Movement patterns and spatio-temporal use of patches by a specialist herbivore, the koala, in a fragmented agricultural landscape

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DECLARATION

I hereby certify that the work presented in this thesis is my own. To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made. This thesis contains no material which has been accepted for the award of any other degree or diploma at another university.

Adrian I. Rus
PREFACE

In accordance with current practice at The University of Sydney, this thesis is presented as a series of stand-alone manuscripts intended for publication in international peer-reviewed journals. These manuscripts were formatted to the requirements of the journals to which they were submitted. Consequently, the formatting of each manuscript is slightly different. Because these manuscripts are similarly themed some repetition was unavoidable.

Most of the ideas contained in this thesis are my own. In other cases, I contributed substantially to the development of the project and conducted the majority of the research (including planning and designing the experiments, collecting and analysing the data, and writing the manuscripts) under the guidance of my supervisors. All contributions from co-authors have been acknowledged by listing the co-author names in the title page of each chapter, as they appear in the submitted versions of the manuscripts. I am first author on all the manuscripts but due to joint-authorship, all the manuscripts are discussed as “we” instead of “I”.

All work was conducted under the approval of the University of Sydney Animal Ethics Committee (AEC; Permit #2016/955) and NSW OEH Animal Ethics Committee (080211/02). Part of the research was funded by an Australian Research Council grant to Mathew Crowther, McArthur and all (ARC# LP140100279).
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Thesis abstract

Understanding how animals use their habitat is an important part of ecology because it links an individual’s life history with movement and resource exploitation. Animals have to move in some form or another to satisfy their energetic and reproductive needs, which is essential for fitness and survival. The patchy distribution of resources (i.e. food, shelter, mates) within heterogeneous landscapes has a strong influence on animal movement. By analysing movement patterns of individuals, we can get a better understanding of the factors influencing the spatio-temporal use of patches. Habitat fragmentation also creates a greater isolation of resource patches, increasing the costs of movement. Therefore, understanding how the distribution and organisation of habitat patches within fragmented landscapes affects the use of patches is crucial for management and conservation of species. My overarching aim was to understand how the internal state (i.e. sex, age, health) and environmental factors influence the movement and patch use of a specialist herbivore occupying a fragmented agricultural landscape. I used free-ranging koalas (*Phascolarctos cinereus*) as a model to explore individual movement, temporal foraging patterns, and periodic use of patches. The koala is a medium-sized arboreal marsupial that is distributed across the eastern and southern parts of Australia. It is currently threatened by habitat loss and fragmentation and disease.

My specific objectives were to investigate:

1) the effects of habitat fragmentation on koala movement and space use
2) the effects of patch quality and fragmentation on temporal foraging patterns
3) the internal and external factors driving periodic use of patches and routine movement.
For Aim 1), I GPS-tracked individuals every 4-hours for four months and calculated their total distance moved, tortuosity and the number of core areas. I used four metrics (proximity, functional connectivity, clumpiness, perimeter-to-area fractal dimension) to quantify landscape fragmentation within koala home-ranges and determine its effects on movement and space use. Functional connectivity had the greatest effect on individual movement and space use. Decreasing connectivity led to longer and more direct movements by koalas and more core areas within an individual home-range, all indicating higher movement costs. I therefore conclude that, for species occupying fragmented landscapes, promoting greater functional connectivity by restoring or protecting resource patches will reduce costs associated with the isolation of resource patches.

For Aim 2), I examined the external, environmental factors associated with tree foliage chemistry, shelter, and habitat fragmentation driving the temporal use of trees by koalas. I used movement patterns to determine the re-use of patches during both day and night, by measuring the number of revisits, average time spent in trees (i.e. Residence Time), and average Time-to-Return. I found that leaf nitrogen is a strong driver for koalas to revisit foraging patches, but habitat fragmentation also plays a role in their foraging decisions. During the night, there was a threefold increase in the number of revisits to trees with low tree connectivity (i.e. higher habitat fragmentation) with high leaf nitrogen content. In contrast, when trees were highly connected, high leaf nitrogen was less of an incentive to revisit. I suggest that from an
individual koala’s perspective, trees that are more isolated (less connected) and also high in
nitrogen could be highly valued. Although nutritional quality of patches attracts herbivores to
revisit patches during the night, I found that shelter and tree size (i.e. diameter at breast height)
have a strong effect during the day. These results suggest that koalas place a higher value on
trees that provide more shelter (i.e. tree canopy cover) because koala revisit to such trees was
greater.

For Aim3), I then investigated whether individual koalas showed periodic re-use of resource
patches and routine movement; and if so, whether there were any internal (i.e. sex, age, body
condition) and environmental drivers explaining these patterns. I used Fourier and wavelet
analysis to detect periodicity, and then I used conditional entropy to examine routine
movement. I found several significant temporal scales of periodicity by individual koalas, with
some differences between males and females; and koalas showed stronger periodic use of
patches during decreased rainfall and lower plant productivity. Koalas also showed a low level
of spatial routine.

Together, my results provide evidence that internal and external factors drive animal
movement patterns and that habitat fragmentation is a strong drive of animal movement and
space use. These insights help advance our understanding of animal movement ecology and
how animals cope with the effects of habitat fragmentation, with implications for management
and conservation of species occupying fragmented landscapes.
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Animal Movement

Movement plays a major role in the survival of most animals, which helps shape the structure and dynamics of population and communities, and ecology and evolution (Dingle et al. 1985; Nathan et al. 2008). As a result, the need to understand and predict animal movement patterns is increasingly recognized in the study of organismal ecology. Nathan et al. (2008) outlined a movement ecology paradigm, which provides a general framework for understanding animal movement by linking the internal state of an organism, its motion and navigation capacities, and external factors. From a mechanistic perspective, motion and navigation capacity help explain where and when animals move; but from an evolutionary perspective, animals move to satisfy their nutritional and reproductive needs, both of which are part of an animal’s internal state (Avgar et al. 2015). The outcome of these life needs is for animals to move away from areas with unfavorable conditions (e.g. high predation and competition) and towards locations with adequate resources such as food, shelter and mates (Avgar et al. 2015). Hence, movement patterns are shaped by both the internal state of an animal and the external environment in which it lives.

Animals can exhibit different types of movement depending on their life stages and ultimate goals, and such movements can vary across spatial and temporal scales. For example, in the early stages of life some individuals disperse over large distances from natal areas to new habitat (Bowler and Benton 2005; Vasudev et al. 2015); and some individuals perform seasonal long-range migrations to overcome seasonal variation in food availability (Dingle 2014; van Moorter et al. 2013). Others may restrict their movements to particular areas, known as home
ranges, that satisfy their needs for food, shelter and mates (Borger et al. 2008; Burt 1943; Van Moorter et al. 2016).

Habitat fragmentation, climate change and introduction of exotic species can complicate how animals interact with and therefore move within their environment. These changes are particularly prevalent today as humans play an increasing role in altering the world’s ecosystems. It is estimated that 1.2 million km\(^2\) of native habitat will be cleared by 2030 due to urban expansion (Seto et al. 2012), and 10 million km\(^2\) of land will be converted for agricultural practices by 2050 (Tillman et al. 2011). Understanding the causes and mechanisms of animal movement is critical for effective management and conservation of species in the response to environmental changes because movement can ultimately shape individual, population and species survival.

Movement Recursion

Animals are commonly considered to forage randomly between resources patches and models of animal movement often assume an individual performs a correlated random walk (Devin et al. 2008). However, this would imply that individuals do not use any internal or external information to navigate (Nathan et al. 2008, Pyke 2015). Contrary to such assumptions, there is evidence that non-dispersing individuals perform non-random movement when foraging, by using memory to locate and return to high quality food patches (Bar-David et al. 2009; Fryxell et
al. 2005). Repeated visits to foraging areas has been referred to as “recursion” and research on recursions has mainly focused on insects, birds and primates (Berger-Tal and Bar-David 2015). These studies have shown recursion is primarily driven by resource renewal and that recursion can help explain why animals return to previously visited areas, which provides insights into space use and foraging strategies.

Since one of the ultimate goals for a forager is energy gain for growth, maintenance and reproduction — and foraging occupies a large proportion of their time — foraging efficiency is expected to be critical for survival and fitness. Revisiting high quality foraging sites is predicted to be an efficient foraging strategy because individuals can minimize the time spent searching for other, lower quality patches and so reduce the distance they need travel between patches (Ohashi 2005).

Studies on large herbivores have suggested that recursion movement behavior is driven mainly by the recovery of food patches, but this has yet to be tested empirically (Berger-Tal and Bar-David 2015). Research on insects (Williams 1998) and birds (Garrison 1999; Gill 1988) provides experimental evidence that individuals time their revisits in relation to resource renewal. For example, bumblebees returned to previously visited flowers in regularly repeated ordered steps that optimised intake of nectar (Williams 1998), and hummingbirds adjusted their visitation rates to feeders in response nectar availability (Gill 1988).
High frequency of revisits to food patches should be advantageous to herbivores as long as the rate does not cause irreparable harm to plants by overharvesting (Watts 1998). In patchy landscapes, movement recursion by mammalian herbivores may therefore be influenced by external factors such as renewal rates, but also, presumably, by the quality of food within food patches. Shelter may also play a role in revisits, since animals use particular areas that provide cover from the environment, and therefore reduce the amount of energy used for thermoregulation. A few studies have examined movement recursion of mammalian herbivores in relation to food quality and shelter in natural environments. In two large herbivores, the Asiatic wild ass (*Equus hemionus*) and red deer (*Cervus elaphus*), number of revisits to foraging sites increased during periods of increased plant productivity (Giotto et al. 2015; Seidel and Boyce 2015) suggesting some form of harvesting strategy. In Mountain Gorillas (*Gorilla gorilla beringei*), frequency of revisits was greater to areas where high-protein food was abundant (Watts 1998), which suggest that particular nutrients (i.e. nitrogen) is an important driver of patch revisits.

**Routine movement**

Movement recursions to individual sites may result in periodic patterns of revisits across time or repeated, ordered sequences among different sites. These movement patterns have been defined as “routine movement behaviours” (Riotte-Lambert et al. 2013; Riotte-Lambert et al. 2017). Migration is one example of large-scale spatiotemporal routine performed by many species (Hobson 1999). Routine movement behavior at smaller scales, such as the daily use of a
grazing areas by large herbivores, has been explored less frequently (Bar-David et al. 2009; Riotte-Lambert et al. 2013) probably because it is less easily observable in animals due to the large locational errors in animal tracking. However, technological advances such as Global Positioning System (GPS) have decreased locational errors in tracking data, making it easier to explore routine movement behaviors in animals even at small scales.

Exploration of smaller-scaled routine movement behavior in herbivores has mainly focused on analyzing path data such as distances and turning angles (Berger-Tal and Bar-David 2015), with most studies exploring whether or not individuals performed routine movement. From the scant studies of routine movement behavior, only one study linked routine movement behavior to internal and external factors. In African elephant, temporal movement routine was linked to social rank and seasonal variation of resources (Wittemyer et al. 2008). Dominant individuals showed higher autocorrelation in movement displacement than subordinates, and all individuals exhibited less autocorrelation during the wet season.

While some individuals return to previously revisited foraging patches (i.e. recursive movements), studies of recursion do not often explore whether there are consistent periodic patterns across time, adding up to routine use of patches. Revisits to areas are likely to be an expression of animals using spatial memory (Fagan et al. 2013) and the spatiotemporal routine may indicate individuals time their use of patches to improve foraging efficiency. Nectivores adjust their timing of revisits to resource renewal rates (Janson 1998; Ohashi et al. 2008),
and/or to defend resources from conspecifics through guarding (e.g., Ohashi et al. 2008; Janmaat et al. 2014; Noser and Byrne 2009). Detecting routine movement in animals and understanding the drivers for this behavior can help answer ecological questions related to spatial memory and foraging efficiency.

**Space Use**

The home range of an animal is the predefined temporal and spatial use of an area to satisfy its foraging and reproductive needs (Burt 1943). As such, a home range can be defined by a collection of animal movements resulting from the interactions between the internal state of the animal and its external environment (Moorcroft 2012). Home ranges may not necessarily restrict individuals to one area. For example, habitat disturbances may force individuals to move and establish home ranges elsewhere, and migration leads to individuals having established home ranges at more than one location (e.g. wintering and breeding sites). Therefore, the definition of a home range can vary with spatial and temporal scales.

Not all areas within an animal’s home range are used equally. Intensely used areas are defined as an animal’s core area (Cederlund and Sand 1994; Samuel et al. 1985). Core areas may contain highly valued resources such as foraging patches, shelter or mates, which are more frequently revisited compared to areas outside the core area (Benhamou 2004).
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As measures of space use by animals, home range and core areas provide an understanding of how individuals interact with their environment. They also help us understand the causes and consequences of ecological processes such as habitat selection (Rhodes et al. 2005), predator–prey dynamics (Lewis & Murray 1993), community structure (Fagan et al. 2013), or disease spread (Kenkre et al. 2007).

Methods for quantifying movement and space use

There are many methods for gathering animal movement data, including direct and indirect observations (e.g. using camera traps) of an individual’s location, radio telemetry (VHF), and GPS datalogging systems that provide high volumes of animal movement data. GPS systems have become common practice for studying animal movement and space use because they are automated systems programmed to record animal locations at a fixed interval with minimal effect on animal behavior (Cargnelutti et al. 2007). The spatial and temporal characteristics of animal location data allow for quantifying a range of metrics of animal movement. Each location point contains a geographic position and the time it was acquired, and points can be connected by straight lines to form paths. Animal paths can then be used to measure total distance moved, while turning angles between paths can be used to measure the convolution of movement paths (i.e. tortuosity).
Movement paths can also be used to analyze recursive patterns of animals to specific locations, such as grazing areas or foraging patches. The method works by placing a circle with a pre-defined radius at a specified location representing a patch. Then, movement data can be used to determine when an animal enters the circle (i.e. number of revisits), amount of time they spend in the circle, and elapse time since last revisit (Benhamou and Riotte-Lambert 2012).

Methods for measuring routine movement involve analyzing the pattern of temporal and spatial repetition of a specific movement parameter, such as the path distance or path turning angles (Polansky et al. 2010; Wittemyer et al. 2008). A recent method allows for identifying temporal routine of resource patches by using GPS data to determine the presence/absence of events in a patch. Fourier and Wavelet analysis are then employed to identify patterns of repetition across time (Riotte-Lambert et al. 2013).

Compared to temporal routine, spatial routine examines the repetition of ordered sequences to important sites. The method for measuring spatial routine was originally developed to understand the repeated use of flowers by nectivores, known as traplining behaviour (Thomson et al. 1997). A recently developed method (Riotte-Lambert et al. 2017) can be used to quantify the level of routine movement behavior in animals displaying recursive movement to predefined patches. This method is based on the concept of conditional entropy and calculates an index of routine, which can be used for comparison of spatial routine between studies (Riotte-Lambert et al. 2017). Using animal movement data and locations of habitat patches, for
each individual animal, a sequence of movements between all the patches is generated. The sub-sequences (i.e. order of movements between two, three and up to all the patches) are analysed for repetitiveness and the routine index is calculated.

For animal space use, there are several common methods for home range and core area estimation using telemetry data (Walter et al. 2015). Minimum convex polygon (MCP) has long been used as a simple estimate of home range size by creating a bounding polygon around each location point (Hayne 1949). The drawback of MCP is that it can overestimate the actual size of the home range (Ross 2015). An alternative to MCP is the Kernel Density Estimator (KDE), which calculates the home range size based on the utilization distribution (UD) of animal locations (Worton 1989). While MCP and KDE methods are appropriate for infrequent, spatial independent location points gathered by VHF telemetry, it became inappropriate for their use on autocorrelated GPS location data. The Brownian Bridge movement model (BBMM) was developed to account for the high degree of autocorrelation in GPS location data (Horne et al. 2007). BBMM assumes a purely diffusive process derived from particle physics known as Brownian motion (Yen 1999) and equates to more of a random walk model (Benhamou 2011). However, home range behavior consists of both random movement and constant returns to previously visited areas. The Biased Random Bridges (BRB) method incorporates an advection process to account for frequent reorientation of animals towards preferred areas, as well as the diffusive process of the BBMM, giving a more realistic home range behavior than BBMM.
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(Benhamou 2011). Using BRB, home ranges can be estimated based on the 95% UD and core areas using 50% UD.

Habitat fragmentation and animal movement

Habitat fragmentation is a landscape process that defines the loss and subdivision of continuous native habitat leading to small, isolated habitat patches (Betts et al. 2007; Fahrig 1997; Schmiegelow and Mönkkönen 2002). Habitat fragmentation can occur naturally or be driven by humans due to changes in land-care practices (Harris and Silva-Lopez 1992; Opdam 1991). One of the main drivers of habitat fragmentation being agriculture. Increasing habitat fragmentation often leads to a decrease in species richness and abundance due to the reduction and increased isolation of native habitat (Fahrig 2003). For example, species richness of four taxa (birds, mammals, reptiles and plants) decreased with increasing habitat fragmentation (Findlay and Houllahan 1997); and the abundance of badgers (Meles meles) was lower in landscapes with less forest cover and increasing habitat isolation (Virgós 2002).

Research of habitat fragmentation has focused mainly on how the amount of native vegetation cover and edge effects impact species richness and abundance, as well as its effects on metapopulation dynamics (Debinski and Holt 2000). But habitat fragmentation can also affect movement processes such as dispersal and migration. For example, increased isolation of habitat patches led to higher mortality in dispersing specialist butterflies (Proclissiana eunomia, Schtickzelle et al. 2006), as well as changes in dispersal behavior such as reduced
propensity to disperse and more directed movement between habitat patches (speckled wood butterfly *Pararge aegeria*, Merckx and Van Dyck 2007), and delayed timing of dispersal in the Crested Tit (*Parus cristatus*, Lens and Dhondt 1994). However, for animals with established home ranges in fragmented landscapes, the effects of habitat fragmentation are less understood, in particular the costs and/or benefits of moving as it relates to foraging and space use. One would predict that if the cost of travel across a hostile matrix is higher than the benefits in terms of resources gained from visiting multiple patches, individuals occupying fragmented isolated patches would have to restrict their home range to one or several habitat patches. On the other hand, if travel costs are low and isolated patches do not provide enough food, individuals would have to increase their movements. There is some evidence for both these predictions. For example, root voles (*Microtus oeconomus*) reduced their home ranges with increasing habitat fragmentation and fewer inter-patch movements because of higher predation rates (Andreassen and Ims 1998). In contrast, raccoons (*Procyon lotor*) occupying fragmented habitats increased their home range to gain access to resources to satisfy their metabolic and reproductive needs (Beasley and Rhodes 2010). However, less is known about how the spatial pattern of habitat (i.e. aggregation and isolation of habitat patches) influences movement behaviors associated with foraging and finding mates, which in turn are expected to influence individual fitness and survival.
Quantifying habitat fragmentation

The majority of studies on habitat fragmentation either use a qualitative approach, i.e., comparing continuous versus fragmented habitat, in exploring the ecological effects; or simply measure the amount of native habitat (Fahrig 2003). The potential weakness of these measures is that they do not provide a quantitative measure of the degree of habitat fragmentation, particularly the distribution and organisation (i.e. size, clustering, and proximity) of patches (Wang et al. 2014). Providing a quantitative measure of habitat fragmentation gives a standardized approach that can be compared across populations and species occupying different landscapes.

Landscape patterns can be measured at three levels: patch, class and landscape (McGarigal and Cushman 2002). Patch-level metrics refer to individual patches of any habitat type and are the basis for calculating class and landscape level metrics. Patch-level metrics provide information about the attributes of a patch such as its size and shape, and when patch attributes are averaged across a habitat type and/or the landscape, they can provide interpretive value at the class and landscape level. Class-level metrics represent the amount and distribution of patches associated with a specific habitat type, such as forest or grasslands. Class-level spatial pattern metrics provide quantitative measures of fragmentation of focal habitat within the landscape, which include patch size and shape, inter-patch distance and patch connectivity (McGarigal and Cushman 2002). Landscape-level metrics are similar to class-level metrics but provide measures of patch characteristics across all class types (i.e. habitat types).
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Research aims and study system

The main goal of this thesis was to investigate the internal and external factors influencing movement and space use of a specialist folivore in a fragmented agricultural landscape. I investigated the temporal and spatial aspects of animal movement, including recursion and routine behavior and space use, using free-ranging koalas.

The koala (*Phascolarctos cinereus*) is a medium-sized marsupial (7-14 kg) that was historically widely distributed across the eastern and southern parts of Australia (Martin and Handasyde 1999). Significant reduction in their distribution due to habitat loss and fragmentation and disease led to its listing as a threatened species in Queensland, the Australian Capital Territory and New South Wales (Lunney et al. 2012; McAlpine et al. 2008). Studies have shown that near the arid and semi-arid distribution of their range, koalas must cope with heat waves and long periods of drought while occupying a fragmented landscape, making their survival less likely under predictive climate models (Davies et al. 2013; Lunney et al. 2012; Sullivan et al. 2003). I conducted my research in a fragmented agricultural landscape to understand the effects of habitat fragmentation on movement and space use, with the applied goal of better management and conservation of koalas and an improved understanding of the future implications of climate change.

Koalas are obligate specialists feeding exclusively on *Eucalyptus* leaves (Moore and Foley 2005), a genus of trees that is the dominant tree species across much of Australia (Pfautsch et al
The leaves of eucalypts are usually low in nitrogen, high in phenolics and often high in toxins, including terpenes and formylated phloroglucinol compounds (FPCs) (Marsh et al. 2014; Moore et al. 2005). Previous studies on tree use by koalas indicate that tree selection is strongly influenced by leaf chemistry such as concentrations of nitrogen and FPCs, and the amount of shelter (Briscoe et al. 2014; Crowther et al. 2014; Moore et al. 2010). Koalas maintain water intake through the consumption of leaves (Nagy and Martin 1985), and leaf moisture level has been found to be a driver of tree selection during periods of decreased rainfall (Ellis et al. 1995). Koalas are mainly solitary with few social interactions except during the mating season (Ellis et al. 2002). Adult males have significantly larger home ranges than adult females and there is some home range overlap, in which male-female overlaps are slightly higher than female-female or male-male (Ellis et al. 2002). While studies have explored movement and tree use by koalas, few have investigated the effects of internal and external factors on movement, particularly the effects of habitat fragmentation, on movement costs and foraging behaviours.

The study area for my research was the Liverpool Plains, near the town of Gunnedah, northwestern New South Wales (NSW), Australia (30°59’S, 150°16’E). The landscape is a matrix of productive agricultural land and isolated open woodland patches, comprising Eucalyptus species including white box E. albens, yellow box E. melliodora, poplar box E. populnea and river red gum E. camaldulensis (Crowther et al. 2014; Dargan et al. 2019; Lunney et al. 2012). The region has a temperate climate, with occasional daily maximum temperatures above 40 °C
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during summer and daily minimums below 0 °C during winter. Annual rainfall ranges from 296 to 1139 mm with a mean of 633 mm (Bureau of Meteorology, 2019, www.bom.gov.au).

Structure of the thesis (Figure 1)

In Chapter Two, I used GPS-tracked koalas to investigate the effects of habitat fragmentation on the long-term movements and space use. This chapter has been accepted for publication in the journal Animal Conservation (accepted 25 March 2020).

In Chapter Three, I investigated the external factors influencing koala recursion to resource trees. Specifically, I investigated the effects of tree quality and habitat fragmentation on the number of revisits, time spent in trees, and time-to-return.

In Chapter Four, I investigated the routine use of resource patches in individuals, and the spatial and temporal scales of routine movements. I also investigated the internal and external drivers of routine movements.

In Chapter Five, I conclude my thesis with a summary of the fundamental implications of movement and space use. I also discuss the ecological consequences and implications of habitat fragmentation from an applied perspective and provide suggestions for future studies.
**Figure 1** Concepts and structure of the data chapters of this thesis.
References


Chapter 1: General introduction


Chapter 1: General introduction


Chapter 1: General introduction


Chapter 1: General introduction


Chapter 1: General introduction


Chapter 2: Habitat fragmentation affects movement and space use of a specialist folivore, the koala
Chapter 2: Effects of habitat fragmentation on animal movement & space use

State of Chapter

Chapter 2 is a manuscript that has been submitted to the journal *Journal of Animal Conservation*, with authors AI Rus, C McArthur, VSA Mella, MS Crowther. The manuscript has been published by the journal.


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Statement of contributions

AIR, MSC and CM conceived the ideas and designed methodology; AIR and VSAM collected the data; AIR analysed the data; AIR wrote the manuscript with feedback from CM, VSAM, and MSC. All authors gave final approval for publication.
Abstract

Habitat fragmentation changes landscape patterns and can disrupt many important ecological processes. Movement allows individuals to find resource patches to maintain their fitness and habitat fragmentation can disrupt this process. We explored the ecological impact of habitat fragmentation on movement and space use of a specialist folivore, the koala (Phascolarctos cinereus). We GPS tracked koala movements within a fragmented agricultural landscape. We calculated the total distance moved across four months and the number of core patches used by each koala. We used four metrics (proximity, functional connectivity, clumpiness, perimeter-to-area fractal dimension) to quantify landscape fragmentation within koala home-ranges and determine its effects on movement and space use. Functional connectivity had the greatest effect on individual movement and space use. Decreasing connectivity led to longer and more direct movements by koalas and more core patches within an individual home-range. Our study provides insight into the effects of habitat fragmentation on animal movement and space use, which can be used by wildlife managers to plan and manage landscapes more effectively. We conclude that restoring or protecting resource patches to promote greater functional connectivity will reduce the costs associated with the isolation of resource patches for species occupying fragmented landscapes. By providing a quantitative relationship between habitat connectivity and movement and space use costs, our results enable managers to set restoration targets, by identifying the most effective way to provide functional connectivity minimising the negative impact on focal species.
Chapter 2: Effects of habitat fragmentation on animal movement & space use

Introduction

Habitat fragmentation changes landscape patterns, reshaping contiguous patches into smaller patches that become increasingly isolated from one another (Schmiegelow & Mönkkönen 2002; Fahrig 2003; Betts et al. 2006). These changes can have significant consequences for many ecological processes such as population dynamics (Arthur, Pech & Dickman 2005), genetic diversity (Hermes et al. 2016, Mekonnen et al. 2018b), predator-prey relationships (Schneider 2001) and dispersal (Entling, Stampfli & Ovaskainen 2011; Banks & Lindenmayer 2014; Awade et al. 2017). Worldwide, changes to natural ecosystems as a result of land clearing has been increasing at an alarming rate. In particular, 10 million km$^2$ of native habitat will be cleared for agricultural production by 2050 (Tilman et al. 2011). The result of these changes is a mosaic of agricultural land and remnant native habitat patches that vary in size and arrangement across the landscape.

The distribution and organisation (i.e. size, clustering, and proximity) of habitat patches within fragmented landscapes can influence movement and space use, with implications to individual fitness and survival (Cattarino, McAlpine & Rhodes 2016). For example, distances moved by prairie voles (Microtus ochrogaster) and deer mouse (Peromyscus maniculatus) increased in fragmented habitats compared to continuous habitats (Diffendorfer et al. 1995). In the specialist arboreal folivore, the greater glider (Petauroides volans), home range size increased with increasing patch size (Pope, Lindenmayer & Cunningham 2004). Movement responses to increasing habitat fragmentation can also vary between species (Fahrig 2017;
Haddad et al. 2017). Some species may be less inclined to cross open terrain as habitat patches become smaller and more isolated. In root voles (*Microtus oeconomus*), increasing fragmentation led to smaller home ranges and fewer inter-patch movements because of the higher predation rates (Andreassen & Ims 1998). A higher threat from crossing open terrain has been observed in many other species (Wilson, Marsh & Winter 2007; Gebauer et al. 2013; Banks & Lindenmayer 2014) and can result in restricted animal movements. In contrast, species with a higher tolerance for modified landscapes, such as the North American racoon (*Procyon lotor*) are less restricted by habitat boundaries and can move longer distances with increasing habitat fragmentation (Beasley & Rhodes 2010).

Based on the Marginal Value Theorem (Charnov 1976), movement decisions of foragers in heterogeneous landscapes should be a function of the size/quality of food patches versus the distance among patches, because both characteristics affect the costs and benefits of moving versus staying in a patch. However, habitat fragmentation leads to more complicated scenarios than simply whether patches are large or small, and near or far from one another. For example, in agricultural landscapes, patches can be clumped (aggregated) or in linear strips along roadways embedded in long stretches of hostile matrix. The cost/benefit outcome of moving is likely to depend, therefore, not only on the size and distance between patches but also the level of patch aggregation and how functionally connected patches are across the landscape. Revealing how patch aggregation and connectivity influence movement decisions depends on effectively quantifying these spatial attributes of fragmented habitats with appropriate metrics.
Habitat fragmentation is usually highly and inversely correlated with habitat abundance (Gustafson 1998; Neel, McGarigal & Cushman 2004; Wang & Cumming 2011). This makes it difficult to differentiate whether differences in animal movement are due to habitat fragmentation and/or habitat abundance. For example, two landscapes may have a similar spatial arrangement of habitat patches but vary in absolute habitat abundance (very low vs. much higher total area). Measuring habitat fragmentation with a metric that emphasizes abundance rather than arrangement would be insensitive and not differentiate the two landscapes. Most studies examine patch size or proportion of habitat, and only few address or account for the sensitivity of fragmentation metrics to low habitat abundance (Saunders 1982; Diffendorfer et al. 1995, Wilson, Marsh & Winter 2007; Beasley & Rhodes 2010; Mekonnen et al. 2017). Habitat fragmentation metrics used by ecologists have been assessed, and several shown to discriminate between habitat fragmentation and amount (e.g. connectivity, proximity, clumpiness index; Wang et al. 2014).

Loss of native habitat due to anthropogenic activities is a global issue affecting many species and will continue to increase into the future (Brooks et al 2002). Agricultural landscapes are one example of landscape modification leading to fragmentation and loss of natural habitat. The negative effects of fragmentation and habitat loss has been well documented across communities and populations (see Fahrig 2003), leading to lower species richness (Findlay and Houllahan 1997, Gibbs and Stanton 2001), higher costs to reproduction (Donovan and
Lamberson 2001, Duplouy et al. 2013), and lower abundance and distribution (Laakkonen et al 2001). But these higher-level ecological effects of habitat fragmentation are the manifestation of impacts on individual animals. For better management and conservation of species, therefore, it is vital to understand how changes to the structure and distribution of native habitat affect movement and, indirectly, fitness and survival of individuals.

In agricultural landscapes, fragmentation of native habitat is likely to influence movement of wildlife. This influence should be particularly strong for tree-dependent species, such as arboreal folivores, because their key resource sits in habitat patches within an effectively barren matrix (Henderson and Broaders 2010). Yet which fragmentation characteristics are the key drivers of movement for arboreal folivores, and what influence they have, is unknown.

Here, our aim was to investigate the effects of habitat fragmentation on movement and space use by a specialist arboreal folivore, the koala *Phascolarctos cinereus*, in an agricultural landscape. The koala is distributed across the eastern and southern parts of Australia but is currently being threatened by habitat loss and fragmentation and disease (Lunney et al. 2012; McAlpine 2015; 2017). As specialist folivores, koalas feed primarily on species of eucalypts of the genera *Eucalyptus*, *Angophora*, and *Corymbia* (Martin, Handasyde & Krockenberger 2008). This food resource is low in nitrogen, high in phenolics and often high in toxins, including terpenes and formylated phloroglucinol compounds (Moore & Foley 2005; Marsh et al. 2014).
Koalas are very selective in the trees they visit to meet their nutritional and shelter needs (Moore et al. 2010; Crowther et al. 2014; Briscoe et al. 2014), and this selectivity is likely to influence their movements across the landscape. Koalas are also a solitary species with adults having established home ranges with some degree of overlap, in which male-female overlaps are slightly higher than female-female or male-male (Ellis et al. 2002). Koala home ranges in mesic forests range from 1 to 300 ha (Ellis et al. 2002, Davies et al. 2014) and 5 ha to 91 ha in agricultural landscapes of southwest Queensland (White 1999). Koalas occupying arid regions of western Queensland had more linear movements and larger home ranges than semi-arid eastern Queensland koalas (Davies et al. 2013). In semi-arid regions of New South Whales, koala home ranges varied from 14 ha to 18 ha (Crowther et al. 2020). Although koala movement and space use has been quantified in natural forest/woodland landscape (Ellis et al. 2002; Ellis, Melzer & Bercovitch 2009; Matthews et al. 2016), the impact of habitat fragmentation on koala movement and space use is untested.

Based on its social structure and strict dietary and habitat requirements, we predicted that in more fragmented habitat individual koalas would: 1) move farther, as the distance between foraging patches and mates increases, 2) have more direct movements, to reduce the cost of crossing an open matrix while moving between habitat patches, and 3) have a greater number of core patches (the most intensely used areas within an animals home range), because of the need to satisfy their specialist diet amongst increased isolation of habitat patches.
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Methods

Study area

We conducted the study on the Liverpool Plains near the town of Gunnedah, north-western New South Wales (NSW), Australia (30°59'S, 150°16'E, Fig. 1). The landscape is a matrix of productive agricultural land and isolated open woodland patches, comprising *Eucalyptus* tree species such as white box *E. albens*, yellow box *E. melliodora*, poplar box *E. populnea* and river red gum *E. camaldulensis* (Lunney et al. 2012; Crowther et al. 2014; Dargan et al. 2019). The climate in this region is temperate with occasional daily maximum temperatures going above 40°C during summer and daily minimums going below 0°C during winter. Annual rainfall ranges from 296 to 1139 mm with a mean of 633 mm (Bureau of Meteorology, 2019, www.bom.gov.au).

Animal tracking

We captured 21 koalas between October 2010 and April 2011 and 58 koalas between October 2015 and November 2017. Koalas were ear-tagged and fitted with GPS collars (average mass 120 g; Sirtrack Ltd., Hawkes Bay, New Zealand) that weigh <3% of their body mass. The GPS collars were set to record one location every 4-hrs for 4-5 months, providing sufficient day and night locations across an appropriate timeframe to capture medium to long term movement patterns (following Davies et al. 2014). We included four months of data for each koala for consistency and ignored dispersing individuals. Movement data ranged from April to August
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(non-breeding season) and September to February (breeding-season). We estimated missing values (<5% of the total set for all individuals) using linear interpolation. We calculated the accuracy of the GPS collars using a static test next to a trigonometric survey mark in Gunnedah (31° 01’ 47.05717″ S, 150° 16 ′ 04.32014″ E, for more detail, see Crowther et al. 2014). The distance root mean square error was calculated to be 9.05 m and we used it as the measure of location uncertainty for estimating koala home range and core patches.

Movement

To calculate the total distance travelled by each koala, we created line segments between each pair of location points using the R package ‘adehabitatLT’ (ver. 0.3.23; Calenge 2006) and then summed the lengths of segments.

Tortuosity represents the crookedness of movement paths, which can vary depending on the movement behaviour of the animal. Convoluted movement paths represent random searches within patches and more direct paths movement between patches (Benhamou 2004). We used sinuosity to determine the tortuosity of koala tracks, calculated using the R package ‘amt’ (Singer, Fieberg & Avgar 2019). Sinuosity measures the actual path length between a starting point and an end point divided by the shortest path length (i.e. Euclidean distance), which represented the start and the end for the entire tracking season (i.e. 4 months). Values can range from 1 (lowest tortuosity) to infinity.
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**Space use**

We estimated koala home ranges (95% isopleths) and core areas (50% isopleths) in R (package ‘adehabitatHR’; ver. 0.4.15; Calenge, 2006). GPS data can be highly correlated, and although we sampled locations every 4 hours, non-dispersing koalas tend to have infrequent short distance movements (Matthews et al. 2016). To overcome the correlation between GPS locations, we used the Biased Random Bridge estimator (BRB). BRB is a modified Brownian bridge approach, which assumes an advection-diffusion process between locations (Benhamou 2011). This method also considers previously visited locations and time spent in each area. Koalas revisit trees across their home range (Matthews et al. 2007), and this method highlights intensively used areas. We counted the number of patches making up the core area within each koala home range, to establish whether habitat fragmentation also fragments core areas (hereafter defined as core patches) of use by koalas (see visual example in supplementary information S1). The total core area (i.e. sum of all core patches) was positively correlated ($r = 0.85$) with the number of core patches, but the two metrics reflect different spatial characteristics.

**Habitat fragmentation**

We used the 2011 NSW woody vegetation extent layer (Office of the Environment and Heritage, NSW) to determine the level of habitat fragmentation within each koalas home range. The layer has a 5 m resolution and classifies vegetation taller than 2 m as woody and everything
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else as non-woody. Since we were only interested in habitat fragmentation within an animals home range, we used ArcMap 10.4 (ESRI, Redlands, CA) to clip the vegetation layer to each animals home range; then we used FRAGSTATS v4 (McGarigal et al. 2012) to analyse the spatial pattern within each animals home range. We selected four class metrics in FRAGSTATS associated with patch aggregation across the landscape (Table 1), 1. Connectivity (Connectance Index), 2. Proximity (Proximity index coefficient of variance), 3. Shape complexity (Perimeter-Area Fractal Dimension), 4. Clumpiness index. These four metrics are useful because they are relatively insensitive to habitat abundance (Wang et al. 2014). The connectivity, proximity and clumpiness index provide different measures of habitat aggregation, which we expected to be important because, in an agricultural landscape, habitat is reduced to fragmented clumps of trees surrounded by agricultural fields. We tested shape complexity because human modified landscape reduces the shape complexity of habitat patches. For example, habitat found near roadways is often represented by linear strips. Connectivity measures the aggregation of patches across the landscape by calculating the percentage of patches considered to be functionally connected based on a patch edge to edge threshold distance. We used 50 m as our threshold because it represented the average step length of our koalas during the night (most movement activity). The proximity index provides a measure of patch isolation by considering the size and distance of all patches within a given radius from the focal patch (we used a 50 m radius). The clumpiness index uses an adjacency matrix, quantifying whether or not pairs of the same habitat type are adjacent, and compares this to a random distribution to determine if habitat is aggregated or disaggregated. For Shape complexity, shapes with simple perimeters are less complex and more complex shapes have convoluted perimeters.
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Statistical analysis

We used an information-theoretic approach to determine the effect of habitat fragmentation on the movement and space use of koalas. We created three sets of models with all possible combinations of the explanatory variables associated with habitat fragmentation, sex, year, and season. Year and season were included because of possible variation in movement between the years due to climate, as well as seasonal variation between non-mating (autumn-winter) and mating periods (spring-summer). We checked for collinearity between explanatory variables using Spearman's rank and found no significant correlations.

We used R Statistical to fitted generalised linear models to test which of the explanatory variables had the strongest influence on total distance travelled, tortuosity and number of core patches. We modeled both additive and interacting effects for sex and season. After examining the quantile plots of several distributions, we found that a gamma distribution with a log-link transformation was the most appropriate for the movement models (total distance travelled and tortuosity) (Zuur, Ieno & Elphick 2010). We used a Poisson distribution for space use models (core area count). We then examined the top models based on the ΔAICc, log-likelihood and Akeike weights (wi) and then calculated model-averaged estimates and standard errors for models with a cumulative wi ≤0.95 (R package ‘MuMln’ ver. 1.42.1; Bartoń 2011). The relative
importance of each explanatory variable by summing the Akaike weights ($\Sigma wi$). More detailed model selection results can be found in the supplementary information (S2).

**Results**

We collected 40,185 GPS locations from 36 koalas (19 females, 17 males), which included 19 during non-breeding season and 17 during breeding season. The koalas travelled an average of 24.3 km (SE = ±2.0) over 4 months, with males travelling 29.8 km (SE = ±3.3) and females travelling 19.5 km (SE= ±1.8). Average tortuosity for males was 0.010 (SE = ±0.006) and for females 0.013 (SE = ±0.009). Average number of core patches for males was 11 (SE = ±2) and for females 8 (SE = ±2). Connectivity ranged from 0.8 to 22.5 percent, with male average of 4.1 (SE = ±0.6) and female average of 6.7 (SE = ±1.1).

**Distance travelled**

All the models within the 95% confidence set included the connectivity variable (wi < 0.95) and six models included both connectivity and sex (S1). Distance travelled by koalas was strongly associated with habitat fragmentation, sex, and year. The connectivity metric had the highest relative importance among all the variables, followed by sex (Table 2). Distance travelled increased with decreasing patch connectivity, and in the most fragmented habitat, koalas travelled over 30 km, or three times more than the least fragmented habitat (Fig. 3). Male koalas moved further than females (Fig. 2).
Tortuosity

There were six models within the 95% confidence interval, all including connectivity. For the top model, the addition of season provided only a small improvement (0.5 AIC) over the connectivity only model (S1). Connectivity was the strongest predictor for tortuosity and had the highest relative importance among all the variables (Fig. 2, Table 2). There was a positive relationship between tortuosity and patch connectivity, and movement was more direct in more fragmented habitats.

Core area count

There were three models within 95% confidence interval, all with connectivity as the most important variable, and with season and year providing a slight improvement to the connectivity only model (S1). The core area count was strongly associated with connectivity, season, and year (Fig. 2). Connectivity had the highest relative importance, with both season and year being second (Table 2). There was a negative relationship between core area count and patch connectivity, seasons and year. The core area count decreased with increasing connectivity of habitat patches and core area count was less during the summer. In 2015, koalas used a greater number of core patches compared to all other years.
Discussion

Of the four habitat fragmentation metrics, patch connectivity had the most substantial effect on both movement and space use. Our results show that koala movement and space use is more sensitive to changes in the functional connectivity between habitat patches than to changes in patch shape, clumpiness, or isolation.

As connectivity between habitat patches was reduced, koalas moved more, supporting our first prediction. One cost of increasing habitat fragmentation for koalas, therefore, is this greater movement cost. This indicates that in landscapes with lower percentage of functionally connected patches, there is a higher cost of remaining in a patch than moving to another patch. This outcome is likely because, as specialist feeders, koalas need a minimum amount of resource habitat because they cannot broaden their diet to satisfy needs within a patch. Since increasing fragmentation divides and isolates suitable habitat, koalas must move longer distances to find resources satisfying their needs. This contrasts with the response of some less specialised species (e.g. Bale Monkeys - Mekonnen et al. 2017; Mekonnen et al. 2018a), which could expand their diet within patches, and hence may not need to move between them.

As connectivity between habitat patches was reduced, koala movement paths were straighter (lower tortuosity). We expect this pattern reflects the dominant need to cross open fields (non-habitat) in search of the next suitable patch. In contrast, in more connected habitat more
tortuous movement likely represents koalas spending more time exploiting resources that are closer together. Similar movement patterns have been observed in elk occupying heterogenous landscapes, which indicated an alternation between different searching modes in relation to resource distribution (Fryxell et al. 2008). When resource patches are aggregated and abundant, animals slow down their movement speeds and increase their turning angles, as opposed to moving faster and more direct when resources are far apart (Benhamou 1992). Our results also provide insight into animal movement in response to patch boundaries, i.e., crossing from a preferred habitat to open matrix. Animals that show a strong boundary response often never leave the patch (Kuefler & Haddad 2006), and movement steps are short and more tortuous (Fahrig 2007). Although we did not directly measure boundary response, we can infer from our results that koalas did not exhibit strong boundary responses because they were willing to move between patches. The cost of crossing an open matrix was therefore less than remaining in the same patch. One cost of crossing open matrix, apart from the energetic costs, is likely a higher risk of mortality. Although predation at our study site is rare, koala deaths have been linked to cars or farming machinery or being crushed by cattle (A. Rus and M. Crowther personal observation). Consistent with the ground being risky for koalas, another arboreal species, the common brushtail possum (*Trichosurus vulpecula*), perceives feeders placed at ground level as riskier than those above ground (Mella et al. 2014).

Our results show a substantial effect of habitat fragmentation — specifically connectivity — on space use by koalas, in terms of core patch use. In highly fragmented habitat, koalas had up to twenty core patches compared with one single area in highly connected habitat. These results support our third prediction and provide additional insight into how fragmentation alters the
use of resource patches. That is, not only do koalas moved longer distance with increasing fragmentation, but they also visit a higher number of resource patches.

The number of core patches used by koalas was also influenced by year and season: higher in 2015 and during the non-breeding season. These results might be explained by variation in rainfall. The non-breeding season is associated with lower levels of moisture, and 2015 showed lower than average rainfall (rainfall for 2015 = 527mm; average rainfall= 633mm; Australian Bureau of Meteorology). Koalas receive most of their moisture intake from their diet (Munks, Corkrey & Foley 1996). But they may drink from pools of water during increased periods of drought, and drink more from water stations with higher ambient temperatures and the more days since it last rained (Mella et al. 2019). Previous research found that captive koalas selected leaves that contained at least 55% leaf moisture (Hume & Esson 1993). Since rainfall can affect the levels of tree moisture and free-standing water, it could also affect space use. We speculate that koalas were actively searching for trees with higher leaf moisture, which led to increasing their number of core patches. Consistent with this, Davies et al. (2013) found that koala home ranges increased with decreasing annual rainfall, which suggests that water availability is an important driver of koala movement during periods of drought. Other less specialised species that are dependent on available water have been found to increase their home ranges in response to a reduction in free water sources due to habitat fragmentation (American Racoon; Beasly et al. 2010).
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*Implications*

Our results provide an insight into the effects of habitat fragmentation on animal movement and space use, which can be used by wildlife managers to plan and manage landscapes more effectively. Our results indicate that koala management programs in fragmented landscapes should focus on increasing functional connectivity of habitat patches, because the distance travelled (hence cost of travel) by koalas was altered considerably by this connectivity. For example, for koalas, managers can focus on restoring functional connectivity between habitat patches to a level that provides the biggest change in the number of core patches. In fig. 4, doubling CONNECT from A to B, reduces the number of core patches by 6, whereas doubling the CONNECT from B to C only reduces core patches by 2. This suggests the greatest gains will be made by restoring habitat from A to B, to increase functional connectivity between resource patches. Such changes would provide koalas with more easily accessible resource patches and reduce the amount of ground travel between patches, with commensurate reduction in travel costs, energetic costs and mortality risk.

The importance of habitat connectivity in a fragmented landscape is relevant beyond koalas, to other threatened or endangered species with specialised diets. Species such as the red panda (*Ailurus fulgens*), Wei et al. 1999; giant panda (*Ailuropoda melanoleuca*), Wei et al. 2015; greater bamboo lemur (*Prolemur simus*), Wright et al. 2008; and woolly flying squirrel (*Eupetaurus cinereus*), Din et al. 2015), for example, have all seen considerable decline in their habitat around the world. Restoring and managing habitat to maintain functional connectivity...
across habitat patches for these threatened and endangered species may help mitigate some of the effects of habitat loss and fragmentation. The principles should also apply to less specialised species, through the responses to different metrics of habitat fragmentation need to be tested. Future studies could use our approach to identify how landscape pattern affects individual movement, in order to develop cost-effective restoration plans.

Our study has provided a link between animal movement and habitat fragmentation in koalas. The next step is to link movement to actual costs. Moving longer distances with increasing fragmentation may satisfy dietary needs for maintenance of individuals but may not provide sufficient resources for reproduction. Future studies can use our findings and include measures of field metabolic rate or stress responses, to better define the costs of movement for species occupying fragmented habitats.

**Acknowledgments**

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Approval for this research was obtained from the NSW OEH Animal Ethics Committee (080211/02) and University of Sydney Animal Ethics Committee (2016/955).
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McGarigal, K., S. A. Cushman, and E Ene. (2012) FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html.


evolutionary history of Bale monkeys (Chlorocebus djamdjamensis) in the southern Ethiopian Highlands. *BMC Evolutionary Biology, 18*, 106.


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Table 1. Description of explanatory variables used for modelling koala movement and space use in a fragmented landscape.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Patch connectivity</td>
<td>Continuous</td>
<td>Connectance index – percentage of functional connections between patches (range 0 to 100; 0 = represents no connected patches, and 100 = one patch)</td>
</tr>
<tr>
<td>Patch isolation</td>
<td>Continuous</td>
<td>Proximity index – variation in the measure of distance and size of the nearest patches. Low variation represents a uniform distribution of patches across the landscape with equal distances and size patches. Value increases with increasing variation of patch distance and sizes.</td>
</tr>
<tr>
<td>Patch shape</td>
<td>Continuous</td>
<td>Perimeter-Area fractal dimension (range: 1 to 2; 1 = simplest geometric shape; and 2 = the most complex shape)</td>
</tr>
<tr>
<td>Clumpiness</td>
<td>Continuous</td>
<td>Clumpiness index (range: -1 to 1; -1 = represents maximum disaggregation, 1 = maximum aggregation, and 0 = random distribution)</td>
</tr>
<tr>
<td>Sex</td>
<td>Categorical</td>
<td>M = Male; F = Female</td>
</tr>
<tr>
<td>Season</td>
<td>Categorical</td>
<td>1 = non-breeding season and 2 = breeding season</td>
</tr>
<tr>
<td>Year</td>
<td>Categorical</td>
<td>Year of capture and tracking (2010, 2015, 2016, 2017)</td>
</tr>
</tbody>
</table>
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Table 2. Ranking of the importance of explanatory variables for koala movement and space use generalised linear models based on the sum of the Akaike weights ($\Sigma w_i$).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Distance travelled</th>
<th>Tortuosity</th>
<th>Core Area Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Connectivity</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Patch isolation</td>
<td>0.1</td>
<td>0.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Patch shape</td>
<td>0.2</td>
<td>0.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Clumpiness</td>
<td>0.1</td>
<td>0.2</td>
<td>-</td>
</tr>
<tr>
<td>Sex</td>
<td>0.7</td>
<td>-</td>
<td>0.1</td>
</tr>
<tr>
<td>Year</td>
<td>0.3</td>
<td>-</td>
<td>0.8</td>
</tr>
<tr>
<td>Season</td>
<td>0.1</td>
<td>0.6</td>
<td>0.8</td>
</tr>
</tbody>
</table>
Figure 1. Map of the study area on the Liverpool Plains, near the town of Gunnedah (New South Wales, Australia) showing the sampled koala locations (grey circles), and primary and secondary roads.
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Chapter 2:

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- Total Distance Travelled
  - Sex (M): 0.29 ± 0.13
  - Season (2): -0.02 ± 0.14
  - Year (2015): 0.44 ± 0.21
  - Connectivity: -0.22 ± 0.07
  - Patch shape: 0.06 ± 0.07
  - Clumpiness: 0.04 ± 0.07
  - Patch Isolation: 0.02 ± 0.08

2. Tortuosity
  - Season (2): -0.24 ± 0.15
  - Connectivity: 0.33 ± 0.08
  - Clumpiness: 0.04 ± 0.08
  - Patch shape: -0.06 ± 0.08
  - Patch Isolation: -0.04 ± 0.09

3. Number of Core Areas
  - Sex (M): -0.32 ± 0.13
  - Season (2): -0.39 ± 0.14
  - Year (2015): 0.40 ± 0.20
  - Connectivity: -0.61 ± 0.11
  - Patch shape: -0.10 ± 0.05
  - Patch Isolation: -0.18 ± 0.06
Figure 2. Diagram showing the effect of the most important variables explaining koala movement: distance travelled and tortuosity; and space use: number of core patches. Continuous lines indicate a positive effect and dashed lines indicate a negative effect. Line width is weighted by the model-averaged standardised parameter values in the generalised linear models, with width increasing with increasing parameter estimate values. Text boxes include the variable names and standardised parameter estimate values with standard errors.
Figure 3. Relationship between distance travelled by koalas ($n = 36$) across 4 months and patch connectivity. Shaded ribbon represents the 95% confidence interval. Image on the left represents a koala home range with one of the lowest level of patch connectivity (1.3), and the image on the right the highest (22.5). Both images have about the same amount of habitat, which is represented in green.
Figure 4. Relationship between number of core patches within koala home ranges ($n = 36$) and patch connectivity. Shaded ribbon represents the 95% confidence interval. Doubling the percentage of connected patches from points A to B represents a 1/3 reduction in the number of core patches in comparison to points B to C.
S1. Example of core areas (shown in orange) estimated using the 50% isopleth of an individual koala occupying a fragmented landscape.
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S2. Results of top ten generalised linear models describing overall movement (A), tortuosity (B), and space use (C) of koalas (n = 36) as a function of habitat fragmentation, sex, seasonality and year. Table includes the likelihood-based $R^2$, log-likelihood (LL), corrected Akaike value ($\text{AIC}_c$), change in $\text{AIC}_c$ ($\Delta\text{AIC}_c$), and weight ($\omega_i$). Habitat fragmentation measured by four metrics: clumpiness, connectivity index, patch shape, and patch isolation.

<table>
<thead>
<tr>
<th>Intercept</th>
<th>CLUMPY</th>
<th>CONNECT</th>
<th>PAFRAC</th>
<th>PROX_CV</th>
<th>Season</th>
<th>Sex</th>
<th>Year</th>
<th>$R^2$</th>
<th>LL</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$\omega_i$</th>
</tr>
</thead>
<tbody>
<tr>
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### Chapter 2: Effects of habitat fragmentation on animal movement & space use

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Chapter 3: Why revisit a patch? Patch quality and habitat fragmentation shape the temporal foraging patterns of a specialist folivore, the koala
Chapter 3: Tree recursion in a fragmented landscape

State of chapter

Chapter 3 has been written as a semi-stand-alone chapter ready to be modified slightly before submitting for publication, with authors AI Rus, C McArthur, VSA Mella, J Lindsay, B Moore, MS Crowther.

Statement of contributions

AIR, CM and MSC conceived the project; AIR, VSAM and JL collected the data; AIR conducted the spatial analysis; AIR and BM performed chemical and statistical analyses; AIR wrote the manuscript with feedback from CM, MSC, and BM.
Abstract

Research on animal use of foraging patches has mostly focused on why herbivores visit or quit patches, and little is known about patch recursion. Food quality and patch characteristics have been demonstrated to affect patch use, and so they should also affect patch revisit. In addition, habitat fragmentation could complicate the foraging decisions faced by herbivores. Here, we aimed to determine how leaf chemistry, shelter and habitat fragmentation affect tree reuse in koalas, a specialist folivore. We GPS-tracked 23 koalas near Gunnedah, NSW; and quantified metrics for revisitation to each tree, including number of revisits, average residence time, and average time-to-return. We measured leaf nitrogen and toxin levels, tree characteristics and tree connectivity level. We also modeled the costs of travel to revisited trees. We found an interactive effect of leaf nitrogen and tree connectivity on number of revisits. Residence time was positively affected by nitrogen level and tree diameter, and time to return was also positively affected by nitrogen level. Tree connectivity negatively affected the costs of travel between patches. We conclude that food quality and shelter are important factors that drive koala tree recursions. This work provides evidence that isolated scattered represent a valuable resource for animals moving across a fragmented landscape and their protection and enhancement is important for animal conservation.
Chapter 3: Tree recursion in a fragmented landscape

Introduction

Foraging herbivores face the dietary decision of how to maintain their nutrient intake while reducing the effects of plant defenses (McArthur et al. 2014). Folivore (i.e. browsers) in particular, must cope with diets that have low levels of essential nutrients, such as amino acids, yet incur high metabolic costs associated with ingesting plant secondary metabolites (PSMs) (Marsh et al. 2007). PSMs such as tannins can bind to protein, reducing their digestibility, and toxins can cause physiological damage (McArthur and Sanson 1991; Shipley et al. 2012; Sorensen et al. 2004). Plant toxins affect herbivore feeding behavior by limiting their food choices (McArthur et al. 1993; Provenza and Malechek 1984) and reducing food intake (Marsh et al. 2005; Moore and Foley 2005; Sorensen et al. 2004; Wiggins et al. 2003) by limiting food bout size and increasing the time between feeding bouts (Wiggins et al. 2006a; Wiggins et al. 2003). The capacity to cope with plant toxins differs between herbivores. Specialist folivores have a higher tolerance for toxins than generalists because they have evolved more efficient pathways to neutralise plant toxins (McArthur and Sanson 1991; Shipley et al. 2012), but they may still have to reduce food intake once toxic thresholds are reached. The consequences of these interactions between plants and herbivores is that nutrients may attract herbivores to food patches, but PSMs drive them away.

Nutritional quality and PSMs vary within patches and across the landscape (Moore et al. 2010), and, in such heterogeneous landscapes, herbivores should aim to visit high-quality patches (e.g. high in nutrients) with low plant defences. Consistent, free-ranging pygmy rabbits (Brachylagus idahoensis) and greater sage grouse (Centrocercus urophasianus) both select for patches with low plant toxin concentrations (Frye et al. 2013; Ulappa et al. 2014). Herbivores also have to
decide when to quit a food patch. The benefit of staying longer in a patch can provide greater nutrient intake but may incur higher costs such as risk of predation or detoxification.

Manipulative experiments have highlighted the effects of plant nutrition and toxins on patch quitting (Bedoya-Pérez et al. 2014; McArthur et al. 2012; Nersesian et al. 2011). For example, common brushtail possums (*Trichosurus vulpecula*) spent more time feeding in safe patches low in toxins and switched to riskier patches when toxins levels were higher in the safe patches (Nersesian et al. 2011).

Foraging is not the only motivator for using habitat patches: shelter can also be important. Herbivores may use shelter to avoid predators or thermoregulate. As a result, herbivores can have different habitat requirements (as food or shelter) within the diel cycle, driving the differential use of patches. In environments with large variation between diurnal and nocturnal temperatures, for example, herbivores may forage more frequently during cooler times of the day and seek shelter during periods of heat. During summer, Beira antelopes (*Dorcatragus megalotis*) use patches associated with increasing tree cover and are more active foraging at night (Giotto et al. 2013). Similarly, bridled nail-tail wallabies (*Onychogalea fraenata*) and red-necked wallabies (*Macropus rufogriseus*) shelter in areas with high plant cover (Fisher 2000; Le Mar and McArthur 2005).

Habitat fragmentation complicates the foraging decisions faced by herbivores. Greater fragmentation may lead to higher movement costs between foraging patches, either because
individuals must travel greater distances, increasing energetic costs, or they must move through open habitat, increasing predation risk. Consistent with this, predation rates were higher in root voles (*Microtus oeconomus*) occupying fragmented habitats with long interpatch distances (Andreassen and Ims 1998). Furthermore, when fragmentation isolates habitat patches, herbivores may have fewer food choices within patches and so need to move more between patches to satisfy their needs. The large cost of needing to travel between patches with reduced food diversity has been demonstrated for common brushtail possums, *Trichosurus vulpecula* (Wiggins et al. 2006b). For this generalist browser, a four-fold increase in travel costs just partially overcame the effects of PSMs on nutrient intake (Wiggins et al. 2006b).

While many studies focus on questions of why herbivores visit or quit patches, an equally important question is why herbivores return to previously visited patches. By incorporating metrics on revisits to patches in studies of foraging, space use and animal movement, we add a temporal component to the cost/benefit analysis that studies on visits *per se* cannot achieve. In doing so, we are better able to understand and measure the quality of the patch from the herbivore’s perspective. Since the quality and abundance of resources can vary across the landscape, individuals may return and spend more time in more favorable areas. The return of animals to previously visited patches is known as recursions (English et al. 2014; Riotte-Lambert et al. 2013; Van Moorter et al. 2016), and recursions are likely to be an important foraging
strategy for herbivores to exploit high-quality patches (Bar-David et al. 2009; McNaughton 1985).

While animal movement studies examining movement recursions are few (Riotte-Lambert et al. 2013), a similar process known as ‘traplining’ has been studied in insects, birds and primates (Berger-Tal and Bar-David 2015). For example, hummingbirds often return to previously visited flowers in regularly repeated ordered steps that optimise intake of nectar (e.g. Gill 1988) (Gill 1988). Few studies have examined the temporal use of patches by individuals in relation to food quality and shelter in natural environments. In two large herbivores, the Asiatic wild ass (Equus hemionus) and red deer (Cervus elaphus), number of revisits to foraging sites increased during periods of increased plant productivity (Giotto et al. 2015; Seidel and Boyce 2015) suggesting some form of harvest strategy. In Mountain Gorillas (Gorilla gorilla beringei), frequency of revisits was greater to areas where high-protein food was abundant (Watts 1998). These studies add to our general knowledge of the temporal foraging patterns of herbivores and re-use of patches.

Here, our aim was to determine how the temporal use — and particularly the re-use — of trees by a specialist arboreal folivore, the koala (Phascolarctos cinereus), is driven by plant chemistry, shelter, and habitat fragmentation in an agricultural landscape. We used the koala as our model species because it is a specialist herbivore that depends on trees for food and shelter (Crowther et al. 2014). Its specialized diet of eucalyptus leaves provides few nutrients and can be high in
toxins and tannins (Eschler et al. 2000; Moore and Foley 2005), limiting their foraging options across the landscape. Toxins such as formylated phloroglucinol compounds (FPCs) can be a strong feeding deterrent in captive individuals (Marsh et al. 2007) and influences tree selection by free-ranging koalas (Marsh et al. 2014; Moore and Foley 2005; Stalenberg et al. 2014).

Koalas can move between trees when canopies overlap but need to move on the ground when habitat fragmentation isolates forest patches or individual trees. Leaf chemistry has been found to affect the number of visits by koalas to particular eucalypts (Moore and Foley 2005) and time spent feeding in trees (Marsh et al. 2014) and koalas are known to return to previously used trees (Hindell et al. 1985; Mitchell 1990). How tree quality and habitat fragmentation affect decisions of when individual return to previous trees, and how often, is unknown.

We hypothesised that factors influencing koala revisits to resource trees would differ between day and night, as koalas are nocturnal (Marsh et al. 2014). We predicted that during the night koalas would revisit trees more often when they are high in nitrogen and low in FPCs. We also hypothesised that tree connectivity would affect the temporal use of patches. We predicted that koalas would revisits would decrease (fewer revisits and less frequently) to trees that were less connected within the landscape. We predicted that during the day, when koalas are resting, koalas would revisit trees that provide more shelter from the daytime temperatures.

We used movement patterns to determine the re-use of patches by measuring the number of revisits, average time spent in trees or Residence Time (RT), and average Time-to-Return (TtoR). For habitat fragmentation, we measured the connectivity of habitat surrounding the used trees.
Chapter 3: Tree recursion in a fragmented landscape

We used least-cost paths (LCP) as an index of the travel costs individuals may experience when revisiting trees and linked it to habitat fragmentation. The cost least-cost paths were based on open vs. forested ground and on the slope of the terrain.

Methods

Study area

We conducted the study on the Liverpool Plains near the town of Gunnedah, north-western New South Wales (NSW), Australia (30°59’S, 150°16’E). The landscape is a matrix of productive agricultural land and isolated open woodland patches, comprising Eucalyptus species including white box *E. albens*, yellow box *E. melliodora*, poplar box *E. populnea* and river red gum *E. camaldulensis* (Crowther et al. 2014; Dargan et al. 2019; Lunney et al. 2012).

Animal tracking

We used the movement data from 23 koalas fitted with GPS collars (average mass 120 g; Sirtrack, Hawkes Bay, New Zealand) between October 2015 and November 2017. The GPS collars recorded koala positions every 4-h for up to 5 months. We only included 4 months of movement data for our analysis to keep it consistent between individuals. Since koalas spend most of the day resting in one tree and move to the next tree during the night, 4-h recordings of their movements provided a balance between being able to identify trees their rested in, and therefore foraged on, and long-term temporal information for identifying revisits to trees. We determined the accuracy of the GPS collars using a static test next to a trigonometric survey.
Chapter 3: Tree recursion in a fragmented landscape

mark in Gunnedah (31° 01′ 47.05717″ S, 150° 16 ′ 04.32014″ E, for more detail, see Crowther et al. 2014. The distance root mean square error was calculated to be 9.05 m.

Koala tree use

We quantified three movement behaviors to examine tree use by koalas: 1) number of visits to each tree, 2) average residence time (RT), and 3) average return time to each tree (TtoR). We used ArcMap to create 5m buffers around the sampled trees, which were used to analyze the level of tree use by each koala. We considered koalas were using the tree when they were within the tree buffer for at least two consecutive location points (i.e. ≥ 4 hours), which was defined as a visit. If an animal left the tree buffer for more than two consecutive location points, it signified the end of the visit. For each sampled tree, we determine the number of revisit by counting the number of visits. RT was calculated as the average time per visit, and the TtoR was the average time between each visit. Singular visits were not used in the analysis of tree revisits, RT or TtoR.

Tree sampling

We used the location data collected by the GPS trackers to identify trees that were visited by koalas. Sampled trees were located using a handheld GPS unit (Garmin eTrex10), which had an accuracy of less than 3 m with most of the readings being within 1m. Due to the level of habitat fragmentation across the site, most sampled trees were more than 10 m from their conspecifics, reducing the uncertainty (due to GPS error) of the true tree selection by the
koalas. We measured physical attributes of the trees: tree height (m), diameter at breast height (~137 cm from ground level; in cm), and canopy cover. Canopy cover of each tree was assessed visually scored based on methods by Crowther et al. (2014) (range 1-3). To determine the leaf chemistry of each tree, we sampled approximately 50 g of mature eucalyptus leaves from the lower one-third of tree canopy. Leaves were placed in zip-lock bags and into a portable freezer at -20°C. Leaves were then freeze-dried and ground in a Foss Cyclotec 1093 mill (ANKOM Technology, Macedon, New York) using a 1mm screen. The dried leaves were stored in the dark in polyethylene vials at room temperature for later analysis.

**Leaf chemistry**

We measured the leaf concentrations of FPCs (mg/g) in 220 samples and total nitrogen (mg/g; hereafter referred to as N) in 412 samples. The spectra of all the dried ground leaf samples were collected from 400 to 2500 nm using a Near-Infrared Spectrometer (FOSS rapid content analyser XDS photospectrometer). Predictive equations were used to determine FPC and N concentrations following the methods used by Moore et al. (2005). A subset of the leaf samples was used to calibrate the predictive equations using partial least squared models with cross-validation.

FPC concentrations were determined using high-performance liquid chromatography (HPLC). Approximately 50 mg ± 1 mg of ground leaf sample was added to 4 ml of extraction solvent
(0.1% trifluoroacetic acid and 0.2 g.L\(^{-1}\) of 2-ethylphenol) and sonicated for two minutes (Wallis and Foley 2005). Samples were then filtered (0.25 µm nylon filter) into an autosampler vial and then loaded into the Agilent 1200 series HPLC. N concentrations of 200mg ± 10mg of freeze-dried ground leaf were determined using a LECO nitrogen/carbon analyser.

**Tree connectivity and least-cost path**

Our approach was to use tree connectivity to represent the level of habitat fragmentation surrounding trees revisited by koalas. When habitat is more fragmented trees are less connected to each other. To quantify tree connectivity, we created a 50 m buffer around each sampled tree and calculated the amount of tree habitat using a woody vegetation layer (i.e. trees > 2 m in height; Office of the Environment and Heritage, NSW, Australia). The buffer distance of 50 m was used because it represented the average daily distance movement by koalas at our study site. Then, we used FRAGSTATS v4 (McGarigal 2012) to analyse the spatial pattern of tree habitat within each buffer using four aggregation metrics: Clumpy, PAFRAC, Cohesion, AI (for more details see Supplementary Information).

We were interested in determining the movement cost of koalas revisiting trees that were more isolated from their conspecifics. The estimation of the movement costs was based on cost surfaces, which represents the index of cost related to energy expenditure and predation risks. We used ArcMap 10.5 (ESRI, Redlands, CA) to create cost surfaces to determine the least-cost
paths and accumulated cost for each sampled tree. Cost surfaces represent the level of landscape resistance that an animal may experience as it moves from one location to another. We modeled koalas moving from the edge of the 50 m buffer to the center (location of sampled tree). LCP can be highly sensitive to the entered resistance values, which can affect the accumulated cost values (Etherington and Penelope Holland 2013). Resistance values are normally inferred from species biology and movement across the landscape (e.g. Jeliazkov et al. 2019). Since there was no information on the cost of movement by koalas, we used the movements of five dispersing koalas to determine the resistance values. We tested two cost surfaces. We choose a resistance value of one as the base cost of koalas moving through tree habitat for both cost surfaces and either two (cost surface A) or eight (cost surface B) for open ground habitat. Cost of two would represent double the cost for koalas moving across open habitat and eight would mean eight times the cost of movement. We also included the costs of koalas moving over sloped terrain using a 5m resolution digital elevation model. After modeling the LCP for the two cost surfaces, we compared the path distances with the observed movement by the dispersing koalas (see supplementary information). We found that cost surface two was closer to the observed values. Therefore, we used the resistance values from the cost surface A to calculate the least-cost for the sampled trees.

Statistical analysis
R version 3.6.1 (R Core Team 2019) was used for all statistical analysis. We compared the concentrations of N and FPCs between the different tree species using a single factor ANOVA test. We then checked diagnostic plots to satisfy the assumptions of the parametric test.

Generalised mixed models were used to determine whether tree characteristics (physical and chemical) and connectivity could explain intensity of tree use by koalas (i.e. number of revisits, RT, and TtoR). We used mixed models to account for the repeat measures to each tree by including the individual animal as a random factor. Diagnostic plots of our data showed a non-normal distribution, and to overcome this, we used a Gamma distribution with a log-link for RT and TtoR, and Poisson distribution with a log-link for number of revisits. We created sets of models combining the external factors (i.e. DBH, Canopy Cover, leaf N, tree connectivity and tree height) with the measures of intensity of tree use. We checked the strength of each model by ranking them using the adjusted Akaike Information Criterion ($AIC_c$) (Anderson and Burnham 2002). We then examined the top models based on the $\Delta AIC_c$, log-likelihood and Akaike weights ($w_i$) and then calculated model-averaged estimates and standard errors for models <2 $\Delta AIC_c$ (R package ‘MuMln’ ver. 1.42.1; (Barton et al. 2015).

We used linear models to determine the effect of tree connectivity (Cohesion) on the cost of movement (i.e. accumulated cost) to revisited trees. We used the accumulated cost as the response variable and Cohesion as the explanatory variable. We used a $4^{th}$ root transformation on the response variable to satisfy the requirements of linear models.
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Results

Comparison of leaf chemistry between tree species

There was a significant difference in the N concentration between species ($F_{6,405} = 10.2$, $p<0.001$, Fig. 1). Concentrations of N were statistically higher in *E. dealbata* than *E. populnea* and *E. albens*. There was a statistical difference in the mean FPC concentrations between species ($F_{6,213} = 6.1$, $p<0.001$). *E. populnea* had the highest mean and was statistically significantly different from *E. albens, E. conical, E. largiflorance* (Fig. 2).

Night tree use

For number of tree revisits our results show an interaction between leaf N and tree connectivity (Fig. 3). Koalas had more revisits to trees that had higher cohesion at lower concentrations of N, and substantially more revisits to trees that had lower cohesion at higher concentrations of N, but not at lower concentrations of N (Fig. 4). Revisits were also slightly higher to trees that had higher cohesion but lower in N. Average time in trees (RT) was influenced by DBH and N (Fig. 3). Koalas spent more time in larger trees, and trees that contained high concentrations of N (Fig. 5). The average TtoR (Time to Return) was only influenced by N, with koalas returning much faster to trees that were high in N (Fig. 5).

Day tree use
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DBH, N, and tree canopy cover were the best predictors for koala tree revisits during the day (Fig. 3). Koalas revisited large trees, trees that contained high leaf nitrogen, and trees that had more canopy cover. Koalas also spent more time in large trees, trees that were less connected, and trees that contained high concentrations of N (Fig. 6). The average TtoR was influenced by DBH and N (Fig. 3). Koalas returned over a shorter period of time to the previously visited trees that were larger and trees that were high in N (Fig. 5).

Least-cost paths

There was a significant relationship between tree connectivity, measured by the cohesion metric, and the accumulated cost of Least-Cost Path ($\beta = -0.078$, SE $= \pm 0.008$, $P < 0.001$, $r_{adj} = 0.42$). Our results indicate a threefold change in the accumulated costs of koala movement to revisited patches between the highest and lowest levels of tree connectivity (Fig. 7).

Discussion

Our results show that tree leaf nitrogen is a strong driver causing herbivores to revisit foraging patches. But importantly, habitat fragmentation also plays a role in their foraging decisions. Surprisingly, during the night, there was a threefold increase in the number of revisits to trees with low tree connectivity (i.e. higher habitat fragmentation) provided they were high in N; and
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in contrast to this, when trees were highly connected, high nitrogen did not result in more frequent revisits. From an individual koala’s perspective, trees that are more isolated and higher in nitrogen were clearly highly valued; consistent with the general pattern that, on average, koalas returned much faster to trees that were higher in nitrogen. Since individuals had established home-ranges, they may revisit these isolated yet valuable trees as a form of resource defence, to deter competitors. Similarly, pied wagtails (*Motacilla alba*) defend their territories against invaders by systematically revisiting foraging spots across their home range, making it harder for invaders to forage on the most valuable areas (Davies and Houston 1981).

The contrasting pattern of reduced revisits by koalas to high N, highly connected trees may simply be due to the availability of more foraging options within close proximity.

The higher rates of revisits to trees that are less connected to their conspecifics might indicate higher costs to individual koalas. A low cohesion index (measure of tree connectivity across the landscape) for the focal tree means that the surrounding trees are far apart, and tree canopies are not interlocking. In such a case there is a higher chance that arboreal species, such as koalas, will need to move on the ground; and this movement across cleared habitat represents a higher risk of mortality. Repeated visits to trees that are less connected must pose a very high cost, either as energetic costs or predation risk. Yet koalas were willing to incur these movement costs for trees that were highly nutritious.
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The repeated use of less connected nutritious trees may also lead to greater browsing pressure on these trees — making them vulnerable to reduced growth rate and perhaps premature death, a longer-term consequence of habitat fragmentation. Koalas are known to defoliate highly preferred trees while leaving others untouched (Hindell et al. 1985), and defoliation and death of vast tracts of eucalypts by koalas occurs in the state of Victoria, Australia, where higher population densities are common (Hindell et al. 1985, Menkhorst 2008).

We also found leaf nitrogen played a role in how much time they spent in a tree (RT) and how quickly they returned (TtoR). Food intake can be related to the quality of food and foragers take advantage of higher quality patches by increasing their food intake. Although we did not directly measure nutrient intake, koalas do eat more when they spend more time in more nutritious trees (i.e. high nutrients and low toxin; Marsh et al. 2014). Koalas may also revisit trees to monitor leaf renewal rates; returning more often to high N trees than low N to do so. Marsh et al. 2014 speculated that koalas might visit unpalatable (low in N and high in FPCs) trees to update their knowledge about the nutritional quality. Leaf quality can fluctuate across time, for example in and out of seasonal or rainfall-driven leaf flush (Duursma et al. 2016; Pook et al. 1997) and as leaves age (Loney et al. 2006). Koalas may therefore optimise their foraging by revisiting trees based on the elapsed time since last visit, although, according to the optimal foraging theory, frequent revisits to profitable areas can increase foraging efficiency independent of food renewal rates (Pyke et al. 1977). For example, ovenbirds (Seiurus aurocapillus) revisited artificial patches with higher density of food more frequently than lower
food density patches when renewal rates were similar (Zach and Falls 1976). The fact koalas revisited more profitable trees (i.e. high in N) faster and many more times than less profitable ones in increasingly patchy habitat, is certainly consistent with hypotheses of efficient foraging.

Contrary to our predictions, the plant toxin concentration was not a strong predictor of tree revisits by koalas. We argue this is because FPC concentrations were much lower than previously reported in other eucalypt populations: >50 mg/g (Moore et al. 2004) compared with 0 - 15 mg/g here. Such low FPC concentrations could be related to environmental conditions, such as the high nutrient soils of this agricultural landscape (Dargan et al. 2019), drought and/or plant genetics. Consistent with this, *Eucalyptus* leaf FPC, nitrogen, phenolic and terpene concentration can all vary as a function of both genetics and the phenotypic influence of fertilizer (Loney et al. 2006; McArthur et al. 2003; O’Reilly-Wapstra et al. 2005); and drought can also lower concentrations of FPCs in *Eucalyptus* (McKiernan et al. 2015).

We found that tree canopy cover and DBH had a strong effect on number of revisits during the day. Our results indicate that koalas placed a higher value on trees that provided more shelter (i.e. tree canopy cover), because they returned more often. This is further supported by previous findings in which koalas used trees with higher canopy cover during the day (Crowther et al. 2014). Apart from shelter, large trees have higher heat capacities than smaller trees and are used by koalas for thermoregulation. During high daily temperatures, koalas were found to use large trees to dissipate heat through conduction with the tree limbs (Briscoe et al. 2014).
Interestingly, average time spent in trees (RT) and average return time (TtoR) during the day were not affected by tree canopy but by the size of the tree (DBH) and its quality (leaf N). Since large trees are favored by koalas for both food and shelter, koalas might revisit particular trees that serve both as a foraging patch during the night and shelter during the day. Such large trees with dense canopies therefore represent a valuable resource for koalas, especially in fragmented habitats, because they can provide both food and shelter.

**Conclusion and implications**

In this study we integrated movement, internal and external factors to explore the ecological question of why individual herbivores revisit resource patches. During nighttime, when koalas are actively feeding, revisits to trees were mainly influenced by leaf nitrogen and tree connectivity, and during daytime revisits were influenced by leaf nitrogen and shelter. Isolated trees high in nitrogen were revisited more frequently than more connected trees, and therefore represent an important resource for koalas occupying increasingly fragmented habitats.

In fragmented habitats, nutritious trees were likely to be revisited more often by koalas, possibly to defend valuable resources from conspecifics. While frequent returns may be
advantages to foragers, the impact on an animal’s fitness may be of concern with increasing density of a population. Loss of such valuable trees may also further fragment habitat and therefore is important to further protect isolated trees and perhaps replant patches of trees. Further research is needed to better understand the effects of increased herbivory on isolated resource patches and their effects on animal fitness and population dynamics. Cost surfaces are an underutilized tool in animal movement ecology and future research should incorporate the physiological costs (i.e. doubly labeled water study) and predation risks into the estimation of the landscape resistance values.

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References


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McGarigal, K., SA Cushman, and E Ene. (2012) FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html.


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**Figure 1.** Comparison of total leaf nitrogen by *Eucalyptus* species sampled across koala home-ranges. Letters were generated for each *Eucalyptus* species, and species sharing the same letter are not significantly different. Boxplots show median (middle horizontal lines), first and third quartiles (box hinges), data range (whiskers).
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Figure 2. Comparison of FPC concentrations by *Eucalyptus* species sampled across koala home-ranges. Letters were generated for each *Eucalyptus* species, and species sharing the same letter are not significantly different. Boxplots show median (middle horizontal lines), first and third quartiles (box hinges), data range (whiskers)
Figure 3. Path diagrams showing the effect of the most important variables explaining koala tree use: number of revisits, residence time and Time-to-Return. Line width is weighted by the model-averaged standardised parameter values of the mixed-effects models, with width increasing with increasing parameter estimate values. Text boxes include the variable names and standardised parameter estimate values with standard errors. Dashed box represents day tree use by koalas and solid box night use. TC = measure of tree connectivity based on cohesion metric; DBH = tree diameter at breast height; Total N = total leaf nitrogen.
Figure 4. Interaction plot representing the number of tree revisits during the night by koalas as a function of the interaction between total concentration of leaf nitrogen and cohesion. Higher cohesion represents higher tree connectivity.
**Figure 5.** Plots representing the effects of N and DBH on the average Residence Time and average Time-To-Return for trees during nightly revisits by koalas. Solid line represents the predicted relationship, and shaded area represents 95% confidence interval for the prediction.
Figure 6. Plots representing the effects of N, DBH and cohesion (measure of tree connectivity) on the number of revisits, average Residence Time, and average Time-To-Return for trees during daily revisits by koalas. Solid line represents the predicted relationship, and shaded area represents 95% confidence interval for the prediction.
Figure 7. The effects of cohesion (measure of tree connectivity) on the accumulated costs modeled by the least-cost paths (LCP). Solid line represents the predicted relationship, and shaded area represents 95% confidence interval for the prediction.
Appendixes

Habitat Fragmentation

We selected four metrics in FRAGSTATS associated with patch aggregation across the 50 m buffer centered on each focal tree, 1. Clumpiness index (Clumpy), 2. Perimeter-Area Fractal Dimension (PAFRAC), 3. Cohesion 4. Aggregation Index (AI). *Clumpy* represents the spatial organisation of patches and measures how far they deviate from a spatially random distribution. *PAFRAC* is a measure of shape complexity, with less complex shapes having simple perimeters and more complex shapes being convoluted. *Cohesion* measures the physical connectedness of the corresponding patch type and increases as the patch type becomes more aggregated in its distribution; hence, more physically connected. *AI* measures the frequency with which different pairs of patch types (including like adjacencies between the same patch type) appear side-by-side on the map and it increases as the focal patch type is increasingly aggregated and equals 100 when the patch type is maximally aggregated into a single, compact patch (for more information see McGarigal et al. 2012).
Chapter 3: Tree recursion in a fragmented landscape

Least-Cost Paths

Table 1. Comparison between least-cost paths (LCP) based on two cost surfaces and observed travel distances by five dispersing koalas. Values of 2 and 8 were used to model LCP for non-tree habitat for Cost Surface 1 and Cost Surface 2 respectively. A value of 1 was used to model LCP for tree habitat for both cost surfaces.

<table>
<thead>
<tr>
<th>Koala ID</th>
<th>Cost Surface A</th>
<th>Cost Surface B</th>
<th>Actual Distance (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DECC014</td>
<td>3923</td>
<td>4195</td>
<td>5387</td>
</tr>
<tr>
<td>DECC141</td>
<td>5493</td>
<td>5578</td>
<td>7345</td>
</tr>
<tr>
<td>DECC201</td>
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<td>6899</td>
<td>7959</td>
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<td>DECC110</td>
<td>2877</td>
<td>2894</td>
<td>3966</td>
</tr>
<tr>
<td>DECC118</td>
<td>2468</td>
<td>2350</td>
<td>2865</td>
</tr>
</tbody>
</table>

Figure S1. Example cost layer for highly fragmented habitat (left) and more contiguous habitat (right). Black lines represent two individual koalas moving in the two types of habitat.
Chapter 4: A specialist herbivore, the koala, shows routine movement behaviour in response to seasonal variations in plant productivity.
Chapter 4: Routine movement by a specialist herbivore

State of chapter

Chapter 4 has been written as a semi-stand-alone chapter ready to be modified slightly before submitting for publication, with authors Al Rus, C McArthur, VSA Mella, MS Crowther.

Statement of contributions

AIR, CM and MSC conceived the ideas and designed methodology; AIR and VSAM collected the data; AIR analysed the data; AIR wrote the manuscript with feedback from CM, MSC and VSAM.

All authors contributed critically to the drafts and gave final approval for publication.
Chapter 4: Routine movement by a specialist herbivore

Abstract

Temporal and spatial routine movements are two types of movement repeatability. While temporal routine defines the consistent revisititation to patches across time by individual animals, spatial routine describes the particular order in which individuals return to patches. Research on routine movement has been conducted mostly on nectar-feeding animals, and little is known about the routine movement behaviours of mammalian herbivores. Here, we aimed to examine temporal and spatial routine of patch revisits in a mammalian herbivore, the koala, and investigate the link between routine movement and internal and external factors. We GPS-tracked 25 koalas for up to 5 months in fragmented habitat in an agricultural landscape near Gunnedah, NSW, in 2015 – 2017. For temporal routine, we identified periodic patterns from time-series of presence/absence in individual core areas using Fourier and Wavelet analyses. For spatial routine, we investigated the systemic use of core areas by calculating the routine index using minimal conditional entropy. We found that 23 of 25 koalas performed temporal routine at 2, 7 and 20-day intervals, and more males had 2-day periodic interval than females. In general, rainfall and normalized difference vegetation index (NDVI) had negative effects on the probability of koalas performing temporal routine. Only 11 koalas performed spatial routine, and for these, there was a positive effect of the number of core patches on the spatial routine index. Despite this, the routine index at the population level was not significantly higher than random movement. Individuals likely visited core patches periodically, especially during less favourable conditions, to revisit highly valued trees. This is the first study to investigate and demonstrate routine movement in koalas, providing novel insights into koalas foraging behaviours.
Chapter 4: Routine movement by a specialist herbivore

Introduction

Movement is essential for the survival of individuals of most animal species by increasing the chance of finding food, shelter and mates (Nathan et al. 2008). In contrast to long range movements, such as dispersal or migration, animal movements can be restricted to small temporally stable areas defined as a home range (Van Moorter et al. 2009). Across an animal’s home range, resources may be clumped, and individuals may repeatedly revisit these particular areas because they are more productive (i.e. greater food quantity) and/or more nutritious (i.e. higher food quality) (Riotte-Lambert et al. 2013). For example, elk (*Cervus elaphus*) returned most frequently to high productivity vegetation patches (Seidel and Boyce 2015) and forest elephants (*Elephas maximus borneensis*) spent more time revisiting productive foraging sites (English et al. 2014).

How often individuals visit resource patches and how regularly the visits are spaced across time are important for understanding the periodic use of habitat as a function of internal (e.g. sex, age/experience) and external drivers (e.g. resource predictability, need to shelter from temperature extremes). At large temporal scales, for example, seasonal changes in resource abundance may lead to repetitive use of patches (Péron et al. 2018).

Movement repeatability, i.e. routine movement behaviour, is a widespread phenomenon across animal species, with theoretical (i.e. computer simulations) and empirical studies across many taxa (Berger-Tal and Bar-David 2015). Routine movement exhibited by individuals can vary temporally and/or spatially in response to external drivers such as resource cycling and
intra-specific competition (Bar-David et al. 2009; Riotte-Lambert et al. 2013; Riotte-Lambert et al. 2017). Routine use of patches can improve foraging performance of animals by enabling them to gain experience about locations and renewal rates of patches, giving them a competitive advantage over random foragers (Garrison 1999; Ohashi 2005; Williams 1998).

Animals can exhibit two types of movement routine: temporal and spatial. Temporal routine defines the consistent revisitation of patches across time by individual animals, and the routine process can be linked to particular drivers (internal or external) influencing the interval of revisits (Bar-David et al. 2009; Riotte-Lambert et al. 2013). In Regent honeyeaters (Xanthomyza phyrgia), for example, temporal routine was associated with rate of food renewal (Burke and Fulham 2003). Individuals avoided short time revisits to nectar feeders and, instead, returned to nectar feeders after a longer time had elapsed since the last visit. On the other hand, spatial routine (also known as ‘trap-lining’ behaviour) describes the particular order in which individuals return to foraging patches (Ohashi 2005). Non-random ordered sequence of revisits to patches — spatial routine — has been observed in Eurasian Griffon vultures (Gyps fulvus) revisiting supplementary feeding stations (Fluhr et al. 2017) and in bumblebees revisiting flower patches (Lihoreau et al. 2012; Thomson et al. 1997). Most knowledge about spatial routine in foraging animals comes from trap-lining research on bees and nectar feeding birds (Berger-Tal and Bar-David 2015), with this research attempting to explain routine behaviour as a mechanism employed by animals to minimize travel between patches while maximizing profitability (Ohashi 2005).
In mammalian herbivores, spatial and temporal routine has been explored through field experiments and computer simulations, in which routine is often inferred from movement behaviours such as path lengths and turning angles (Péron et al. 2018; Polansky et al. 2010; Wittemyer et al. 2008). Only a few studies have quantified the routine use (temporal and/or spatial) of habitat patches and linked them to internal and external factors. For example, impala (Aepyceros melampus) periodically used grazing areas every 24 hrs, 7 days and 30 days, which was associated with periods of decreased predation and reduced human disturbance (Riotte-Lambert et al. 2013). Black-tailed deer (Odocoileus hemionus) showed high spatial routine when moving between habitat patches (Riotte-Lambert et al. 2017). Whether routine use of patches by herbivores is influenced by seasonal variations in resources (both food and water) or variation in plant renewal rates has yet to be determined. Movement routine in the use of habitat patches, or lack thereof, can enhance our ability to understand the factors influencing habitat use.

We investigated the spatio-temporal patterns of patch use by a specialist arboreal herbivore, the koala (Phascolarctos cinereus), occupying a fragmented agricultural landscape, and linked these patterns to internal and external factors. Koalas are obligate specialists feeding exclusively on Eucalyptus leaves (Moore and Foley 2005). Tree selection by koalas has been found to be influenced by leaf nitrogen, toxin and tannin concentrations (Marsh et al. 2007; Moore and Foley 2005; Moore et al. 2010). Koalas maintain water intake through the
consumption of leaves (Nagy and Martin 1985), and leaf moisture is a driver of tree selection during periods of decreased rainfall (Ellis et al. 1995). We have also demonstrated that koalas revisit previously utilized trees, and their revisits are primarily driven by trees with higher leaf nitrogen, larger diameter, and increasing level of habitat fragmentation (see Chapter 2).

Here, we focused on two main questions:

1. Do koalas show any temporal routine and/or spatial routine of patch revisits, and if so, at what scales?

2. If koalas exhibit spatial and/or temporal routine, are there any internal and external drivers that may explain such patterns?

Since spatial and temporal routine is seen in nectar feeding insects and birds feeding on renewable, stationary, and predictable resource patches, we predicted that koalas also employ a similar strategy when foraging on trees, which are also renewable, stationary, and predictable resource patches. Revisiting patches routinely could improve foraging performance through experience, by knowing which patches are of high value, and by preventing competitors from depleting them.

We examined whether internal factors (sex and age) influence koala routine movement between foraging patches. Koalas are solitary and not known to be territorial (Ellis et al. 2009). However, field observations and movement data at our study site indicate that male koalas may exhibit some form of territoriality due to limited home range overlap (approximately 5%)
Chapter 4: Routine movement by a specialist herbivore

and observed confrontation between males. Male and female koala home range overlap can be as much as 50% and Female and Female overlap up to 20%. We therefore predicted that territoriality would drive temporal routine movement in males more than females. We also predicted that age would influence spatial routine. From lack of experience, younger, non-dispersing animals may be less efficient at foraging than older animals and therefore move more randomly between patches, hence show less routine.

Routine movement by koalas may be influenced by seasonal variations in rainfall and tree productivity. Since, tree leaf moisture varies in relation to moisture-holding capacity of the soil (Davidson and Reid 1989) and genetics of individual trees may also play a role in how adaptable trees are to periods of drought (Li and Wang 2003), there may be a variation in amount of leaf moisture and leaf productivity between trees and/or patches. We therefore predicted that seasonal variation in rainfall would lead to an increase in routine movement, because during periods of water scarcity individuals would consistently move between predictable patches that maintain an adequate amount of leaf moisture.

Habitat fragmentation may also be an important driver of routine movement since it reduces and isolates trees (i.e. patchy habitat), which may be more predictable to koalas since there are fewer trees to choose from. We used a measure of tree connectivity across an animal’s home range (calculated in chapter 2) to test whether habitat fragmentation influences routine movement. We predicted that animals occupying habitats with lower tree connectivity would show a higher probability of routine movement between patches, because employing a
consistent order of revisits, as well as timing of visits, would help individuals minimize travel costs (i.e. energy expenditure and/or predation) while increasing food profitability.

**Methods**

*Study site*

The study was conducted on the Liverpool Plains, surrounding the town of Gunnedah, northern New South Wales (NSW), Australia (30°59′S, 150°16′E). The landscape is a matrix of productive agricultural land and isolated open woodland patches, comprising *Eucalyptus* species including white box *E. albens*, yellow box *E. melliodora*, poplar box *E. populnea* and river red gum *E. camaldulensis* (Crowther et al. 2014; Dargan et al. 2019; Lunney et al. 2012). The climate in this region is temperate with occasional daily maximum temperatures going above 40 °C during summer and daily minimums going below 0 °C during winter. Annual rainfall ranges from 296 to 1139 mm with a mean of 633 mm (Bureau of Meteorology, 2019, www.bom.gov.au). This region had an extreme heatwave in 2009 after a long period of drought, which killed an estimated 25% of the Gunnedah population (Lunney et al. 2012).

*GPS tracking*

We used the movement data from 25 adult koalas (9 males and 16 females) that were not dispersing. Individuals were fitted with GPS collars (average mass 120 g; Sirtrack, Hawkes Bay,
New Zealand) and tracked between October 2015 and November 2017. The GPS collars recorded koala positions every 4-h for up to 5 months. We only included 4 months of movement data for our analysis to keep it consistent between individuals. We estimated missing values (<5% of the total set for all individuals) using linear interpolation. Detailed information about the timelines over which different individuals were monitored can be found in the Appendix Fig. S2 and plots of movement tracks in Appendix Fig. S3.

**Temporal routine**

To examine temporal routine, we analysed the periodic use of core areas. Core areas represent geographic patches that delineate intensively used or most revisited areas by animals (Benhamou and Riotte-Lambert 2012). We delineated core areas using the 50% contour of the cumulative frequencies of the utilization distribution (estimated using the Movement-based Kernel Density Estimation method; Benhamou 2011). For each animal, we built up a binary presence/absence time-series by attributing a “1” if the individual was present in a particular patch and a “0” when it was absent. Fourier periodograms were computed for each animal’s time-series, with peaks in the spectrum indicating which frequencies contribute the most to the variance of the series (Cazelles et al. 2008). Significant periodicities were determined using a permutational test that retained the number of transitional events of entering (i.e. 0 -> 1) and leaving a patch (1->0) (for more details see Riotte-Lambert et al. 2013).
We only considered Fourier periods that were significant at $p=0.05$ (see one example Fig. 1a). Though Fourier periodograms provide useful information about the dominant frequencies (i.e. frequencies with large peaks), but they assume that the properties of the time-series are stationary (i.e. do not vary with time; Cazelles et al. 2008). However, ecological processes are rarely stationary (Cazelles and Hales 2006). Wavelet analysis is often used as a second step in the process of analysing periodic patterns because it overcomes the problems of non-stationary ecological data, providing information about constancy of the dominant frequencies along the entire timeseries (Riotte-Lambert et al. 2013). We used wavelet analysis to determine the significant periodicities and how consistent they were across time. We used a permutational test similar to the one used for the Fourier analysis to determine the significant thresholds ($p=0.05$).

**Spatial routine**

We investigated spatial routine by assessing the degree of repetitiveness in sequences of visits to core patches using conditional entropy (Riotte-Lambert et al. 2017). For each koala, we created an ordered sequence of the visited patches from the presence/absence time series used for temporal routine. For each sequence, we computed the index of routine, which ranges from 0 (no spatial routine) to 1 (pure spatial routine). Because of home ranging constraints, routine movement may still be possible for individuals moving at random between core patches (Fluhr et al. 2017). To overcome this, we followed the approach of Fluhr et al. (2017) and ran computer simulations for each individual by simulating biased correlated random walk.
constrained by the individuals home range. The simulated movement tracks were biased towards the core patches using a landscape resistance raster (supplementary information Fig. S1). We compared the routine movement index of the actual versus the simulated tracks using a paired t-test.

**Internal and external determinants of routine**

We used multiple generalized linear models with a binomial distribution and a logit-link function to determine the relationship between the dominant frequencies detected by the Fourier transform (response variable) and explanatory variables sex, age group, and connectivity (see Table 1 for more details). We used a connectivity metric to quantify the level of habitat fragmentation within each koala’s home range (see chapter 1 for more details).

We created sets of models using generalized linear mixed models to test the probability of an individual visiting core patches periodically (response variable), as determined by the wavelet analysis. Then we linked the probability of koalas performing routine movement to internal factors of sex and age, and external factors of connectivity, rainfall and mean normalized difference vegetation index (NDVI). We obtained monthly rainfall from the Gunnedah Airport weather station ([www.bom.gov.au](http://www.bom.gov.au)). We used ArcMap to create the NDVI layers for the study site using monthly 30 m Landsat 8 multispectral images. We then clipped the core area patches from the NDVI layer to determine the average NDVI for each animal. We used NDVI because it is a longitudinal metric of plant productivity (Rasmussen 1998). We used the ‘glmer’ function in R with a binomial distribution and a log-link function with individual koala as the random effect.
Chapter 4: Routine movement by a specialist herbivore

We checked the strength of each model by ranking them using the adjusted Akaike Information Criterion (AIC$_c$) (Anderson and Burnham 2002). We then examined the top models based on the ΔAIC$_c$, log-likelihood and Akeike weights ($w_i$) and only considered the models <2 ΔAIC$_c$ as support for temporal routine (R package ‘MuMln’ ver. 1.42.1; Barton et al. 2015).

Results

Temporal Routine

The number of core patches within an animal’s home range varied from 3 to 19 (mean = 8, SD = 4; Table S1). The Fourier spectrum of the presence/absence time series revealed several significant periods (p < 0.05) across individual koalas (Fig. 1a). However, the temporal scales of the periodicities varied, and two individuals (females) out of 25 showed no significant movement periodicity. There was a tendency for more males to show periodicity at the smallest scale (i.e. 2-day periodicity) than females, and more females to show a periodicity at the largest scale (i.e. 20-day periodicity) than males (Fig. 2). The number of koalas exhibiting significant periodicities varied throughout time (Fig. 3). There was a significant sex effect for the 2-day periodicity, with a higher probability of males showing periodicity than females ($\beta = 3.20$, SE = 1.10, p < 0.010). We found no significant effects of age on the probability of routine (p > 0.1) or habitat connectivity (p > 0.1) on the probability of koalas exhibiting 2, 7 and 20-day periodicities.

During 2016, the number of individuals with periodic patterns was highest at the beginning of winter (April) and decreased each month until September. During the winter of 2017, the pattern was reversed. In terms of monthly variation in number of animals showing periodicity in
Chapter 4: Routine movement by a specialist herbivore

2016 and 2017 (Fig. 3) several models were within 2 ΔAICc, which included a combination of rainfall, NDVI, year and habitat connectivity (Table 2). The probability of koalas having significant periodicity increased with decreasing 3-month lag rainfall (β = -0.017, SE = 0.006; Fig. 3). There was an interaction between year and average NDVI (β = -2.24, SE = 1.07). In 2016 there was little change in the probability of periodicity in response to average NDVI, and in 2017 there was a higher probability of periodicity with decreasing average NDVI (Fig. 6).

Spatial Routine

Only 11 (4 males and 7 females) of 23 koalas had significantly higher routine than expected by a random movement (Appendix S1). There was a significant negative relationship between the number of core patches and the routine index (β = -0.017, SE = 0.007, P = 0.04). Individuals that had fewer core patches had a higher level of routine than ones with a greater number of core patches. At the population level, the global values of routine movement were low (mean = 0.28, SE = 0.1), and not significantly higher than those expected by random movement between core patches (mean = 0.26, SE = 0.2; paired Wilcoxon-Mann-Witney test; V_{25} = 177, p = 0.65; Fig. 4).
Discussion

This is the first study to quantify temporal and spatial routine in a specialist herbivore occupying a fragmented landscape. We found that most koalas have some temporal routine, varying to some extent among individuals and between males and females. There was no effect of age of animal on the periodic use of patches. Interestingly, core patches were more likely to be visited periodically during periods of decreased rainfall and lower plant productivity. At the population level, spatial routine was very low as only a few individuals moved significantly more routinely than expected by chance.

Our results indicate that koalas perform temporal routine, with males and females showing different periodicities. Males tended to routinely visit core patches at shorter intervals compared to females, and there was a higher probability of males exhibiting a 2-day periodicity than females. A 2-day cycle may indicate frequent patrolling of territory by male koalas by constant movement in and out of core patches, with less time spent in each core patch compared to female koalas. Core areas are known to contain highly valued food patches and they is known to be visited quite frequently by individuals (Benhamou and Riotte-Lambert 2012). Routine movement to these patches by male koalas could be a strategy for individuals to
appear more predictable, avoiding direct confrontation with neighbors and therefore reducing the risk of harm. Male koalas are known to use vocalization to deter rival males to avoid direct confrontation during mating season (Charlton et al. 2013). Perhaps individuals routinely move throughout their home range and use vocalization to avoid direct confrontations. Consistent with this, other territorial species have been shown to patrol their home ranges at a particular interval to mark their territory (Briscoe et al. 2002; Potts et al. 2012) and evict any intruders (pied wagtail Motacilla alba (Davies and Houston 1981); chimpanzees Pan troglodytes (Watson and Watson 2015). In contrast, female koalas having greater periodicities (7, 20-day) may indicate less frequent switching between core patches and perhaps more time spent in each patch to forage rather than to patrol.

The results from wavelet analysis, which we used to look at consistency of routing across time, showed seasonal variation in resource abundance impacted the probability of koalas exhibiting temporal routine. The increase in probability of koalas exhibiting temporal routine during periods of water scarcity (i.e. lower than average rainfall; Fig. 5) may indicate a water conservation strategy. Available water is very important for koalas because they get most of it from their diet; and only occasionally drink from open pools of water, particularly during heatwaves (Ellis et al. 2010; Ellis et al. 1995). It is possible, then, that during periods of water scarcity, temporal routine between core patches may be associated with accessing trees with leaves with high moisture content. Such trees may occupy soils with higher water capacity and/or be able to maintain higher leaf moisture than their conspecifics, though this has yet to
be tested. Consistent with our finding, other herbivores demonstrate routine behaviour in movement patterns during seasonal droughts. African elephants, for example, showed strong autocorrelated movements during periods of drought compared to more random movements during the monsoon season (Wittemyer et al. 2008) and Asiatic wild ass (*Equus hemionus*) revisits to artificial water sources were driven by decreased rainfall (Giotto et al. 2015).

Our results also showed strong support for plant productivity (mean NDVI) having an effect on the probability of koalas performing temporal routine, with koalas showing a negative relationship between probability of routine and mean plant productivity (Fig. 6). High probability of routine during reduced plant growth suggests that koalas could be using routine movement behavior to improve foraging efficiency, which may be essential for their daily energetic needs. By revisiting core patches routinely at particular intervals may benefit individuals by reducing the amount of time and energy spent searching for food. In addition, routine visits may also allow koalas to adjust their return to food trees after resources have renewed. However, it is important to note that the effect of reduced plant productivity was strongest during 2017, which suggests that plant productivity may have been affect by other factors such as yearly rainfall. As such, seasonal variations in resource abundance can be important factor in driving routine use of foraging patches and may be an indication plant renewal rates may drive routine movement in herbivores.
Chapter 4: Routine movement by a specialist herbivore

Our results showed that at the population level, koalas showed low levels of spatial routine when revisiting core patches; and only several individuals had an index of routine movement higher than simulated random movements. The index of routine was far below that observed in bumblebees (Lihoreau et al. 2013), hummingbirds (Tello-Ramos et al. 2015) and black deer (Riotte-Lambert et al. 2017). While we predicted that koalas would show high routine (both temporal and spatial) because they forage on stationary renewing food patches, having a particular order to revisiting food patches (e.g. spatial routine) may not matter as much as the timing for revisiting patches (e.g. temporal routine). It is possible koalas perform spatial routine when revisiting individual trees within the patches (i.e. revisiting trees in a particular sequence), but that question was beyond the scope of this study.

Our findings do raise some interesting questions about the spatial scale of routine movement, which has yet to be explored in the field of movement ecology. We know that the index of spatial routine by our koalas was much lower than for black deer, a generalist herbivore (Riotte-Lambert 2017). This difference may be explained by difference in the spatial scale of the food patches relevant to specialists and generalists. To generalists, larger spatial scales (e.g. patches containing various plant species) may represent predictable renewable resources driving high spatial routine. In contrast, at smaller spatial scales, such as the level of individual plants, generalists might forage at random between the different plant species, providing little advantage by performing routine movement. Specialists, such as koalas, on the other hand, may benefit from performing routine movement at the spatial scale of individual trees because
their food choices are limited. Although specialist should also have high routine at the larger spatial scales to optimise travelling, our counterintuitive results indicate that there might be other unexplained behaviours, such as being less predictable to predators when moving between patches.

For koalas that showed significant spatial routine, we found that only the number of core areas had a significant negative effect on the level of spatial routine. This may simply reflect that with fewer core areas (e.g. 3 core areas), there are fewer combinations of sequences available, forcing a higher routine index. For individuals with more core areas (e.g. 19 core areas), the choices among core patches are higher. With more combinations of sequence available, performing perfect routine movement could become too complex, unnecessary and even perhaps too energetically costly in terms of investing in spatial memory. Consistent with our results, in a manipulative experiment, hummingbirds showed higher spatial routine when they were presented with fewer feeding stations, and lower spatial routine with more feeding stations (Tello-Ramos et al. 2015). Interestingly, although we previously found a positive effect between the number of core areas and the level of habitat fragmentation (Rus et al. 2020, Chapter 2), habitat fragmentation did not affect the degree of spatial routine.

To conclude, our results demonstrate how internal and external factors affect the routine use of resource patches by a specialist herbivore, the koala. The next steps could be to examine routine behaviour at the scale of individual trees and explore the effects of plant renewal on
Chapter 4: Routine movement by a specialist herbivore

spatial and temporal routine in koalas. Investigating routine in response to plant renewal would provide insights into animal foraging efficiency. Expanding this type of study into a range of specialist and generalist herbivores would also enable a test of our suggestion that the scale of the patch may differ in importance.

We acknowledge that perhaps routine movement might be influenced by intraspecific interactions, where male koalas might have been visiting females. The movement data that we analyzed was before the breeding season and across several months, which would limit the effects of intraspecific interactions. While the effects of intraspecific interaction were beyond the scope of this paper, we suggest that future studies should include the interactions between males and females during the breeding season to determine its effects on spatial and temporal routine.

Acknowledgments

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(HWRE2017R1NEW197). Approval for this research was obtained from the NSW OEH Animal Ethics Committee (080211/02) and University of Sydney Animal Ethics Committee (2016/955).
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References


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**Chapter 4: Routine movement by a specialist herbivore**

**Tables**

**Table 1.** List of explanatory variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>CONNECT</td>
<td>Continuous</td>
<td>Connectance index – percentage of functional connections between patches (range 0 to 100; 0 = represents no connected patches; and 100 = one patch); Patches were considered connected if they were within a Euclidian distance of 50 meter of each other.</td>
</tr>
<tr>
<td>NDVI</td>
<td>Continuous</td>
<td>Mean monthly normalized difference vegetation index</td>
</tr>
<tr>
<td>Rainfall</td>
<td>Continuous</td>
<td>3-month lag in the average monthly rainfall</td>
</tr>
<tr>
<td>Sex</td>
<td>Categorical</td>
<td>M = Male; F = Female</td>
</tr>
<tr>
<td>Age Group</td>
<td>Categorical</td>
<td>Koala age group: A &lt; 3 years; B = 3 – 6 years; C &gt;6 years; Age was determined by the measure of tooth wear.</td>
</tr>
</tbody>
</table>
**Table 2.** Effect of internal and external variables on the probability that an individual shows temporal routine of core patches, using generalised linear mixed models (GLMM). Internal factors are sex and age, and external factors are connectivity, monthly NDVI and monthly Rainfall. Table includes coefficients, the corrected Akaike value (AIC$_c$), change in AIC$_c$ (ΔAIC$_c$), weight ($\omega_i$), and log-likelihood (LL).

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC$_c$</th>
<th>ΔAIC$_c$</th>
<th>$\omega_i$</th>
<th>LL</th>
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<tr>
<td>rainfall</td>
<td>126.75</td>
<td>0</td>
<td>0.25</td>
<td>-60.24</td>
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<tr>
<td>NDVI x Year</td>
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<td>0.48</td>
<td>0.2</td>
<td>-59.4</td>
</tr>
<tr>
<td>rainfall + Year</td>
<td>127.59</td>
<td>0.84</td>
<td>0.17</td>
<td>-59.58</td>
</tr>
<tr>
<td>Connect + Rainfall</td>
<td>128.67</td>
<td>1.92</td>
<td>0.1</td>
<td>-60.12</td>
</tr>
<tr>
<td>Rainfall + Age Group</td>
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<td>2.74</td>
<td>0.06</td>
<td>-59.41</td>
</tr>
<tr>
<td>Sex</td>
<td>130.51</td>
<td>3.76</td>
<td>0.04</td>
<td>-62.12</td>
</tr>
<tr>
<td>NDVI</td>
<td>130.57</td>
<td>3.83</td>
<td>0.04</td>
<td>-62.16</td>
</tr>
<tr>
<td>Null</td>
<td>130.58</td>
<td>3.84</td>
<td>0.04</td>
<td>-63.23</td>
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<td>3.89</td>
<td>0.04</td>
<td>-61.1</td>
</tr>
<tr>
<td>Connect</td>
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<td>5.77</td>
<td>0.01</td>
<td>-63.13</td>
</tr>
<tr>
<td>Year</td>
<td>132.55</td>
<td>5.8</td>
<td>0.01</td>
<td>-62.06</td>
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<tr>
<td>Connect + NDVI</td>
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<td>0.01</td>
<td>-62.1</td>
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<td>Connect + Sex</td>
<td>132.68</td>
<td>5.93</td>
<td>0.01</td>
<td>-62.12</td>
</tr>
<tr>
<td>Age Group</td>
<td>134.34</td>
<td>7.6</td>
<td>0.01</td>
<td>-62.95</td>
</tr>
<tr>
<td>NDVI + Age Group</td>
<td>134.37</td>
<td>7.62</td>
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<td>-61.86</td>
</tr>
<tr>
<td>Connect + Age Group</td>
<td>136.1</td>
<td>9.35</td>
<td>0</td>
<td>-62.72</td>
</tr>
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</table>
**Chapter 4: Routine movement by a specialist herbivore**

**Figures**

**Figure 1.** Fourier power spectrum for presence/absence time series (a) for one individual koala. The red dashed line represents the 5% significant threshold. Large peaks represent periodicities with higher power. (b) Wavelet power spectra for presence/absence time series (b) for one individual koala. Solid black lines represent 5% significant thresholds. The cone of influence (stripped area) indicates where spectrum values are unreliable due to edge effects. The time series spectra show 7-day significant periodicity that is consistent from July to September based on the significance threshold and the power.
**Figure 2.** Bar chart representing the number of male (blue) vs female (orange) koalas that had significant periodicities at the 2, 7, and 20-day intervals.
Figure 3. Number of koalas showing significant periodicities during winter in the year 2016 (blue) and 2017 (orange) based on the wavelet analysis.
Figure 4. Comparison of routine index between observed vs. simulated use of core patches by 25 koalas in a fragmented landscape.
Figure 5. Logistic regression relationships between probability of periodicity (temporal routine) by koalas and the 3-month rainfall lag for months of April-September.
Figure 6. Logistic regression relationships between probability of periodicity (temporal routine) by koalas and the interaction between year (2016 in red and 2017 in blue) and average monthly NDVI.
**Appendixes**

Table S1. Spatial routine of core patches and movement characteristics by 25 koalas in a fragmented landscape: home range (HR) size in ha, observed routine index (RI), simulated routine index (RI).

<table>
<thead>
<tr>
<th>Animal ID (sex)</th>
<th># Patches</th>
<th>HR Size</th>
<th>Observed RI</th>
<th>Simulated RI</th>
</tr>
</thead>
<tbody>
<tr>
<td>DECC004 (M)</td>
<td>19</td>
<td>44.2</td>
<td>0.14</td>
<td>0.05</td>
</tr>
<tr>
<td>DECC016(M)</td>
<td>14</td>
<td>52.8</td>
<td>0.08</td>
<td>0.13</td>
</tr>
<tr>
<td>DECC017(M)</td>
<td>3</td>
<td>25.1</td>
<td>0.05</td>
<td>0.42</td>
</tr>
<tr>
<td>DECC021(M)</td>
<td>4</td>
<td>8.6</td>
<td>0.30</td>
<td>0.51</td>
</tr>
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<td>DECC027(M)</td>
<td>4</td>
<td>18.4</td>
<td>0.46</td>
<td>0.30</td>
</tr>
<tr>
<td>DECC050(M)</td>
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<td>10.3</td>
<td>0.18</td>
<td>0.16</td>
</tr>
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<td>DECC052(M)</td>
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<td>3.7</td>
<td>0.47</td>
<td>0.14</td>
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<td>DECC053(M)</td>
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<td>36.6</td>
<td>0.09</td>
<td>0.10</td>
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<td>15.7</td>
<td>0.03</td>
<td>0.07</td>
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<td>DECC108(F)</td>
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<td>5.0</td>
<td>0.39</td>
<td>0.38</td>
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<tr>
<td>DECC129(F)</td>
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<td>9.2</td>
<td>0.39</td>
<td>0.22</td>
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<tr>
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<td>9.5</td>
<td>0.24</td>
<td>0.43</td>
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<td>0.44</td>
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<td>DECC139(F)</td>
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<td>3.6</td>
<td>0.48</td>
<td>0.42</td>
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<tr>
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<td>0.16</td>
<td>0.20</td>
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<td>DECC154(F)</td>
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<td>7.5</td>
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<td>0.22</td>
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<tr>
<td>DECC161(F)</td>
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<td>10.9</td>
<td>0.22</td>
<td>0.25</td>
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<tr>
<td>DECC167(F)</td>
<td>7</td>
<td>6.5</td>
<td>0.21</td>
<td>0.29</td>
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<tr>
<td>DECC173(F)</td>
<td>9</td>
<td>4.2</td>
<td>0.43</td>
<td>0.18</td>
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<tr>
<td>DECC180(F)</td>
<td>5</td>
<td>12.3</td>
<td>0.23</td>
<td>0.32</td>
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<td>DECC181(F)</td>
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<td>52.8</td>
<td>0.43</td>
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<td>DECC195(F)</td>
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<td>8.0</td>
<td>0.29</td>
<td>0.07</td>
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<tr>
<td>DECC198(F)</td>
<td>5</td>
<td>10.9</td>
<td>0.46</td>
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<tr>
<td>USYD001(F)</td>
<td>12</td>
<td>8.4</td>
<td>0.30</td>
<td>0.10</td>
</tr>
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</table>
Figure S1. Example of simulated movements (blue) for one individual koala within its home range. Landscape resistance is represented by the colour gradient with resistance of 0.0 representing the core area patches and resistance of 1.0 home range boundary and beyond.
Figure S2. Graphic of the timelines of koala movement data for 25 individuals monitored between 2015 and 2017.
Figure S3. Plot of the movement tracks for 25 individual koalas used in the analysis.
Chapter 5: General discussion
This thesis presented a series of mensurative studies investigating the drivers of movement in a specialist mammalian herbivore, the koala, in a fragmented agricultural landscape. First (Chapter 2), I investigated the internal and external factors affecting movement in terms of distance travelled, tortuosity of movement paths, and resulting core area characteristics. Specifically, I used landscape pattern metrics to quantify habitat fragmentation to examine how the distribution and organisation of habitat patches affect animal movement. Second (Chapter 3), I investigated the external factors influencing tree use by individual koalas by linking movement recursion (revisits to trees) to tree characteristics in terms of food quality (leaf chemistry) and shelter (canopy cover). I then used least-path costs to examine the effects of tree connectivity on the travel costs of movement recursion. Third (Chapter 4), I applied methods newly developed in the literature to investigate routine use of habitat patches and the internal and external drivers of routine behavior.

In Chapter 2, I found that functional connectivity of habitat patches affected how individual koalas move and how they use their space. Decreasing connectivity led to longer and more direct movements by koalas as they moved between patches, and to more core areas within an individual’s home-range, both indicating higher movement costs with increasing habitat fragmentation.

In Chapter 3, I found that factors influencing revisits by koalas to trees differed between night and day. At night, leaf nitrogen was a strong driver for koalas to revisit foraging patches, but
importantly habitat fragmentation also played a role in the foraging decisions. During the night, trees with the combined characteristics of low connectivity to others and with high leaf nitrogen were revisited three times as often as trees with high connectivity and high leaf nitrogen. When trees were highly connected, leaf nitrogen was less of an incentive to revisit. During revisits to trees, the amount of time koalas spent in a tree increased with increasing leaf nitrogen levels and with the size (diameter) of the tree. During the day, tree diameter, amount of shelter and leaf nitrogen all influenced the number of revisits, average time spent in trees and average return times. Koalas had more visits, spent more time in and returned more often to large trees, trees with greater shelter and trees high in nitrogen.

In Chapter 4, I found koalas showed significant temporal routine movement when revisiting core patches and some koalas also showed significant spatial routine. Temporally, more male koalas had 2-day significant periodicities than female koalas. Koalas also showed higher probability of temporal routine during times of decreased rainfall and, for one of two years, lower plant productivity (measured by NDVI). About half of the koalas showed significant spatial routine and koalas showed stronger routine when moving between fewer patches.
**Chapter 5: General discussion**

**Ecological implications of movement in a fragmented landscape**

*Consequences of habitat fragmentation*

I found that the level of connectivity between habitat patches was a strong determinant of how far koalas move. The outcome of fragmentation is the division and reduction in amount of suitable habitat, as well as increasing distance between habitat patches. As a result, koalas increased the number of intensely used areas (i.e. core areas) with decreasing connectivity between patches (Chapter 2). When individuals spend more time travelling between patches to fulfill their needs, such as energetic requirements and mates, I speculate that individuals would incur higher metabolic costs and result in higher physiological stress than individuals spending less time travelling between patches. Consistent with this, in Carnaby cockatoo (*Calyptorhynchus latirostris*), individuals occupying a fragmented landscape had to travel longer distances to find food, which lowered their breeding success (Saunders 1980; Saunders 1982).

Since koalas travelled more across several habitat patches in fragmented landscape, such a behavior might have an adverse effect on their fitness.

I speculate that the cost of travel across open habitat for koalas occupying a fragmented landscape is high. In terms of energetic costs, when patch isolation increases, individuals face the added cost of further to travel to reach the next tree. What we found is that koalas occupying least connected habitats showed a threefold increase in the total distance travelled compared to koalas in the most connected habitats (Chapter 2). Such an increase in total distance not only translates to high energetic costs because of the increased movement, but
also, likely, to other movement costs and risks associated with habitat fragmentation. For example, koalas, as an arboreal species, are presumably very vulnerable when crossing long stretches of open habitat on the ground when moving between habitat patches, because they lack the ability to quickly escape predators. Furthermore, for an arboreal species, especially for a specialist, the distinction between habitat and non-habitat is very clear, the lack of trees literally means no habitat, so there is no chance of supplementing food intake in any way while crossing this “desert”.

If increasing habitat fragmentation increases the risks and costs of travel between habitat patches, why do koalas still choose to move? It seems that trees within patches have abundant foliage, hence koalas should have abundant resources to exploit from within a patch. Previous studies have demonstrated that there is variation of leaf nutrients between trees in habitat used by koalas, and koalas select for those trees that are large and with leaves that have a high concentration of leaf nitrogen and low toxin concentration (Moore et al. 2010). One explanation of why koalas choose to move between patches might be that increasing habitat fragmentation results in fewer nutritious trees within a habitat patch, forcing koalas to move more to meet their nutritional needs. Since the concentration of leaf nutrients was the primary driver of tree visits (chapter three), koalas are willing to travel longer distances to visit other patches if the benefits of foraging on more nutritious trees across several habitat patches outweigh the cost of remaining in the same patch. This effect of habitat fragmentation on animal movement is not to understate the importance of other factors, such as reproduction.
and territory defense, which also drive animal movement (in particularly for males; Davies et al. 2013; Ellis et al. 2009; Chapter 2); but in the landscape of my study system, habitat fragmentation seems to be a strong factor.

Isolated trees that were high in leaf nitrogen had a higher number of revisits than less isolated trees, even though the cost of travel to these trees was much higher than less isolated trees (Chapter 3). Barth et al. (2019) also showed higher use of isolated scattered trees by koalas, although they did not explore the nutritional value of such trees. My findings suggest that from the perspective of an individual koala, trees that are more isolated (less connected) and high in nitrogen are highly valued. Therefore, there may be a benefit for koalas revisiting highly valued trees and even defending them as part of the territory. Consistent with the travel costs in fragmented landscapes, my results also showed that the least-cost path — an indirect measure of travel costs such as predation and energetic costs — increased with increasing tree isolation (Chapter tree). Koalas that occupied habitats with fewer trees that were far apart from one another prioritized the use of the trees that provided them with more nutritious leaves and shelter. In contrast, koalas that occupied habitats that were less fragmented had more trees to choose from, were therefore not restricted to visiting only a few trees, and so spread visits among trees of high leaf quality. Consistent with this, studies on koala movement and tree use in continuous forests found that individuals switched trees regularly and only rarely used the same tree twice (Ellis et al. 2009; Marsh et al. 2014). Rather than isolated trees being insignificant to koalas (which may be the intuitive conclusion), the patterns and importance of revisits that I found to these isolated trees indicates, in contrast, that they are extremely
important as food and shelter. Protection of such trees may be critical to ensure the survival of individual koalas in fragmented habitat.

More generally, my results suggest that species occupying fragmented habitats may be at risk from the effects of climate change, such as prolonged periods of drought and heatwaves. Smaller isolated patches can increase the exposure of animals to extreme environmental conditions (i.e. solar and wind exposure) because of reduced shelter. Ambient temperatures in forest fragments also have higher fluctuations in their minimum and maximum daily temperature than in continuous forest due to higher absorption of solar radiation by the surrounding cleared fields (Didham and Lawton 1999; Young and Mitchell 1994). Animals occupying fragmented habitats may have to use more energy for thermoregulation to overcome weather extremes, which may mean a reduction in fitness.

Coping with habitat fragmentation

I found some evidence that koalas employ several behaviours for coping with increasing habitat fragmentation. While they traveled more in more fragmented habitats, they also had more direct movements (Chapter 2). This direct movement reduces energy expenditure during travel and may also reduce the risk of predation by limiting the amount of time spent crossing a hostile environment. Similar behaviours have been observed in deer mice Peromyscus maniculatus (Stapp and Van Horne 1997), darkling beetles Eleodes obsolete (McIntyre and
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Wiens 1999), and butterflies Lepidoptera sp. (Cant et al. 2005), which all displayed more direct movements and spent more less time when travelling across risky open habitat (Stapp and Van Horne 1997). The added energy spent travelling between isolated patches may increase the metabolic costs of individual koalas, particular the males since they are larger and there is evidence that metabolic rate scales with body weight in mammals (Weibel et al. 2004). Males also travel longer distances compared to females, which can be more energy demanding (Chapter 2). The movement behaviours seen from koalas suggests that individuals may be able to cope with the energetic costs of movement in a fragmented landscape by spending more time and revisiting highly nutritious trees more often compared to koalas occupying less fragmented habitats (Chapter 3).

While increased time spent in nutritious isolated trees may benefit koalas, it could also have long-term effects to the trees themselves it is results in intense browsing; and any decline in tree health or worse still, tree death, may in turn have longer term detrimental effects on the browser (in this case koalas) and the ecosystem more broadly. Such impacts of overbrowsing by koalas have been seen elsewhere. For example, overabundant populations of koalas in Southern Australia have defoliated Eucalyptus trees (Menkhorst, 2008). Recent findings on the koala gut microbiome suggest that populations occupying habitats with E. viminalis and E. ovata may have become highly specialized on these particular species and may lack the capability to switch to other eucalypt species (Blyton et al. 2019). Intense herbivory by overabundant koala populations has led to starvation and widespread tree death (Menkhorst

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2008; Whisson et al. 2016). Furthermore, the effects of canopy defoliations have been found to negatively impact bird species diversity and richness (Whisson et al. 2018). Intense herbivory and its effects on ecosystems have been observed in other species - and is has been linked to overpopulation and increased browsing rates in the absence of predators (Ripple and Larsen 2000).

The behaviours I detected — less torturous movements between habitat patches and revisiting and spending more time in highly valued trees (Chapters 2 and 3) — that seem to help koalas cope with movement across a fragmented landscape may reflect evolutionary adaptations for occupying a naturally fragmented landscape. Since the pre-European landscape at my study site was dominated by native grassland and woodland habitat (Debus et al. 2017), some koala populations in the area would have occupied naturally patchy woodland habitat. Evolutionarily, animal populations living in a continuous habitat are slower at adapting movement parameters that can cope with changes in their environment (Fahrig 2003), compared to populations that have always had to move in a patchy woodland and grassy landscape.

Management implications for koalas in fragmented landscapes
My results suggest that koala management programs in fragmented landscapes should focus on increasing functional connection of habitat patches, because the distance travelled (hence cost
of travel) by koalas was substantially altered by this connectivity (Chapter 2). For example, managers could focus on strategically planting trees to restore functional connectivity between habitat patches to a level that provides the greatest change in the number of core areas, to provide one, or several, intensely used areas by individual koalas. A reduction in the number of core areas may also be advantageous by lowering energetic costs and predation risk, because koalas would spend less time moving between habitat patches.

Scattered isolated trees were highly valued by koalas, having the dual purpose of providing food and shelter while also providing a stopover between habitat patches (Chapter 3). Therefore, I suggest it is important that managers target such trees for protection and restore habitat around isolated trees to increase functional connectivity. Since folivores, including koalas, rely on leaf moisture to maintain hydration (Ellis et al. 1995), isolated high leaf nitrogen trees may be valuable for koalas not only from their provision of nutrients, but also by providing water supplementation. However, during heatwaves and periods of drought, isolated trees may not provide enough leaf moisture, and further water supplementation may be necessary. Evidence shows that koalas use water supplementation stations extensively throughout the year, particularly when daily temperatures were high (Mella et al. 2019). Providing supplemental water to koalas occupying highly fragmented habitat may mitigate water loss due to greater movement and exposure to the environment.
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The importance of habitat connectivity in a fragmented landscape is relevant beyond koalas, to other threatened or endangered species with specialised diets. Species such as the red panda (*Ailurus fulgens*) (Wei et al. 1999); giant panda (*Ailuropoda melanoleuca*) (Wei et al. 2015); greater bamboo lemur (*Prolemur simus*) (Wright et al. 2008); and woolly flying squirrel (*Eupetaurus cinereus*) (Din et al. 2015), for example, have all seen considerable decline in their habitat. Restoring and managing habitat to maintain functional connectivity across habitat patches for these threatened and endangered species may help mitigate some of the effects of habitat loss and fragmentation. The principles should also apply to less specialised species, through the responses to different metrics of habitat fragmentation need to be tested.

Future Research

I suggest future studies could build on the findings from my thesis to directly examine the costs of movement of animals occupying fragmented landscapes, in particular the risks of predation and physiological stress. Although I used the koala as a model species, the following suggestions and ideas can be adapted to other species:

1. Investigate the survival and reproductive rates of individuals as a function of habitat fragmentation. Habitat fragmentation affects how animals move in the landscape (Chapter 2, 3), and has been demonstrated to affect individual physiological stress levels (Johnstone et al. 2012). Consequently, the combined effects of habitat fragmentation and stress could ultimately affect individual survival and reproductive
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rates. Understanding the population dynamics arising from these impacts on individual animals could help in management and conservation of species in a fragmented landscape.

2. Investigate the link between recursion to foraging patches and plant renewal rate. Studies of recursion have only implied that plant renewal rates could be the driver for the timing of revisiting patches in herbivores. Understanding the plant renewal rate could provide novel insights into the mechanisms of patch revisitation and routine movement. In addition, monitoring the plant renewal rate across years could help determine how climate change affects plant physiology, and ultimately, animal foraging behaviours.

3. Investigate inter-individual variation and how animals respond to different level of habitat fragmentation. Studies have linked inter-individual variation in animal personality to inter-individual variation in movement and space use (Dingemanse et al. 2003; Wat et al. 2019) but not to habitat fragmentation. It may be the case that bold arboreal folivores may be more inclined to go to the ground and move long distances between patches, which would make them better able to cope with increasing habitat fragmentation. But perhaps it will also make them more susceptible to predation risk and other risks associated with moving on the ground. A link between habitat fragmentation and animal personality would add to our
understanding of how resilient certain personality traits are at dealing with the stressors of habitat fragmentation, and likely shifts in personality profiles of populations over time or in different landscapes.
**Figure 1.** Summary of the effect of habitat fragmentation on animal movement. The pictures on the left represent two examples of koala home ranges and the distribution of tree habitat (green). Habitat fragmentation, measured by tree connectivity, is increasing from the bottom to the top. For each movement parameter on the right the effect of habitat fragmentation is shown by an up arrow (positive effect), down arrow (negative effect), and no effect (flat line).
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References

Barth, B.J., FitzGibbon, S.I., Gillett, A., Wilson, R.S., Moffitt, B., Pye, G.W., Adam, D., Preece, H. & Ellis, W.A. (2019) Scattered paddock trees and roadside vegetation can provide important habitat for koalas (<i>Phascolarctos cinereus</i>) in an agricultural landscape. *Australian Mammalogy*, -.


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