ground activity and use of alternative den resources by *C. penicillatus* and *M. gouldii* compared to that of *P. ariel*, has made these species more exposed to predation by the feral cat.

The second hypothesis is that the lower energetic requirements of gliding (relative to quadrupedal locomotion) (Scheibe *et al.*, 2006) has enabled *P. ariel* to continue to access resources over a larger area where resource availability has declined due to altered fire regimes. This hypothesis is based on findings in Chapter Four, where I showed *P. ariel* has a disproportionately large home range size relative to body size due to regionally low resource availability. Several other gliding mammals have also been shown to exhibit large variability in home range size, especially in areas of low resources (Hanski *et al.*, 2000; Weigl, 2007). Altered fire regimes in northern Australia may have simplified the habitat structure of the tropical savannas, reducing habitat structural complexity and hollow abundance (Williams *et al.*, 1999; Russell-Smith *et al.*, 2003b; Woolley *et al.*, 2018), i.e. availability of food and shelter for arboreal mammals. Thus, it is possible that *P. ariel* might be better able to accommodate changes in resource availability as the species expends less energy and can move faster over greater distances compared to other arboreal mammals.

Testing these hypotheses requires quantitative data on the movement behaviour of arboreal mammals in northern Australia. However, they are consistent with the three main theories proposed to explain the evolution of gliding, i.e. (1) gliding enhances ***predator avoidance***, (2) gliding reduces travel time for ***optimal foraging*** and (3) gliding is energetically less expensive therefore reducing the ***cost of foraging*** (Jackson, 2012). Hence, it seems likely that gliding may have helped slow the rate of decline of *P. ariel*, relative to non-gliding arboreal mammals.

Insights for arboreal mammal decline in northern Australia

Although my thesis primarily describes aspects of the ecology of a little-known species, I have highlighted how the substantial environmental gradient over northern Australia impacts arboreal mammals through variation in resource availability and habitat structure. I have demonstrated that arboreal mammal populations in the southern, drier areas of the tropical savannas may be persisting in somewhat marginal habitat, which unsurprisingly leaves these populations more vulnerable to novel threats. My findings support previous studies that nominate altered fire regimes and feral cat predation as the primary drivers of small mammal decline in northern Australia. However, my thesis adds to the existing body of research by: (1) demonstrating the pattern of decline in northern Australia from south to north is linked to variation in resource availability and habitat structure (Chapter Two, Four and Five), and (2) suggesting the disproportionate decline of arboreal mammals is due to their shared use of the three-dimensional habitat structure in the tropical savannas which provides food, shelter and cover from predation for arboreal mammals (Chapter Two, Four and Five).

In my study, both large eucalypts and shrubs were found to be important resources for arboreal mammals in the tropical savannas (Chapter Two and Five). Therefore, land managers should act to conserve and promote these resources throughout the tropical savannas to prevent further declines of arboreal mammals. Controlling feral cats is also an appealing management recommendation. However, it is likely to be extremely challenging to achieve. Despite on-going research into effective cat-removal methods (Read, 2010; Read *et al.*, 2014), the only examples of where cats have been successfully eradicated are from isolated areas, such as cat-free enclosures and islands (Doherty *et al.*, 2017). Some success has been gained in reducing cat densities through broad-scale poison baiting but there are severe practical and financial constraints to these methods (Read *et al.*, 2014; Doherty *et al.*, 2017). Thus, regional cat control is a limited management solution and cannot offer the swift resolution required to prevent imminent mammal extinctions in northern Australia. As arboreal mammals have fared better in more structurally complex habitats, it may be more feasible for conservation managers to focus on enhancing, or at least maintaining, structural complexity in the tropical savannas. The feasibility of existing methods that provide protection and shelter for animals in urban environments, such as installing next boxes and tree planting, warrants further investigation as a short-term solution to restoring and/or enhancing shelter for arboreal mammals in localised areas.

Additionally, developing the shrub layer and protecting large eucalypts through targeted fire management is a long-term management option for providing greater structural complexity throughout the tropical savannas.

Limitations and future research directions

The outcomes of my research would be strengthened by a better understanding of the proportion of terrestrial versus arboreal behaviour of other arboreal mammals in northern Australia. Furthermore, this research relied on the theoretical impact of fire regimes and predation by feral cats on arboreal mammals. Detailed studies that quantify the rate of predation by feral cats on arboreal mammals and the rate of change in habitat structure that has occurred over the savannas would have strengthened my research.

I found evidence that *P. ariel* may be in decline, at least at the drier, southern end of its range. This finding should prompt increased monitoring of *P. ariel* populations throughout the tropical savannas. Further studies should also seek to detail additional aspects of the species' basic ecology that were not recorded here. For example, it would be useful to obtain a detailed assessment of *P. ariel* diet and the importance of various food items for each population; thus, future studies should aim to address this gap in knowledge. It is also important to determine the social structure of *P. ariel* since social structure can influence local population size and density. My observational data from stag-watching and nocturnal radiotracking suggests that social groups are larger in areas of high rainfall than in areas of low rainfall. However, data obtained here was limited, so more detailed behavioural and genetic studies are required.

Concluding remarks

My primary goal of identifying factors that influence the distribution, abundance and ecology of *P. ariel* was accomplished. I highlighted how a complex interplay between altered fire regimes, feral cat predation and resource availability likely explains the disproportionate decline of arboreal mammals in the southern, drier areas of northern Australia. I suggest arboreal mammals are more vulnerable to decline than ground-dwelling mammal's due to their shared use of the three-dimensional habitat structure, and susceptibility to threats is greater in areas of low rainfall due to lower resource availability and less habitat connectivity. The unique nature and drivers of decline of small mammals in northern Australia relative to declines elsewhere in Australia and globally will require novel solutions. Here, I suggest maintaining and, if possible, restoring habitat structural complexity throughout the tropical savannas, especially in drier regions, should be an immediate priority for land managers. More broadly, my thesis highlights the adaptive advantages of gliding in areas where there is a discontinuous canopy layer and structural connectivity is limited. Although I did not seek to examine the evolutionary drivers of gliding in marsupials, *P. ariel* provides an example where gliding has potentially facilitated the survival of a species in a rapidly changing environment.

Appendix I

Pilot-study comparing the efficacy of camera trapping, live-trapping and spotlighting for detecting *Petaurus ariel* in the tropical savannas of northern Australia.

Appendix I cover page images were created by First Dog on the Moon for sale during the Unknown Glider crowdfunding campaign

Objective

As there have been few targeted studies on arboreal mammals in northern Australia, I conducted a pilot to determine the most effective method for detecting the savanna glider (*Petaurus ariel*) using different fauna survey methods in the tropical savannas. Camera-trapping, live-trapping and spotlighting have all been used previously for detecting gliders and/or other arboreal mammals (Rees, 2004; Brown, 2006; Harley *et al.*, 2014). However, I do not believe the effectiveness of these methods for detecting gliders has previously been compared. In this pilot-study, I adjusted each method slightly to better suit the habitat structure (mainly smaller diameter and shorter trees) typical of the tropical savannas.

Methods

Study area

The study took place in the Shark Bay region of Melville Island (-11.33°, 130.57°). This large island (5,786 km^2) is located off the coast of the Northern Territory, north of Darwin and is an Aboriginal reserve managed by the Tiwi Land Council (Fig. A.1). Less than five percent of the island has been cleared for forestry plantations of introduced *Acacia mangium*. Eucalypt forests dominate Melville Island, with occasional rainforest patches associated with perennial freshwater springs. The Tiwi Islands receive the Northern Territory's highest annual rainfall, with mean annual rainfall exceeding 1500 mm and more than 90% falling during the summer wet season (*ca*. December–April, inclusive). Mean annual temperature on the island is around 32˚C. All surveys were conducted within nine experimental fire plots established and managed by the Commonwealth Scientific Industrial Research Organisation (CSIRO) at Shark Bay (Richards *et al.*, 2012). Each plot varied slightly in size but all were at least 50 ha. All surveys were conducted in September 2015.

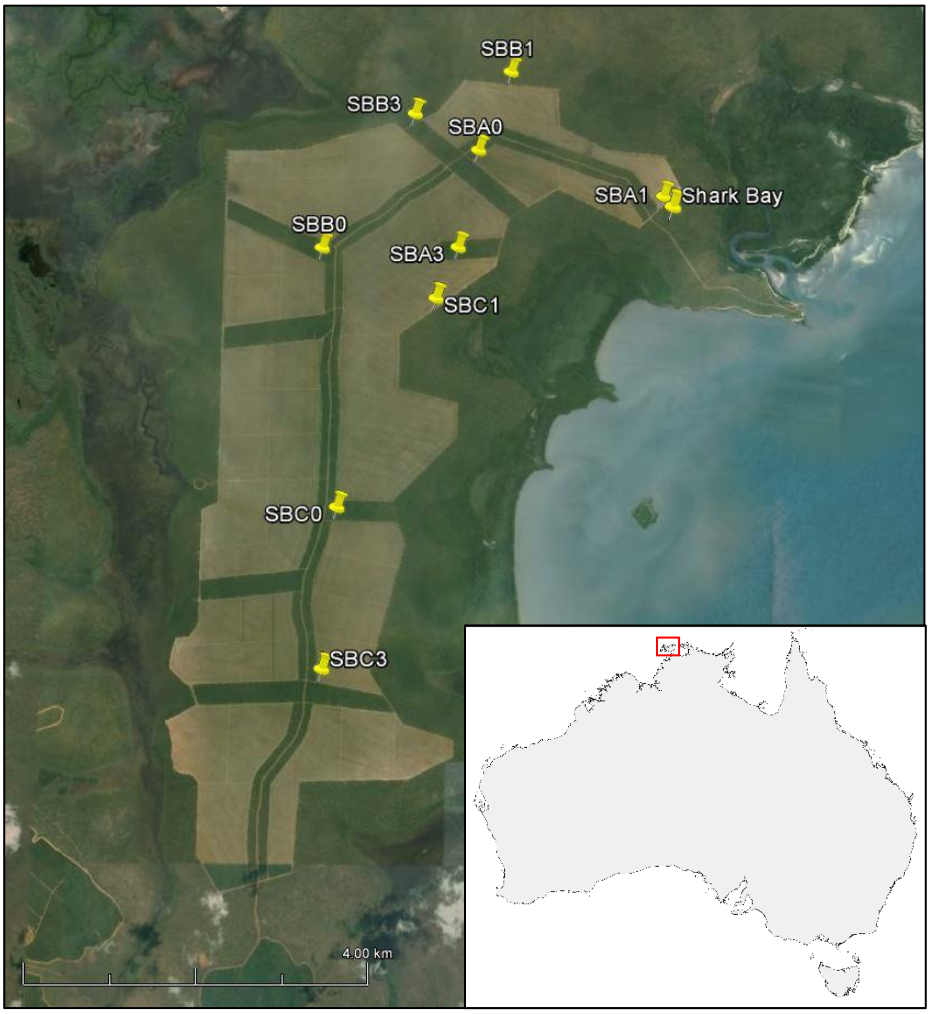


Figure A.1: Map showing layout and location of CSIRO's experimental fire plots at Shark Bay, Melville Island ; © Google Earth 2016. Square inset highlights location of Melville Island (in red) relative to Australia.

Live trapping

Five medium Elliot (aluminium box) traps (Type A) were set within each plot. Traps were attached to brackets with tape, and the brackets were secured to trees 3–4 m above ground with three galvanised nails. Traps were placed so that the entry faced the tree with a gap of 10 cm between the entrance of the trap and the base of the tree to act as a landing platform (Fig. A.2). Traps were baited with a mixture of peanut butter, honey and rolled oats. Additionally, a solution of honey and water (ratio 1:5) was sprayed on the tree from the base of the trap to the canopy of the tree to attract gliders. Traps were set on larger, mostly hollow-bearing trees spaced a minimum of 50 m apart. Traps were set each evening before sundown and checked the following morning at first light for 3–5 consecutive nights.

Figure A.2: Example of arboreal live-trapping methods : photograph of (a) metal bracket with wooden platform attached, (b) trap attached to bracket and (c) final trap position after instalment.

Captured animals were transferred to calico bags for processing. All animals were weighed, sexed and aged on site. The reproductive condition of both sexes was noted, and used to distinguish adults from sub-adults and juveniles. Males with a developed head scent gland were classified as adults (Jackson, 2003). Females that showed signs of being reproductively active, i.e. pouch with loose skin, elongated or lactating teats, or had pouch young, were classified as adults (Jackson, 2003). Animals were released at the point of capture, either within an hour of capture or at last light in the evening.

Camera trapping

Three camera-traps (Reconyx Hyperfire 400) were deployed for 5–6 nights in each plot. Cameras were fixed to trees 3–4 m above ground using two elasticised octopus straps. A solution of honey and water was sprayed on an adjacent tree as a lure. Adjacent trees were 1–3 m away and directly in the camera’s field of view. The honey spray was refreshed every second day.

Prior to using the solution of honey and water, I tested the effectiveness of different lures at a site close to Darwin (Blaydin Point) where *P. ariel* is known to occur. For this I compared three lure types: a container holding a bait ball of peanut butter, honey and oats (with honey water sprayed above); a rodent water bottle filled with honey and water (with honey water sprayed above) and an empty container (no honey water spray) to act as a control. Fifteen cameras were deployed for 21 days at each plot.

I found no obvious difference in *P. ariel* detectability with lure type. However, observations from camera-trap images, suggested that gliders were most likely to be detected within the first few days of installation and appeared to be attracted to areas where honey water had previously been sprayed. The lack of a clear preference and the ease of installing a camera on one tree and spraying an adjacent tree with honey water (rather than install a baited lure), meant that cameras deployed on Melville Island were ‘baited’ with honey water.

Spotlighting

Each of the nine plots on Melville Island was surveyed on foot, along a 1 km transect (approximately around the perimeter of the plots) for 1 hour at three different survey times. Transects for each plot were surveyed at 0.5, 2.0 and 3.5 hours after sunset. No plot was surveyed more than once in a night. The order in which each plot was surveyed was randomly allocated.

Results and discussion

Based on data collected from the plots surveyed on Melville Island, spotlighting was considered much better method for detecting *P. ariel* than either camera-trapping or live-trapping (Table A.1). Camera-trapping and live-trapping only detected *P. ariel* at two of the nine plots, although they were detected at all plots with spotlighting. Based on these preliminary results, spotlighting was deemed a far more efficient and effective method for detecting *P. ariel*.

Another finding based from spotlighting data was that *P. ariel* detectability was highest 0.5 hrs after sunset (Fig. A.3), with detections declining in the following 2 and 3.5 hours after sunset surveys. Notably, no spotlight survey returned a zero detection of *P. ariel*, suggesting Melville Island likely supports high numbers of *P. ariel.*

Table A.1: Raw data of *Petaurus ariel* detections using camera-trapping, live-trapping and spotlighting survey methods in the Shark Bay plots on Melville Island.

Site	Method		
	Camera-trapping	Live-trapping	Spotlighting
SBA 0	0	0	15
SBB 0	1	0	13
SBC 0	0	3	12
SBA 1	0	0	12
SBB 1	0	0	15
SBC 1	2	0	26
SBA 3	0	0	10
SBB 3	0	0	12
SBC 3	0	6	18
TOTAL	3	9	133

Spotlighting was the most appropriate technique for broad-scale assessment of *P. ariel* presence/absence and density estimates (coupled with an appropriate analytical approach such as distance-sampling). Although spotlighting proved the most efficient method for detecting gliders, live-trapping was also used in this study to obtain morphological measurements and for collaring animals for radiotracking. Where possible, live-trapping was used in conjunction with spotlighting to increase confidence in any 'no detection' result. Camera-trap surveys were not used further in this study due to poor detectability of *P. ariel*.

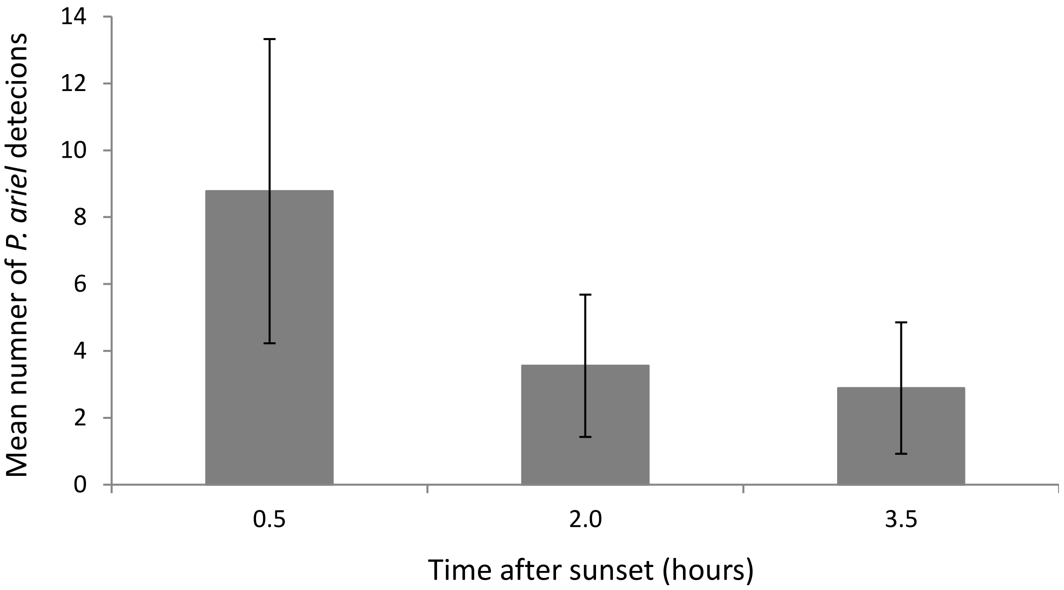


Figure A.3: Mean number of *Petaurus ariel* detections (with standard error bars) during three spotlight survey times at Shark Bay, Melville Island.

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