THE IMPACTS OF ENVIRONMENTAL CHANGE ON DISPERsal
OF LARGE-SEEDED FOREST SPECIES BY THE EMU

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This thesis is presented for the degree of Doctor of Philosophy for
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I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary education institution.

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ABSTRACT

Seed dispersal is a critical stage in the life-cycle of plants. It is the process by which seeds escape the potentially deleterious density-dependent effects of deposition beneath conspecifics and other individuals. Long distance dispersal (LDD) – the movement of seeds considerable distances away from the parent plant – strongly influences plant population structures and dynamics. In response to global environmental change, LDD is a key mechanism by which species may be able to establish in new habitats and climatic ranges.

The emu (*Dromaius novaehollandiae*) is an important LDD vector in Australian ecosystems, capable of traversing many kilometres over a few days, and retaining large amounts of seed within the gut for up to a few weeks. In this thesis, the population dynamics of four large-seeded species within the jarrah (*Eucalyptus marginata*) forests of southwestern Australia was investigated within areas of contrasting high/low emu abundance. The focal plant species could all be dispersed by the emu and represented different life histories; *Leucopogon nutans* (Ericaceae), a fire-killed, short-lived seeder shrub, *Persoonia elliptica* (Proteaceae), an epicormic resprouting tree, *Macrozamia riedlei* (Zamiaceae), a long-lived, apical resprouting cycad, and *Podocarpus drouynianus* (Podocarpaceae), a long-lived, basal resprouting coniferous shrub.

Plant demographic assessment revealed that there was no difference in population structure, demographic rates or spatial structure for any of the species in contrasting sites of high/low emu abundance. A spatial simulation model and Bayesian change point analysis highlighted the difficulties in detecting a change in spatial structure following dispersal agent loss. For the three larger species, extreme plant longevity and environmental heterogeneity make it difficult to detect a change in plant spatial pattern following dispersal agent loss. For the shorter-lived *L. nutans*, high seed production and low frequency of removal masks any effect of whether emus are present or not in terms of population structure.

Visitation and fruit removal rates were generally low for each species, irrespective of emu abundance. The dispersal agent community was depauperate, with only a few vertebrates acting as local dispersal agents for each focal species. The emu was observed to ingest all of the focal species except *P. elliptica*. Telemetric tagging of *M.*
riedlei seeds revealed that the Australia Raven (*Corvus coronoides*) acts as a novel LDD vector, regularly dispersing individual seeds > 300 m from the parent plant.

Spatially-explicit simulation modelling of emu movement, informed from the Global Positioning System (GPS) tracking of birds within jarrah forest showed that the emu is a highly mobile and effective LDD vector, and could disperse many seeds > 1500 m from the parent plant and up to a maximum dispersal distance of ca. 7000 m during a 1000-hr simulated period. Modelling also revealed that the emu (and subsequent seed dispersal) is highly sensitive to changes to landscape configuration and composition. Simulated increases in habitat fragmentation and disconnection substantially reduced seed dispersal distances and collapsed LDD.

The emu is a highly effective seed dispersal agent (in terms of both quantity and quality of seeds dispersed), yet remains directly persecuted in some agricultural areas, and faces the same population pressures from habitat loss as other large organisms. The emu has shown a remarkable resilience to these pressures, and provides a pathway for plant species to expand their ranges under global environmental change. However, in order to fulfil this function, the emu requires a relatively contiguous landscape. Future work should focus on understanding the long-term (seasonal) movements of the emu to provide a complete picture of how this species contributes to seed dispersal in a changing landscape.
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Plate 6.1 Left, fish implant two-stage radio transmitter inserted into an *M. riedlei* seed (right, red arrow). Photographs from Gerlach (2012)

Plate 7.1 Attachment of the cuff above the ankle joint of a released emu
CHAPTER ONE

THESIS STRUCTURE AND SIGNIFICANCE

1.1 GENERAL INTRODUCTION

The dispersal of diaspores is a key, and the only vagile, component of plant demographic processes. The seeds of most plant species show physical adaptations supposedly designed to facilitate dispersal away from the parent, including endozoochory (diaspores carried within an animal), exozoochory (diaspores carried outside an animal), myrmecochory (seed dispersal by ants), explosive ballochory (explosive), hydrochory (water) and anemochory (wind), although some show no obvious mechanism (barochory) (Wright et al. 2007). Of these, particularly sophisticated dispersal mutualisms are observed to have evolved between plants and frugivores. Frugivores are the key dispersal agent for numerous large-seeded species within many tropical and temperate ecosystems and provide opportunities for both short and long-distance dispersal (LDD) (Clark et al. 1999a; Corlett 2007). The quality and quantity of seed dispersed by frugivores directly influences the population success of plants (Schupp 1993; Schupp et al. 2010), with limited dispersal often linked to negative demographic consequences.

Many frugivore/plant dispersal mutualisms are under threat as a result either of direct or indirect anthropogenic pressures. Large frugivores are especially threatened by direct persecution from hunting (Corlett 2007). For example, the African elephant (Loxodonta spp.) is an iconic large frugivore that provides LDD opportunities for many tree species (Dudley 2000), yet faces unprecedented direct threats from poaching and displacement from unprotected habitat. Populations of large frugivores are most at risk from anthropogenic impacts due to their typically large area requirements and the impacts that they in turn may have on human land-use activities (e.g. damage to crops). Habitat fragmentation, declining habitat quality, altered fire regimes, climate change and the interactions between these pressures have affected many large frugivore populations on most continents (Corlett 2007). Within Australia, populations of two large ratites capable of LDD - the Southern Cassowary (Casuarius casuarius) in Northern Queensland rainforests and the emu (Dromaius novaehollandiae Latham) in southern Australian forests and woodlands - face such threats (Calviño-Cancela et al. 2006; Bradford and Westcott 2010).
The evolutionary significance of LDD and the impact of a loss of LDD vectors cannot be overlooked. LDD is thought historically to have driven island colonisation and offers a means for plants to establish populations outside their existing ranges in response to climate and other global environmental changes (Nathan 2006). Dispersal is generally characterised through "dispersal kernels", which describe the probability of dispersal events occurring at, or beyond, specific distances (Nathan 2006; Nathan 2007). These kernels take the form of decay functions (Lognormal, Weibull, Exponential, etc; Hirsch et al. 2012b) with the probability of dispersal events occurring at long distances assumed to be low. The assumed rarity of these events is partially attributable to insufficient dispersal data (Nathan 2001) and insufficient knowledge of individual species' behaviours. Emerging and advancing technologies are now allowing researchers to fill the void in dispersal data, with radio telemetry, genotype analysis, censored tail reconstruction, satellite telemetry and nuclear marking allowing increasingly complete "total dispersal kernels" to be derived (Mack and Druliner 2003; He et al. 2009; Campbell et al. 2012; Hirsch et al. 2012b). This complete dispersal information can then be used in sophisticated simulation models to predict the likelihood and extent of plant range expansions and shifts in response to climate and other global environmental changes.

Dispersal kernels alone do not allow us to completely understand how plants may "move" in response to global environmental change. Detailed information is required on the behaviour of the frugivores that disperse the seeds. Unfortunately, historically there has been a poor meeting between animal and plant ecology (Nathan et al. 2008a). The emerging movement ecology paradigm seeks to ask why, how, when and where organisms move, providing a framework for understanding the behaviours of animals (including frugivores) and how they link to plant demographic processes, especially dispersal (Nathan et al. 2008a). If we can disentangle individual plant biology (including reproductive biology and seed ecology) and identify, describe and quantity frugivore seed dispersal agents and behaviours, then there is a unique opportunity to assess how frugivore loss or decline may affect populations of species under the impact of global environmental change.
1.2 PROJECT AIMS

The aim of this project is to assess the impact of the loss of the assumed sole extant large-seed disperser, the emu, on population dynamics of large-seeded species in the jarrah (*Eucalyptus marginata*) forests of southwestern Australia. This project describes the reproductive biology of these species and identifies both seed dispersal vectors and seed predators. Dispersal kernels for species dispersed by the emu are derived, which reveals how frequent and to what extent LDD events are. The seed ecology of each species is examined to assess to role of the dispersal vectors, in particular emu, on seed germination requirements. The impact of passage through the gut on seed viability and germination success is varied for many species consumed by ratites (Bradford and Westcott 2010), and a determination is made as to whether passage through the emu gut has a promotive or inhibiting effect on seed germination. Interactions between passage through the emu gut and other typical seed germination cues in fire-prone southwestern Australia (heat and smoke in particular) (Dixon *et al.* 1995) are also examined. The movement ecology of emu is investigated in a continuous northern jarrah forest fragment via satellite telemetry to define home ranges and movement behaviours/potentials that contribute to LDD. The reproductive biology of individual species, seed ecology, dispersal vector identity, dispersal kernels and *D. novaehollandiae* movement ecology is used to construct spatially-explicit agent-based simulation models that are used to predict the impact of changes in landscape configuration and composition on LDD.

1.3 GENERAL OBJECTIVES AND HYPOTHESES

1.3.1 Seed Dispersal

Objective (1): Quantify the frequency and distance of dispersal events for four large-seeded forest species with contrasting fire response and recruitment strategies for sites with contrasting emu abundance (high/low) using satellite tracking, radio telemetry and motion-sensitive, infra-red (IR) cameras.

Hypothesis (1): LDD is reduced/eliminated where emu abundance is low/absent i.e. there are no other long distance dispersers for the key study species.

Objective (2): Identify other seed dispersers and dispersal distances for target plant species using motion-sensitive IR cameras, radio telemetry and marked seeds.
Measure dispersal distances, construct and contrast seed dispersal curves for different dispersers.

Hypothesis (2): There will be a decrease in density and distance of LDD seeds as emu density declines. Other animals (native and invasive) will act as local (short-distance) dispersers or seed predators, thus changing the shape of the dispersal kernel.

1.3.2 Plant Demography

Objective (3): Quantify target plant species demographics, including population structures, recruitment, growth, survival and fecundity rates with and without fire (two of the four species show fire-stimulated fruiting, producing seeds mostly or only in the first year after fire).

Hypothesis (3): Where emu abundance is low there will be measurable deleterious plant demographic consequences (more evident in non-sprouter than resprouter species), including:

- More strongly aggregated spatial pattern
- Reduced fecundity and recruitment

1.3.3 Seed Ecology

Objective (4): Assess viability and germination requirements of animal-dispersed forest species, including the role of passage through the emu gut and of complex interactive factors (e.g. heat, smoke, temperature stratification and time) on germination.

Hypothesis (4): Dispersal is the major role played by seed passage through the emu gut, with additional subsequent (multiple) triggering factors necessary for germination.

1.3.4 Simulation Models

Objective (5): Construct and test computer simulation models of population (spatial) dynamics for target species incorporating dispersal kernels, and compare these for forests with and without the emu. Timescales of change will be investigated in relation to future change scenarios.

Hypothesis (5): Where emus are absent, plant species population structures will become more aggregated.
Objective (6): Construct spatially-explicit models using GPS telemetry data of emu movement to generate seed dispersal kernels in increasingly disconnected and impassable habitat.

Hypothesis (6): The extent and occurrence of LDD events by the emu will decrease as the landscape becomes increasingly fragmented (disconnected) and as the proportion of impassable habitat increases.

1.4 THESIS STRUCTURE

This thesis is presented as a series of stand-alone chapters, with a literature review following this general introduction. The literature review provides an overview of the impact of dispersal on plant demographic processes, with particular attention given to endo- and exozoochory. The review describes frugivores as agents of LDD and highlights the processes directly and indirectly threatening their populations. The review then elucidates the uncertainty surrounding passage of seed material through the gut of frugivores, specifically ratites, on seed germination requirements. The ways in which dispersal vectors may be identified and dispersal distances determined are examined. The review brings together this information to provide guidance as to how seed dispersal has been modelled in past work, and how the emerging movement ecology paradigm guides approaches to future studies.

The third chapter provides an overview of the distribution and ecology of the individual plant species included in this study as well as the ecosystems in which they are found. Attention is given here also to the distinctive biology of the emu, which makes it such a successful potential LDD vector. This chapter reveals the methods used to undertake assessments of the emu populations at sites of high and low emu abundance.

Chapter four presents the demography for each species at sites of contrasting high/low emu abundance, including population size structures, cone/flower production and seed/fruit production. For those species with a soil seed bank (SSB), the quantity and quality of soil-stored seeds is presented.

Chapter five examines the spatial pattern of each species at each site, analysed for evidence of aggregation in relation to disperser presence/abundance. A spatial
simulation model is also presented that highlights the difficulties in detecting a change in plant spatial pattern following dispersal agent loss.

Chapter six deals with the seed ecology of individual species. This includes analysis of the role of passage through the emu gut on seed germination and viability, and the germination requirements for selected species. The sixth chapter also identifies the local and LDD vectors for each species at contrasting sites of high/low emu abundance. Seed predators are identified. The distances that individual fruits/seeds are dispersed are presented following the use of radio telemetry and analytical methods.

Chapter seven presents the movement ecology and behaviours of emus within continuous northern jarrah forest. This chapter describes the extent and variation of their movements and behaviours as it influences potential LDD events.

Chapter eight describes the spatially-explicit agent-based simulation models. The simulation models provide a means of assessing the impact of changing landscape composition and configuration on LDD by the emu and for other models of animal movement typically used in the ecological literature.

The final chapter presents the conclusions of the study and synthesises each chapter to give an overview of the importance of improved understanding on rates of LDD and movement ecology. Future research directions are proposed.

1.5 PROJECT SIGNIFICANCE

Through the innovative estimation of the frequency, spatial scale, and consequences of LDD, where species traits and external (e.g. vector) factors that affect LDD are identified, significant advances in our understanding of the movement dynamics of plant populations are delivered. The integration of plant-animal interactions, plant demography and dispersal modelling is innovative and will lead to new insights into the importance of LDD and of dispersal vector disruption. It will contribute significantly to ecological theory by providing novel and strong empirical evidence on the frequency, extent and biological significance of LDD within the unified theoretical framework of movement ecology, and contribute to increasingly sophisticated and accurate models of threats to biodiversity from environmental change.
CHAPTER TWO

LITERATURE REVIEW

Introduction

This review discusses the importance of seed dispersal, particularly long distance dispersal (hereafter LDD), to the population persistence of many large-seeded forest species in the face of global environmental change. It provides a framework for understanding the components of dispersal that are relevant to the thesis; investigating seed dispersal of large-seeded jarrah forest species by the emu (*Dromaius novaehollandiae* Latham) and their persistence under global environmental change. The seeds of most plant species show physical adaptations supposedly designed to facilitate dispersal away from the parent through; endozoochory (diaspores carried within an animal), exozoochory (diaspores carried outside an animal), myrmecochory (seed dispersal by ants), ballochory (explosive), hydrochory (water), anemochory (wind) and barochory (no obvious mechanism/beneath the plant) (Wright *et al.* 2007).

While most seeds fall close to the parent plant, these adaptations play a primary role in range expansion through colonisation of new habitat. This expansion requires LDD through a variety of vectors, although the frequency at which seeds are dispersed long distances is thought to be rare (Nathan *et al.* 2003). Non-standard dispersal vectors (where the primary dispersal adaptation is not primarily associated with the vector) are also thought to contribute significantly to rates of LDD. LDD through non-standard vectors is likely then to also provide plants with increased resilience under global environmental change.

The southwest botanical province of Western Australia is recognised as a global biodiversity hotspot, owing not only to a biodiverse flora, but also exposure to a number of processes threatening ecological structure and function (Myers *et al.* 2000). Among these, land clearance, habitat fragmentation, grazing pressure, invasion by exotic flora and fauna, salinity, anthropogenically-altered fire regimes and hydrological cycles, and climate change, are the most significant processes threatening long-term species persistence within the region (Sattler and Creighton 2002; Burgman *et al.* 2007). The improved contemporary understanding of the significant impact these threatening processes may have on plant population dynamics has contributed to an increased and renewed interest in LDD, with LDD identified as playing a key role in linking spatially disjunct populations (Opdam and Wascher 2004). Moreover, Nathan *et al.* (2008a)
suggest that “the long-distance movements of various organisms can greatly impact the spatial dynamics of local populations and communities, driving species’ responses to fragmentation, playing a key role in species invasions, responses to climate change, and other global concerns”. In defining LDD, a basic problem remains in deciding how far is ‘far enough’. Due consideration needs to be given to the scale involved (Nathan et al. 2003). In plant ecological studies, LDD is generally considered to include those infrequent dispersal events that fall in a high percentile (e.g. 95th or 99th) of a specific cumulative dispersal probability, or where diaspores have been transported to a distance greater than 100 times mature plant height (Nathan et al. 2003). Following this, it becomes important to highlight that the modern resurgence of interest in LDD follows a past limited perception of its importance owing (1) to its perceived rarity, (2) the difficulty in quantifying its occurrence, and (3) the argument that LDD is not the selective “reason”, in both an evolutionary and ecological context, for diaspore vagility (Howe and Smallwood 1982; Higgins et al. 2003). There are now improved methods for determining LDD, such as the use of molecular markers to assign parentage to dispersed seeds and/or seedlings to obtain estimates of realised LDD (He et al. 2004; Lesser and Jackson 2013). The use of radio telemetry and satellite technologies also permits accurate determination of the possible distances of LDD within various ecosystem types (Nathan et al. 2003; Griesser et al. 2014). There is emerging evidence to suggest that LDD is occurring in systems at surprisingly high rates, at least within species-rich shrublands, with key LDD vectors dispersing a number of plant species irrespective of their dispersal morphologies and regeneration responses (He et al. 2004; Krauss et al. 2006; He et al. 2009). Consequently, plant species may be endowed with a stronger resilience to global environmental change (particularly climate change, habitat fragmentation and anthropogenically-altered fire regimes) than previously considered.

Rates of LDD need to be determined within and among vegetation types with different structural properties, different disturbance regimes, varying taxa, and for a range of dispersal vectors in order to test the applicability of emerging generalisations regarding LDD and its potential to assist plant population resilience to global environmental change (Peterson et al. 1998; Corlett and Westcott 2013). For instance, diaspore (a spore, seed or structure that functions in plant dispersal) dispersal by vertebrates as LDD vectors, both through endo- and exozoochory, has been shown to result in dispersal distances greater than those recorded for wind, myrmecochory or unassisted
dispersal (Takahashi and Kamitani 2004). For plants responding to a changing climate, zoochory has been shown to be more important for range expansions, in comparison to anemochory (Cunze et al. 2013). Plants whose seeds and/or pollen are able to move between habitat fragments (or colonise new habitats) will likely maintain genetic diversity and viable metapopulations (Hamrick 2004; Bacles et al. 2006; Uriarte et al. 2011). However, this resilience is reliant on disperser populations remaining intact. Humans alter the dispersal of seeds both directly, through impacts on frugivores (herbivore or omnivore where fruit is a preferred food), and through land use conversion (Wright et al. 2007). There is also a recognised synergism between direct and indirect anthropogenic disturbances, with direct persecution of animals (i.e. hunting and pest management) increasing in fragmented landscapes (Peres 2001). This synergism may affect seed dispersal by altering the abundances and behaviours of animals, with resulting trophic cascade (i.e. top-down) effects. However, whether the incidence of seed dispersal is increased or reduced may be species-specific (Dennis et al. 2005). Generally, species of plants with large, animal-dispersed diaspores will experience inhibited dispersal resulting from direct and indirect anthropogenic influences because of the strong relationship between the size of a species and its susceptibility to anthropogenic impacts (Wright et al. 2007; Moura et al. 2014). Moreover, large, flightless frugivores are especially susceptible to population decline and local extinction due to their generally long generation times, low reproductive capacities, large territories or home ranges and preference as game species (Cardillo et al. 2005; Corlett 2007). This will likely lead to reduced fitness and population decline in plant species dependent on them. For example, in tropical north Queensland more than 100 different plant species are considered to be dependent on the endangered cassowary (Casuarius casuarius), a large flightless frugivorous bird, to disperse seeds and enhance germinability of seeds as a result of retention in the gut (Bradford and Westcott 2010). In this instance, cassowary population decline would threaten the persistence of many tropical plant species. Similarly, within the jarrah forests of southwest Western Australia, the emu is the putative sole extant large seed disperser. Other important dispersers within the jarrah forests for key large-seeded species have been lost, with the now extinct megafauna disappearing in the first few thousands of years after the arrival of Aborigines on the continent (Enright and Thomas 2008). The emu has the capacity to retain diaspores in its gut for from several days to many months, and transport these diaspores over distances potentially of tens to hundreds of kilometres (but likely much less in the wetter, forested parts of SW Australia where local resource levels are higher)
(Calviño-Cancela et al. 2006; Dunstan et al. 2013). However, although emus are known to consume a variety of seeds with varying dispersal morphologies, their role as seed dispersers has received little attention and potential effects on plant communities are largely indeterminate. There is limited evidence on the role of the emu as an LDD vector, with much of the recent literature focussing on the dispersal morphologies of seeds found in emu scats (Calviño-Cancela et al. 2006). More attention needs to be given to ascertaining the viability of these ingested seeds and assigning parentage to obtain true rates of LDD.

LDD is very important for plant population dynamics at both the local and landscape scales in relation to the activities of specialist LDD vectors (such as large flightless frugivores), and population resilience, especially when considering global environmental change (Calviño-Cancela et al. 2008; Corlett and Westcott 2013). To better understand how the complex movement of these specialist vectors influences plant population dynamics (through LDD), it is useful to apply an integrative scheme that can link movement to ecological processes. The study of LDD may be considered within the conceptual framework of ‘movement ecology’, which provides an integrated conceptual, theoretical, methodological and empirical basis for examining the movement of organisms to elucidate the synergies between the internal state of an organism, its motion and navigation capacity and any other external factors influencing movement (Nathan 2008).

**Anthropogenic Impacts on Dispersers and Plant Demographic Consequences**

The dispersal of seeds has a profound impact on the structure of vegetation at multiple scales, with the dynamics of seed dispersal mediating numerous plant processes, including the maintenance of species diversity, colonisation, metapopulation preservation, regeneration and succession (Howe and Smallwood 1982; Wang and Smith 2002). Traditionally, the dispersal of seeds has been broadly divided into two categorical states; namely short and long distance dispersal, with the latter particularly difficult to quantify (Nathan et al. 2003). Following from this, primary seed dispersal vectors/mechanisms can be further allocated into categories which aid our understanding of their behaviours and susceptibility to anthropogenic disturbance; these include bats, small birds (< 300 g body mass), large birds, non-volant mammals (variously categorised as zoochory), ballochory, hydrochory, wind and barochory (Wright et al. 2007). These primary seed dispersal agents, or vectors, interact with
plant diaspores to facilitate seed dispersal, promoting the long-term survival of individual species and maintenance of local and landscape-scale diversity. Through seed dispersal, and especially LDD, seeds are transported away from parent plants, germinating and establishing in new locations, often with increased rates of survival owing to an escape from density-dependent effects (i.e. competition) encountered under the canopy of parent plants or conspecifics (Antonovics and Levin 1980; Nathan 2006). Anthropogenic influences may directly and/or indirectly impact seed disperser populations (Corlett 2007), affecting seed dispersal and leading to negative demographic consequences (Andreazzi et al. 2012). A single dispersal agent may transport a variety of diaspores (e.g. Jordano et al. 2007; Calviño-Cancela et al. 2008) or the diaspores of an individual species may be potentially transported by a varied and dynamic disperser community (e.g. Burbidge and Whelan 1982). As a result, anthropogenic disturbance impacts both directly on disperser communities, and indirectly on ecological processes, with the underlying interactions between these likely to have a profound impact on the long-term persistence of many species (Blendinger et al. 2011).

A great deal of empirical evidence suggests that anthropogenic influences, especially habitat fragmentation combined with increasing urbanisation, negatively impact disperser communities and lead to a decline in disperser abundance, fruit removal, seed dispersal and subsequent recruitment (Rodríguez-Cabal et al. 2007). Within southwestern Australia, approximately 90% of the original great western woodlands have been cleared for agricultural purposes (Wardell-Johnson and Calver 2005). The jarrah forests, southwest of these woodlands, have also suffered extensive disturbance. It is perhaps surprising then that there is emerging evidence to suggest that urbanised and fragmented environments in addition to degraded agroecosystems may either facilitate dispersal (via anthropochory) or remain intrinsically resilient to disturbance impacts (Von Der Lippe and Kowarik 2008; Breitbach et al. 2010). For instance, Auffret (2011) identified non-standard, human-mediated dispersal vectors such as clothing and motor vehicles as transporting the seeds of European grassland species, with numerous dispersal morphologies, over extensive distances. Wace (1977) was perhaps the first to describe the transportation of seeds attached to the undercarriage of motor vehicles in the Australian Capital Territory. Unfortunately and conversely, these very same human-mediated dispersal vectors also provide opportunities for the transport of exotic species (Barney 2006; Pickering and Mount 2010). In general,
habitat fragmentation alone has not been seen to substantially reduce dispersal distances, visitation and seed removal rates for seeds dispersed by large frugivores (Uriarte et al. 2011; Markl et al. 2012.). However, the capacity of species to move within and between fragments will have an effect on the impact of fragmentation on seed dispersal.

**Dispersal Vectors and LDD**

The diaspores of plant species are generally considered to have particular morphologies to enhance dispersal by specific vectors that facilitate long term population persistence (Soons and Ozinga 2005). These adaptive traits contribute to the persistence of individual species by allowing them to escape the density-dependent effects of competition and avoid local predators and pathogens through the occupation of new habitat (Howe and Smallwood 1982; Nathan and Muller-Landau 2000). To fully appreciate the importance of LDD within numerous ecosystems, one needs to understand that some diaspores, regardless of their dispersal morphologies, are capable of being dispersed long distances by multiple vectors (Nathan et al. 2008b) and that the incidence of LDD by non-standard vectors may not be as rare as originally presumed (Nathan 2006). For instance, Calviño-Cancela et al. (2006) investigated the diaspore matrix of emu scats in the floristically biodiverse sandplains of southwestern Australia, revealing seed material with diverse dispersal morphologies including vertebrate endozoochory, exozoochory, anemochory, myrmecochory and barochory. Ratites such as the emu possess seed and fruit consumption and digestion characteristics that lead to the gentle processing of seed material, long gut retention times and the capacity to move seeds over long distances (Davies 2002). They are thus appropriately recognised as non-standard vectors contributing to LDD for many plant species. However, Higgins et al. (2003) argue that the link between dispersal syndromes and LDD is poor because of the often complex and multiple mechanisms involved in seed dispersal, and it remains uncertain whether LDD events in plants are usually caused by non-standard means of dispersal or not. Nevertheless, LDD events are important to the maintenance of populations. For example, in agroecosystem landscapes such as the wheat-belt of Western Australia, natural vegetation remnants have become disconnected and degraded, with native perennial vegetation largely replaced by annual crops and pastures (Hobbs 1993). Here, LDD of many native species occurs by highly mobile
organisms (such as large frugivorous birds, especially ratites) and is likely to be important in maintaining ecosystem function (Breitbach et al. 2010).

**Demographic Consequences of Disperser Decline**

Before it is possible to determine how a reduction in, or removal of, dispersers might affect the demography of individual plant species, it is important to understand the complexity of the dispersal process; from fruit selection, to dispersal, secondary and subsequent dispersal, seedling emergence and survival, and how all these components of the seed dispersal system can have a profound influence on vegetation structure (Wang and Smith 2002). Dispersal effectiveness generally has been split into two components; the quantitative, i.e. the number of seeds removed (and subsequently dispersed), and the qualitative, which describes the quality and characteristics of seeds dispersed and the sites into which they are deposited (Schupp 1993; Schupp et al. 2010). It is necessary to address how a reduction in frugivore populations might impact these quantitative and qualitative elements and how these individually, and the interplay between them, play a role in plant demographic processes (Rodríguez-Pérez and Traveset 2010). While much attention has been paid to the quantitative component and potential impacts on plant demography following disperser reduction (e.g. Schupp 1993; Corderio et al. 2009), less attention has been given to the qualitative components (Schupp and Fuentes 1995; Vidal et al. 2013; Benítez-Malvido et al. 2014). This disparity in the literature is perhaps attributable to difficulty in the measurement of variables pertaining to fruit selection, impact of endozoochory on seed viability and germinability, patterns of seed deposition at varying spatio-temporal scales, and ensuing seedling emergence and survival (Rodríguez-Pérez and Traveset 2010). If we consider these difficulties in conjunction with the often-cited challenges of measuring LDD (Nathan 2001) and the important implications that it has on plant population survival and structure, especially within anthropogenically-altered landscapes (Bohrer et al. 2005), the qualitative aspects of endozoochory in relation to LDD become increasingly intriguing and demanding of further investigation. As severed dispersal mutualisms will significantly impact dispersal effectiveness (both in quality and quantity of seeds dispersed), populations of plant species that rely on these mutualisms will be directly affected (Rodríguez-Cabal et al. 2007). The importance of each component of the seed dispersal system and dispersal effectiveness requires assessment to determine how plant species and broader communities will respond to disruption (Howe and Miriti 2004).
Seed dispersal contributes to improved demographic performance by releasing seeds and emergent seedlings from the competitive pressures (e.g. allelopathy, intraspecific competition and pest facilitation) of establishment beneath the canopy and in the vicinity of parents and closely-related conspecifics (Wright 2002). However, negative demographic performance under conspecifics is not uniform, exhibiting temporal variation and a dependence on specific environmental conditions and community diversity (Wright 2002; Rodríguez-Cabal et al. 2007). For instance, Rodríguez-Cabal et al. (2007) observed higher seedling survival of Daphne rodriquezii, a small Mediterranean evergreen shrub, under heterospecifics after dispersal by its sole disperser, the lizard (Podarcis lilfordi), in comparison to seedlings located under conspecifics. Concordant patterns of seedling survival under heterospecifics and conspecifics have also been reported in other Mediterranean regions (see Rey and Alcantara 2000), although, they note that observations varied with climatic conditions, with the higher seedling survival in years of average rainfall, while under drought conditions seedling survival was independent of deposition under conspecifics or heterospecifics. Similarly, Lázar et al. (2006) suggest that hydric stress can be the most significant bottleneck to regeneration, with the inconsistencies in regenerative effects at microhabitat and temporal scales making determination of patterns at larger scales problematic. Ultimately, it is clear that the selection for or against dispersal and subsequent demographic benefits or consequences varies across, and interacts with, spatial and temporal scales, environmental gradients and inter and intraspecific interactions. Even within a species considerable variation may be observed, further confounding the selective influences on dispersal. Increased dispersal reduces density-dependant mortality as a result of high seed and seedling density. Dispersal also allows plants to escape inbreeding depression (due to reproduction between genetically-similar individuals), which leads to negative fitness outcomes such as reduced flowering and fruit production. Strong Allee effects (where small populations have a critical size or density) may also be avoided through dispersal (Stephens et al. 1999). Species without specific adaptations for dispersal (such as Silene diclinis, Montesinos et al. 2006) may be particularly vulnerable to global environmental change, but LDD via non-standard vectors may provide the means for long term persistence and population survival for these species. Due attention needs to be given to the spatial patterns of recruitment in relation to disperser populations and activity, particularly considering periods of environmental stress, such as those encountered under global environmental change. Spatial patterns of seed dispersal and recruitment aid in not only the deconstruction of
potential LDD vectors but also assist in predicting the survival, persistence and reproductive capacity of individuals, depending on their spatial arrangement (Clobert et al. 2009; Fedriani and Wiegand 2014).

While LDD may facilitate the persistence of different plant species, the impact of a fragmented landscape and other anthropogenic effects on LDD rates is so far largely indeterminate, with the effect of fragment or matrix degradation on LDD and colonisation largely unknown (Hodgson et al. 2011). Additionally, populations within anthropogenically-altered landscapes may already be suffering from general detrimental demographic impacts including reduced fitness, expressed as lowered fecundity and other vital rates (growth, survivorship) essential for long term species persistence (Fahrig 2003). For example, Cordeiro and Howe (2003) found fewer juveniles of *Leptonychia usambarensis*, an endemic African tree of submontane Tanzanian rainforest, recruited within forest fragments, in comparison to those within continuous forest. As a result, any area that has already experienced the negative effects of habitat fragmentation (or other threatening ecological processes) is likely to be increasingly susceptible to a loss of dispersers and subsequent negative demographic consequences (Chapman and Chapman 1995).

The impact of a reduction or removal of dispersers within an ecosystem is not uniform and may depend on plant and diaspore traits and their mutualisms with dispersers. Both large and small-seeded species may be expected to respond differently to a change in disperser community composition, with large-seeded species generally exhibiting an increased susceptibility to an absence of dispersers, particularly if large-seeded species have selected for LDD (Andreazzi et al. 2012). Additionally, there is evidence to suggest that large-seeded species may be selected for dispersal, be more resilient to seed predation (Cousens et al. 2010b) and exhibit greater fitness and competitiveness in relation to their small-seeded counterparts owing to a greater metabolic reserve in resource-poor environments (Marshall 1986). However, seed size alone should not be used as the sole predictor of the success or extent of dispersal, either local and long distance, with gut residence time found to be independent of seed size in some frugivores (Wilson 1989). With increasing evidence suggesting that seed traits or size may not be used to successfully predict potential improvements in germinability following frugivore ingestion (Traveset et al. 2001), it appears more likely that both small and large-seeded species may be vulnerable to decline in disperser populations.
due to the disperser’s own vulnerability to various anthropogenic influences (Nuñez Iturri and Howe 2007). Direct and species-poor frugivore-diaspore mutualisms are also likely to result in negative demographic consequences, with seeds dispersed by only a few or single species likely to be removed repeatedly to similar microhabitats, with many habitats suitable for colonisation remaining unused (Hampe 2003). Vander Wall and Longland (2004) suggest that diplochory, where there is sequential seed dispersal via different modes, has important implications for the fate of seeds, with the benefits of seed dispersal combined with a reduced likelihood of seed mortality through the partitioning of dispersal risks. The importance of diplochory to LDD, however, remains largely unknown (Nogales et al. 2012).

**Genetic Consequences of Disperser Decline**

For plant species that undergo rapid range expansions, such as might result from species migrations in response to global environmental change, LDD events may be one of the most important factors in spatial genetic structuring at local and regional scales of genes that are maternally inherited (Le Corre et al. 1997). Importantly, levels of inbreeding and inbreeding depression can depend on this spatial genetic structuring, influencing demographic processes such as fecundity, growth and survival (Epperson and Alvarez-Buylla 1997). Interactions between inbreeding depression and stochastic disturbances may lead to local extinctions, particularly if the sizes of populations are not large enough to resist the effects of deleterious gene mutations (Tanaka 1997). Disperser decline may further limit the movement of genetic material both locally and, in the case of LDD, at the landscape scale (Calviño-Cancela et al. 2012).

**Dispersal, Spatial Arrangement and Demography**

With dispersal having already been identified as playing a significant role in the demographic processes of individual plants and the broader communities in which they reside, it is pertinent to consider the explicitly spatial processes and consequences of dispersal, particularly the function that spatial dynamics play in population processes (Nathan and Muller-Landau 2000). Dispersal is the most significant factor determining spatial demography, with dispersal and spatial arrangement not only influencing recruitment success, but subsequent success owing to factors such as predation, competition and mating. For instance, the spatial arrangement of individuals may determine the susceptibility of a habitat to invasion by exotic species, with Marchetto et
al. (2010) identifying the importance of incorporating spatial realism in invasive species spread models to achieve better management outcomes. Franklin (2010) suggests that the spatial arrangement of organisms, especially sessile plants, may not only be used to predict subsequent dispersal patterns, establishment, competition, mortality, facilitation and growth, but that spatial patterns may be used to reveal the importance and presence of these processes to past populations. With increasing attention being given to space, spatial arrangement and, in particular, the role of ‘empty space’ as a limiting resource (with spatial partitioning in itself a measure of other resource partitioning in ecological communities; Grams and Lüttge 2011), it becomes necessary to continue to attempt to disentangle how dispersal may influence plant demographic processes. A reduction in dispersers is likely to lead to an aggregation of individuals within a population (Choo et al. 2012), arising from limited dispersal opportunities, particularly if a diaspore has a very specific dispersal morphology (Morales and Carlo 2006). Although the spatial arrangements of plant populations are critical to demographic processes, the patterns of distribution have been historically considered difficult to quantify (Clark and Evans 1954). Traditional methods for determination of spatial arrangement have centred around the measurement of the distances between nearest neighbours (a form of spatial autocorrelation measurement), producing a statistic describing the degree of aggregation as uniform, random or aggregated (Clark and Evans 1954). Other methods used to measure spatial arrangement include spatial interpolation, spatial regression, spatial interaction and simulation modelling. Spatial analysis of the genetic diversity of plant populations is increasingly being used as a tool for plant conservation, allowing an integration of genetic, demographic and ecological perspectives (Escudero et al. 2003). Bacles et al. (2006) used a genealogical reconstruction to show seed dispersal to be the main vector for gene flow across remnant vegetation, revealing an insufficient emphasis of seed-mediated gene flow as a resilience mechanism, particularly within fragmented ecosystems. Ouborg et al. (1999) also describe how molecular approaches can be used to determine genetic differentiation in spatially disjunct populations.

**Frugivory, Seed Processing and Germination Success in fire-prone Ecosystems**

The resilience of plant species of fire-prone habitats to global environmental change may depend on the interplay between LDD, particularly by large frugivores (such as ratites; Noble 1975), and plant propagule dormancy mechanisms (such as those broken by smoke and fire; Ooi et al. 2006). The jarrah forest of SW Australia, which has
experienced an extremely variable fire history over the past 250 years, primarily owing to changes as a consequence of European settlement (Ward et al. 2001), contains many species that have evolved traits related to a fire-prone environment (Bell et al. 1987). A simple classification can be applied to woody plant species in relation to their response to fire. Plants may be killed by fire (nonsprouters), reproducing only by seed, either from a soil stored seed bank or from seeds held in the canopy (serotiny), or reproduce from aerial or subterranean regenerative buds (resprouters) (Gill 1981). Any effects of disperser decline on plant population dynamics are likely to be more readily recognisable in nonsprouters in comparison to resprouters owing to their shorter generation times. Dixon et al. (1995) report that smoke and smoke-derived compounds have a promotive effect on the germinability of many Western Australian plants. The maintenance of plant species diversity following fire is largely attributable to an extensive soil seed bank (Koch et al. 2009). The passage of diaspores through the gut of frugivores may also break dormancy and enhance germinability, i.e. an increased rate of germination, greater overall germination percentage, or both (Noble 1975; Calviño-Cancela 2004). Here, I focus on the potential impacts of frugivory by the emu, the putative sole extant disperser of large-seeded species within the jarrah forests of southwest Western Australia (Calviño-Cancela et al. 2006), on germinability of ingested (gut-processed) seeds.

The enhancement of germination rate in seeds dispersed by frugivores is not universal and depends on both the dispersing agent and the plant species being dispersed (Traveset 1998). Germination enhancement may occur as a result of removal of the pericarp and abrasion of the seed coat, which becomes more rapidly permeable to gases and water, or through the removal of other material containing germination inhibitors (Traveset 1998). Renison et al. (2010) report variable germination enhancement for both large and small-seeded species consumed by Rhea americanca, a large South American ratite, with observed germination enhancement attributed to the breaking of physical dormancy mechanisms in some species. Similar occurrences of germination enhancement following gut passage have been observed in seeds eaten by other ratites, particularly the cassowary (Webber and Woodrow 2004; Bradford and Westcott 2010), and emu (Noble 1975), but with limited attention in the literature given to the latter. The passage of seeds through the intestinal tract of frugivores may also result in decreased germinability owing to the destruction of seed (extreme abrasion/scarification) (Traveset 1998). However, one would not expect to find many
examples of germination inhibition if the frugivore-plant relationship had evolved over a long period of time. For example, Bradford and Westcott (2010) recognise that for the cassowary, despite its relatively long gut retention time (mean ca. 5 hrs), the absence of an avian crop (as common for all ratites) and short digestive tract results in the gentle processing of diaspore material, leading to limited seed destruction via internal mechanical and chemical scarification. Nevertheless, it should be noted that seed dispersers may also function as seed predators, and so the mutualisms that they have developed in their plant-frugivore interactions will intrinsically contain some degree of inhibitory effect (Tsuji et al. 2010). Overall, with the germination response of species so inconsistent both within and between frugivores (Traveset 1998), it may be argued that the primary effect of frugivory (especially in ratites), is simply to facilitate dispersal away from the parent plant (Bradford and Westcott 2010; Renison et al. 2010). Other germination cues are then required following dispersal. In some environments the provision of moisture may be sufficient to stimulate germination, however, in fire-prone ecosystems more complex triggers are often required (such as heat or smoke) to ensure germination does not occur during a time unsuitable for recruitment (Dixon et al. 1995). Additional dormancy-breaking mechanisms such as cold (temperature) stratification and time (weathering) may also be required (Baskin and Baskin 1998). The complex requirements needed to break dormancy reveal that it may be non-adaptive for the seeds of species to be stimulated to germinate by gut passage. Rather, germination needs to be timed to coincide with fire so that there is the longest possible time after fire for plants to grow and accumulate seeds before the next fire.

**Modelling Seed Dispersal**

With the dispersal of seeds and other plant propagules recognised as a complex and multi-step process (Vander Wall and Longland 2004), models used to estimate seed dispersal, both empirically and mechanistically, require large amounts of data and an appropriate understanding of underlying processes (Cousens et al. 2010a). Considering that seed dispersal fundamentally mediates the spatial structure and dynamics of plant populations and, indeed, metapopulations (Russo et al. 2006), the development of suitable models that capture and predict dynamic seed dispersal processes are paramount in order to improve our understanding of plant population resilience to global environmental change. Although there have been numerous advances in our understanding of dispersal of plant propagules by wind over the past decade or two
(Okubo and Levin 1989; Bullock and Clarke 2000) there has been an unfortunate lack of attention paid to the prediction of dispersal by animals (Cousens et al. 2010a), though see Caughlin et al. (2014). In the context of LDD, given that both large and migratory animals are recognised as having a significant impact on vector seed load and displacement velocity (Nathan et al. 2008b), the creation of models predicting seed dispersal, based on component processes, becomes increasingly important. With the movement ecology paradigm permitting the examination of seed dispersal in relation to these component processes, it is perhaps unsurprising that this iterative ideological shift has led to recent advances in the development of increasingly complex mechanistic models of seed dispersal by frugivores (Anderson et al. 2011; Caughlin et al. 2014).

**Dispersal Kernels and Estimated LDD**

The probability of seeds being distributed over particular distances from parent plants is frequently described by functions referred to as dispersal kernels (Nathan and Muller-Landau 2000). Dispersal kernels are often considered as a component of general ‘seed shadow’ models, which includes, in addition to the kernels, estimations of fecundity or seed production (Clark et al. 1999a). These seed shadows estimate seed movement across varying spatial scales, with fine-scale dispersal often associated with competitive effects and, at coarse scales, colonisation of new habitats (Clark et al. 1999a). It has been suggested that plant migrations and colonisations during periods of directional climate change (e.g. in response to glacial-interglacial cycles; Davis and Shaw 2001), and potentially other anthropogenic disturbances, is controlled by the ‘tail’ of these probability distributions (Clark 1998). However, the tails of these dispersal kernels are notoriously difficult to quantify, which has far-reaching implications for understanding the spatial dynamics of plants (Bullock and Clarke 2000). Perhaps as a consequence of the difficulties and complexities of measuring the tail of the curve, there are limited examples in the literature of studies that measure LDD and the tail of the curve, with few determining the shape and extent of the tail with any degree of surety (Willson 1993; Bullock and Clarke 2000). Moreover, spatial models of seed dispersal have been historically plagued by erroneous dispersal data, over-simplified or incorrect conceptual and mechanistic understandings of the dispersal process (Silvertown 1991). While molecular methods have been developed in response to the dearth of suitable methods through which LDD may be examined (see He et al. 2004; He et al. 2009), there is some lingering criticism that molecular methods alone may not be sufficient, with
Bullock and Clarke (2000) suggesting that molecular markers alone simply establish long distance emergence and establishment and may underestimate the rates of LDD. Moreover, the collection of genetic information can be cumbersome and expensive if all potential parents within a LDD study location require genotyping (Nathan et al. 2003).

Of all the methods used to quantify and explain the pattern, rate and range of dispersal of plant and animal propagules, the Eulerian and Lagrangian movement/redistribution methods are the most popular, with both methods enjoying increasing contemporary attention in the literature (Cain et al. 2000; Gillespie 2001). The Eulerian approach is concerned with populations of individuals and how they are redistributed in large numbers across specific points in space, while the Lagrangian approach characterises the magnitude (spatial extent), speed and direction of individual movements (Nathan et al. 2003). Both methods have enjoyed an ecological renaissance of sorts owing to rapidly improving technology, facilitating increasingly accurate methods of mark/recapture using markers, tracers and isotopes, or improved satellite and radio telemetry equipment (Nathan et al. 2003). Mack and Druliner (2003) used radio transmitters and temperature loggers inserted into baits, placed at the base of fruiting forest species within Papua New Guinea, to be consumed by C. bennetti (pygmy cassowary). The recovery of the transmitters following ingestion and excretion provided an indication of both point-to-point dispersal distances and gut residence time. Unfortunately the recovery rate of the radio transmitters was poor, with only 30% of the ingested transmitters recovered (Mack and Druliner 2003). ‘Cafeteria-style’ experiments are also commonly used to measure dispersal distance and determine dispersal vectors (Guitián et al. 2002; Hirsch et al. 2012a). Smith et al. (1989) used cafeteria experiments to determine the rate of seed dispersal by ants for two deciduous forest species in Indiana, noting a greater likelihood of seed removal when seeds of one species were offered in smaller quantities in comparison to the other species. Cafeteria experiments may be used in conjunction with camera trapping, seed marking and radio telemetry to determine: 1) preference of seed removal, 2) dispersal vectors and 3) distances dispersed.

In order to fully capture the complex and long distance movement patterns of organisms, particularly large vertebrate avian frugivores, the employment of satellite telemetry is considered the most accurate and resource (including cost) effective, and is perhaps more reliable than radio tracking in estimating LDD (Powlesland et al. 2011).
However, satellite telemetry alone is not sufficient to comprehensively gather information regarding disperser communities, particularly where vectors may exhibit complex behavioural patterns (such as seasonal variations in feeding behaviour; Davies 2002) or where a single diaspore may be dispersed by numerous vectors. In this instance, it is appropriate to consider the use of camera trapping to quantify the frequency and extent of frugivory by animals to complement the use of satellite telemetry (Prasad et al. 2010). Snow and Walter (2007) successfully used motion-sensitive infrared camera traps to determine the dispersal vectors of the cycad Macrozamia lucida in a Brisbane forest, discovering only two dispersal agents. Snow and Walter (2007) also described the feeding behaviour of the visiting dispersers, noting the bush rat (Rattus fucipes) did not generally damage the seed kernel. Nathan et al. (2003) recommend that a combination of ever-advancing methods be appropriately utilised in order to provide improved insight into LDD. Unfortunately, the use of multiple methods may not be practical, for instance, it would likely be impossible to use mark/recapture methods on large vertebrates, with satellite tracking (of a small sample of individuals) being the most practicable method (Nathan et al. 2003). Careful attention needs to be given to the potential methods utilised to determine rates of LDD.

Seed Dispersal and Population Viability Analysis

Population viability analysis (PVA) is frequently applied as a tool in conservation biology to compare alternative management options or to assess potential impacts of changing environmental conditions (global environmental change) on individual species and ecological processes (Beissinger and Westphal 1998). Improved information regarding the rates of LDD within different ecosystems and the incorporation of enhanced knowledge regarding the movement behaviour of organisms will likely significantly influence the manner in which PVA is conducted (Reed et al. 2002). Spatially-explicit, individually-based PVA models require data on how organisms disperse across various habitat-types, often over large scales (Reed et al. 2002). Use of LDD in PVA has typically proven problematic due to a lack of data and the use of assumed rates that may be far from true (Baker et al. 1995). The development of radiotelemetry, particularly miniaturisation of radio transmitters and advanced satellite telemetry (as previously discussed) increasingly permits the incorporation of spatial dispersal data into PVA (Cohn 1999; Reed et al. 2002). Ultimately, as the empirical evidence regarding rates of LDD in various ecosystems increases, modelling studies
will permit the assessment of errors (sensitivity analysis) regarding dispersal parameters and their influence on the performance of modelling efforts (Reed et al. 2002).

Movement Ecology

The emerging movement ecology paradigm aims to provide a structure for the study of the movement of all types of organisms, resulting from an increasing appreciation and understanding of the significance of the movement of organisms to many ecological and evolutionary processes (Nathan 2008). Movement ecology seeks to remove the previous demarcations of movement research, such as the random, biomechanical, cognitive and optimality approaches, instead unifying these individual paradigms into a single cohesive theory of organism movement (Nathan 2008). Included then in this integrative movement ecology theory is the recognition that the paradigm’s framework can be applied to passively transported organisms (such as plants), in an evolutionary context. It also has application to self-propelled sentient organisms (Nathan 2008; Nathan et al. 2008a). For instance, Wright et al. (2008) applied the essential components of movement ecology; the motivation for an organism to move, its motion and navigation capacity (representing how and where the organism may move) and external factors affecting movement, to understand how seeds may be dispersed under differing atmospheric conditions. Furthermore, the framework of movement ecology may be used to assist comparisons between this and congruous studies when considering the complex interactions between plant traits and external dispersal factors (Wright et al. 2008). Spatially, the movement of organisms may be inhibited by threatening ecological processes, such as habitat fragmentation, resulting in negative demographic effects (Cordeiro and Howe 2003). Furthermore, movement ecology is being used as a useful framework for guiding and scaling seed dispersal investigations (Côrtes and Uriarte 2013).

Movement ecology also provides a unified framework for understanding why, how, where and when organisms move, presenting an opportunity to reassess the significance of LDD and its numerous ecological consequences (Nathan et al. 2008a). In response to global environmental change, including habitat fragmentation, altered fire regimes, exotic species invasion, climate change and the potential interactions between these threatening processes, conservation biologists have been reluctant to engage with the movement behaviour literature (Doerr et al. 2011). This oversight is perhaps unsurprising, with early movement literature omitting important connections between
organism movement behaviour and threatening processes, specifically habitat fragmentation and landscape connectivity (Doerr et al. 2011). Yet movement ecology (Nathan 2008) provides an excellent basis for modelling and conserving habitat connectivity, through robust and inclusive examination of an organism’s movement throughout the landscape (Doerr et al. 2011). With considerable debate in the literature continuing over the most suitable measures for conservation in the face of global environmental change (Hodgson et al. 2009; Doerr et al. 2011; Hodgson et al. 2011), a more complete and thorough understanding of how organisms move and the implications of this for population resilience (mediated through LDD) is necessary.

Conclusions

Global environmental change poses a significant risk to biodiversity (Thomas et al. 2004), especially within highly biodiverse areas such as SW Australia (Myers et al. 2000; Midgley et al. 2002). In order to maintain population, species and ecosystem-level diversity, species will be required to adapt to a changing climate. This could be by dispersing into suitable habitat through fragmented and increasingly degraded landscapes (Pearson and Dawson 2005), and/or through exhibiting strong resilience in existing habitat – this latter likely to be most possible where levels of genetic diversity are high (buffering effect) – also a result of genetic mixing over longer spatial distances. LDD may provide the suitable means through which species may be able to achieve these important realised dispersal outcomes, especially with increasing evidence suggesting that dispersal via standard means is unlikely to keep pace with the rapid range expansions and changes required (Pearson and Dawson 2005). Moreover, the importance of LDD is further increased with recognition that as the need for LDD within a system increases, the importance of habitat connectivity and quality for dispersal potential decreases (Pearson and Dawson 2005). Improved understanding of LDD as a non-standard dispersal vector will not only inform how native species may respond to global environmental change, but also illuminate just how threatening ecosystem-degrading processes may be, highlighting the vagility of the diaspores of exotic species (Cleland 2011). With non-standard vectors of LDD transporting species with disparate dispersal morphologies, increasing consideration needs to be given to the impact of direct and indirect anthropogenic influences on disperser communities, with a loss of dispersers likely to lead to negative demographic outcomes at local and landscape levels (Bohrer et al. 2005). The reduction or loss of disperser populations
will not only lead to decreased plant mobility in response to global environmental change, but will directly result in increased negative demographic consequences, driven largely by density-dependent mortality. Ultimately, an improved understanding of LDD within various ecosystem types and its impact on ecological processes needs to be achieved to better inform future conservation strategies and will add to our understanding of the way dispersal processes contribute to species population dynamic behaviour.

In Chapter Three, a description of the study sites used in this study, and target species dispersed by the emu is presented. It provides the background information for this study of seed dispersal by the emu in the jarrah forests of southwestern Australia.
CHAPTER THREE
STUDY SITES AND STUDY SPECIES OVERVIEW

3.1 INTRODUCTION

Southwestern Australia is a global biodiversity hotspot, owing not only to substantial floral diversity and endemism, but also threats to ecological processes from climate change, changing fire regimes and habitat fragmentation (Myers et al. 2000). The jarrah (Eucalyptus marginata Sm.) forest that lies within this area has been substantially altered since European settlement, namely through widespread clearing for agricultural and pastoral purposes. Continuing urban expansion, previously restricted to the coastal plain, places further pressure on an already vulnerable area. The northern extent of the forest is classified as open forest, with the wetter southern extent considered tall open forest Dell et al. (1989). The overstorey is dominated by E. marginata and Corymbia calophylla and the understorey consists of small trees between 4 - 7 m. Beneath this, the ground layer is dominated by a variety of woody shrubs and grass-trees (Dell et al. 1989). Fire plays a key role in the life cycle of plants within the forest and is the key stochastic process that shapes plant demography. The plants of the jarrah forest have evolved different strategies to regenerate following fire. Species may regenerate from above-ground (epicormic or apical) buds or a subterranean storage organ (lignotuber). Species that exhibit these traits are typically referred to as resprouters (Gill 1981). In contrast, individuals may be killed by fire and subsequently regenerate from a soil-stored seed bank or from canopy-stored seeds (serotinous). These species are typically referred to as seeders (Gill 1981). While the dichotomy between these two general reproductive strategies is not always readily delineated, they provide a useful method of understanding how species in the forests respond to fire and how changing fire regimes may impact population persistence.

The importance of fire on ecosystem properties and function has been extensively documented (Bond and Van Wilgen 1996). Much of the flora in fire-prone, Mediterranean-type ecosystems has evolved adaptive traits in response to a regime of frequent fires (Gill 1981) with fire-promoted flowering in perennial plants as one of the key responses (Lamont and Downes 2011). If fire-stimulated reproduction (fsr) occurs only in the first 1 - 2 years after fire, and is followed by a period of dormancy or only vegetative growth through the remainder of the inter-fire period, the species is
considered to exhibit obligate fsr (Lamont and Downes 2011). Up to 154 different species within the Mediterranean regions of Australia and South Africa are thought to exhibit obligate fsr (Lamont and Downes 2011). Such species may be particularly susceptible to changes in fire regimes that are discordant with their flowering phenologies and associated cueing and resource availability.

Prior to the settlement of Australia by Aborigines, SW Australian jarrah forests are thought to have experienced fires of moderate to high intensity, on average every 30 - 100+ years (Enright and Thomas 2008). Conditions in SW Australia are normally conducive to fires over a 4 - 8 month period, with lightning strikes a major source of ignition during summer and early autumn, resulting in intense and wide-spread fires (McCaw and Hanstrum 2003). The arrival of Aborigines in the late Pleistocene instituted an anthropogenic fire regime, with a shortened estimated fire interval of 10 - 15 years or less in heavily occupied areas (Hassell and Dodson 2003). Fires were typically ignited from October to June, with most recorded for the hottest months from December to March (Abbott 2003). Current land management practices by forestry and conservation authorities favour a regime of short interval burns, delivering low intensity fires in spring or autumn that reduce surface layer fuels and are readily controlled (Enright and Fontaine 2014).

Current fire regimes in SW Australia are predicted to shift on a landscape scale as a result of climate change, and at a local scale are being altered as a result of habitat loss and fragmentation (Cochrane 2001; Williams et al. 2001). Modelled future climates within the region (Bates et al. 2008) project a decline in rainfall and an increase in temperature. These climate shifts will result in increasingly prevalent severe fire weather conditions, increasing the likelihood of ignitions, with more frequent fires over a longer fire season (Bradstock et al. 2002). Species whose reproductive strategies have evolved in response to recurrent (predominantly summer) fires are potentially threatened by changes to fire regimes that are discordant with their life histories.

Changing fire regimes are only one impact of the local and landscape-level changes that have occurred following European settlement and increasing urbanisation. In increasingly fragmented landscapes, large organisms, which may play a disproportionately important role in ecosystem dynamics, are displaced either by direct persecution or from indirect effects (Corlett 2007). The emu (Dromaius
*novaehollandiae* Latham), is a large ratite and the putative sole remaining disperser of large-seeded and -fruited species within the jarrah forest, following the extinction of most of the Pleistocene megafauna over the past 50 ky (Hall and Walter 2013). Its ability to ingest large amounts of seed material, retain these for long periods of time (potentially many weeks; Davies 1978) and move potentially hundreds of kilometres during this time (Davies *et al.* 1971), make it a key seed dispersal agent and long distance dispersal (LDD) vector. As LDD events are paramount in shaping plant population dynamics (Nathan 2006), it is important to understand how the loss of a LDD vector in the jarrah forest, in conjunction with crucial environmental processes (especially fire), may potentially impact populations of particular species and their resilience to future global environmental change.

This chapter provides the essential background information pertaining to the general study sites and species used in this research project. It presents climate, topographic, soil, ecosystem dynamics (i.e. vegetation and its natural disturbance regimes - especially fire), information and land use history, for each of the study sites. Given that the overarching aim of this thesis is to examine the potential impacts of loss of the key primary seed dispersal agent, the emu, on plant populations and their resilience in the face of global environmental change, the biology and ecology of emu is also described.

The aims of this chapter are to

1. Describe the biology of the primary seed dispersal agent, the emu
2. Describe the key characteristics and provide a general description of the four large-seeded/fruited plant species investigated in this study
3. Explain the location, general vegetation, geomorphologic and climate information for each of the study sites of comparative high/low emu abundance in which each key plant species is found
4. Elucidate the method by which each study site was assessed as either high/low emu abundance via scat assessment

**3.2 STUDY SPECIES**

Nomenclature used throughout this thesis for plant species follows Paczkowska and Chapman (2000). Plant demographic studies focus on four species; *Leucopogon nutans* E. Pritz (Ericaceae), *Persoonia elliptica* R. Br (Proteaceae), *Macrozamia riedlei*
(Gaudich.) C.A.Gardner (Zamiaceae) and *Podocarpus drouynianus* F. Muell (Podocarpaceae). These four understorey species in the jarrah forests of southwestern Australia were selected for use in this study because of; their relatively large seed or fruit size in relation of other co-occurring species, substantial interspecific variation in seed/fruit size, range of regeneration responses to fire (a key process in shaping plant dynamics in fire-prone ecosystems) and previous evidence of dispersal of seeds of these species by *D. novaehollandiae*.

This thesis recognises and discusses a single species of Australian emu (*Dromaius novaehollandiae*) and not the four disputed sub species; *D. novaehollandiae novaehollandiae*, *D. novaehollandiae woodwardi*, *D. novaehollandiae diemenensis* and *D. novaehollandiae rothschildi* (Davies 2002).

### 3.2.1 Primary dispersal agent

*Dromaius novaehollandiae* (emu)

The emu is a diurnal, large flightless bird (ratite) (Plate 3.1) that is distributed over most of mainland Australia (Davies 2002). The emu prefers heavily forested vegetation and will typically avoid arid areas except in the instances where heavy rain has fallen. Pairs of birds are driven apart for between 2 - 3 km by intraspecific competition, although resource abundance will result in the co-location of larger groups of individuals. Like other large frugivores, populations of the emu are under pressure from direct persecution by land-users, as well as indirectly via habitat fragmentation, land-use change and other environmental changes (Corlett 2007). The emu exhibits substantial sexual dimorphism, with females of the species heavier on average than their male counterparts (36.9 kg vs. 31.5 kg; Davies 1967). Pairing and preparation for laying occurs between January to May, with egg laying occurring between March and May (Davies 2002). The male incubates the solitary nest and bears sole responsibility for raising the chicks, with the clutch size varying between 4 and 24 chicks, with 9 chicks on average per clutch (Marchant and Higgins 1990).
Plate 3.1 An emu foraging in the understorey of jarrah forest near Nannup, SW Australia

Despite its preference for dense forest, the emu's biology makes it well-adapted to semi-arid environments, where resources are scarce and available only periodically (Davies 2002). It has the capacity to sustain itself on minimal quantities of water (though will drink freely when water is available, and requires succulent food to compensate for low water availability) and can derive sustenance from even the poorest of vegetation (Herd and Dawson 1984). The emu is a generalist (Dunstan et al. 2013), omnivorous feeder and will select for the richest nutrient source in its environment. It feeds on fruits, seeds and flowers from all plant life forms and will also consume insects, including beetles and grasshoppers (Davies 2002). This generalist feeding behaviour results in the ingestion of a large amount of seed that lacks specific morphologies for dispersal by frugivores (Calviño-Cancela et al. 2006; Calviño-Cancela et al. 2008). As such, the emu possesses great potential as a non-standard seed dispersal vector for many plant species (Calviño-Cancela et al. 2006).

Ingested material passes through a relatively short (ca. 6.55 m) alimentary system, through a gizzard that retains a large amount of gravel for assisting in processing low quality organic material (Davies 1978), and which does not include an archetypal avian crop (Herd 1985). The reported retention time of ingested material is highly variable. It is short for the fluid and particulate phases of the diet (4.1 ± 0.2 hr and 5.5± 0.4 hr, respectively; Herd and Dawson 1984), but can be much longer for larger food items. Davies (1978) reports retention of wheat for between 3 and 50 hrs, and gut passage time for other material between 1 - 2 days on average. Davies (1978) also reports gut
retention times of ca. one week for pseudo seeds with specific gravities similar to native seeds. In rare instances some (artificial - marbles) material may be held for upwards of 100 days (Davies 1978). However, this outlier observation would likely not reflect the retention time of the seeds of most, if not all, native species owing to the very large difference in specific gravity of these materials. The impact of gut passage on seed fate is variable, with some species responding positively to ingestion (Noble 1975), while others may be impeded or show no significant effect (Dunstan et al. 2013).

Movement of the emu is best described as somewhat nomadic and is principally driven by the availability of resources. Some birds have been observed to stay within a small area for over a year (ca. 1 km²), whereas other (banded) birds have moved hundreds of kilometres over a few months (Davies 2002). Beyond the recapture of a small number of banded individuals, little is known about the landscape-scale movement potential of emus or daily variations in their behaviour and movement. Nevertheless, given the bird's substantial gut retention time for seeds of many species and their capacity to traverse large distances, the emu has great potential as a long distance seed dispersal vector.

3.2.2 Plant species

The species selected for study here encompass major patterns of variation in demographic traits, influencing plant population dynamics for large-seeded (and fruited) woody plants in a dry sclerophyll forest environment. Each species can be dispersed by the emu.

*Leucopogon nutans*

*L. nutans* is a small erect shrub growing to 1.5 m high (Plate 3.2). *L. nutans* is found in the understorey of the northern jarrah forests region near Perth, SW Australia. It is an obligate seeder shrub that is short-lived (c. 15 yrs), killed by fire, and regenerates from a soil-stored seed bank (Allan et al. 2004). Seedling recruitment in the inter-fire period, as for other obligate seeder species, is uncommon. It commonly produces a solitary flower per leaf axil between April - June that develops into an ovoid drupe on average 6 × 5 mm by August. The hard and woody endocarp contains five locules, though over 50 % of these often contain no seed (Allan et al. 2004). Seeds of *L. nutans* often dominate emu scats (along with other Ericaceous species), and no animal other than *D.*
*D. novaehollandiae* has been observed to consume them (Andrew Nield, *unpublished data*).

**Plate 3.2** (a) *L. nutans* flowering at Avon Valley, Western Australia and (b) developed *L. nutans* fruit retained on shrub

*Persoonia elliptica*

*P. elliptica* is an understorey tree reaching up to 7 m height (Plate 3.3) that is widely distributed throughout the jarrah forest region of SW Australia. Mature individuals are fire-tolerant, resprouting from epicormic buds on major branches in the plant crown. *P. elliptica* also recruits from a soil-stored seed bank following fire (Abbott and Van Heurck 1988). A fruit crop is generally produced each year in mature plants, excepting the year following fire. Flowers are produced between October - February. The fruit of *P. elliptica* is a fleshy drupe (c. 1 cm length × 0.5 cm width) and is released from the plant over the course of a few months following maturation. Recruitment failure over the last 50 years or more has been reported for this species (Abbott and Van Heurck 1988), with seedlings and saplings absent from most populations. *D. novaehollandiae* is the assumed primary disperser of *P. elliptica*, however, its seeds have been observed also to be consumed by the currawong (*Strepera graculina*) and western grey kangaroo (*Macropus fuliginosus*) (Abbott and Van Heurck 1988).
Plate 3.3 (a) Mature *P. elliptica* tree at Sawyers Valley, Western Australia and (b) mature fruits recently fallen from the canopy, some with flesh removed by kangaroos. Photographs: S Monaco

*Macrozamia riedlei*

*M. riedlei* is a long-lived, apical resprouting cycad that is widespread in the understorey of the jarrah forests of southwestern Australia. The stroboli (cones) are produced at the stem apex (Burbidge and Whelan 1982) (Plate 3.4). Fire appears to stimulate fruiting, with seeds generally produced 12 - 18 months following fire. Fruiting may be fitful, with mature plants fruiting after some fires but not others (Ornduff 1985; Ornduff 1991). Male cones mature in 5 - 6 months, whereas female cones mature in 10 - 11 months. Although fire stimulates cone production in this cycad (Pate and Dixon 1982; Pate 1993), coning in the absence of fire may also occur from time to time, with mature individuals producing stroboli and seed cones on average every 3 - 6 years according to one study (Baird 1939). Seeds are large (c. 5 cm length × 2 cm width), covered in a red sarcotesta, and germinate readily, within 12 - 18 months following dispersal. Seeds of *M. riedlei* have been observed to be dispersed short distances by possums (*Trichosurus vulpecula*), ravens (*Corvus coronoides*) and western grey kangaroos (*Macropus fuliginosus*) (Burbidge and Whelan 1982), but the emu is assumed to be its only potential long-distance disperser.
Plate 3.4 (a) *M. riedlei* with immature female cones at Sawyers Valley, Western Australia and (b) mature *M. riedlei* seed with sarcotesta

*Podocarpus drouynianus*

*P. drouynianus* is a dioecious, resprouting shrub that grows in fire-prone areas of southwestern Australia, primarily in the southern jarrah forests (Chalwell and Ladd 2005) (Plate 3.5). The species is unusual within the Podocarpaceae, being one of only two fire-tolerant species in the family in Australia (*P. spinulosus* in eastern Australia being the other; Gibson *et al.* 1995). Although fire-tolerant, *P. drouynianus* retains some life history characteristics of its fire-sensitive relatives, such as large seeds exhibiting limited dormancy (Chalwell and Ladd 2005). *P. drouynianus* resprouts rapidly after fire from its lignotuber, with most shoot growth observed in the first year following fire. Production of female and male sporophylls, borne in the leaf axils of the new shoots, follows fire, with a pattern similar to many other species that exhibit fire-stimulated reproduction (Chalwell and Ladd 2005; Lamont and Downes 2011). The production of cones can occur within 8 months of fire, but varies depending on the season of burn, with seeds ripening and shed in autumn (Chalwell and Ladd 2005). The production of a small amount of seed in the second year after fire has been observed in some instances, with little reproduction evident subsequently through the inter-fire period. Seeds are large (c. 2 × 2 cm) and are accompanied by a fleshy aril, attractive to
vertebrate dispersal agents. Seeds of *P. drouynianus* are recalcitrant, with germination coinciding with the arrival of winter rains. No species other than *D. novaehollandiae* has been observed to disperse the seeds of *P. drouynianus* (Chalwell and Ladd 2005).

Plate 3.5 (a) *P. drouynianus* shrub at Nannup, Western Australia and (b) mature seeds with fleshy purple aril

### 3.3 STUDY SITES

Five study sites were used to assess the impact of the loss of the key dispersal agent, the emu, on plant demographic attributes for the four large-seeded species described above. Location of each study site and general climate information are provided in Figures 3.1 and 3.2, respectively. Sites were selected based on the presence of the target large-seeded species and differences in the abundance of the assumed primary seed dispersal agent, the emu. Relative emu population abundance at each study site (Table 3.1) was determined via scat counts, the methodology for which is described below. Not all study sites contained all four target plant species, necessitating use of additional study areas (i) Nannup for *P. drouynianus* and (ii) Kings Park and Hill River for *M. riedlei* as detailed below.
Figure 3.1 Location of each of the study sites within southwestern Australia (general region indicated by the red star). Image: Google Earth (2014)

Table 3.1 Presence of each study species in relation to study site and relative emu abundance

<table>
<thead>
<tr>
<th></th>
<th>Avon Valley&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Sawyers Valley&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Nannup&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Kings Park&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Hill River&lt;sup&gt;b&lt;/sup&gt;</th>
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<td>&lt;i&gt;L. nutans&lt;/i&gt;</td>
<td>✓</td>
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<td>&lt;i&gt;M. riedlei&lt;/i&gt;</td>
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<td>&lt;i&gt;P. elliptica&lt;/i&gt;</td>
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<tr>
<td>&lt;i&gt;P. drouynianus&lt;/i&gt;</td>
<td>✓</td>
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<sup>a</sup> High emu abundance
<sup>b</sup> Low emu abundance
<sup>c</sup> No emu population
Figure 3.2 Summary climate information for study sites in southwestern Australia including (a) mean monthly rainfall, (b) maximum temperature and (c) minimum temperature
3.3.1 Avon Valley National Park

The Avon Valley National Park (31.63°S, 116.19°E) and surrounding Moondyne Nature Reserve, located c. 50 km NE of Perth, Western Australia was selected as a high emu abundance study site and contained three of the four target plant species; *L. nutans*, *M. riedlei* and *P. elliptica*. The Avon Valley lies at the northern end of the Darling Scarp on the transition between the northern extent of the jarrah (*Eucalyptus marginata*) forest and the drier wandoo forest (*Eucalyptus wandoo*). In relation to topography and soils, *E. marginata* is associated with lateritic hill tops and ridges, and *E. wandoo* with the clay/loam soils of the valleys (Department of Environment and Conservation, DEC 2012). The understorey vegetation is sparse, with common species including *Xanthorrhoea preissii*, *Grevillea bipinnatifida*, *L. nutans* and *M. riedlei*. The Avon Valley receives a mean annual rainfall of 816 mm, which follows a Mediterranean climate type rainfall pattern, largely confined to the winter months (June - August). Climate information is from the nearest meteorological station (Lower Chittering, 31.61°S, 116.11°E) that has > 10 years of available data (Bureau of Meteorology, BOM 2014). The average fuel age (an analogue of fire history) of the Avon Valley at the commencement of the study was between 10 - 13 years (Department of Parks and wildlife, pers. comm.). However, the patchiness of fire, both prescribed and natural, results in a mosaic of fire ages.

3.3.2 Sawyers Valley State Forest

Sawyers Valley State Forest (31.90°S, 116.20°E), located c. 30 km E of Perth, Western Australia, was selected as a low emu abundance study site and contained all four target species; *L. nutans*, *M. riedlei*, *P. elliptica* and *P. drouynianus*. Sawyers Valley is also a part of the northern Darling Plateau, with lateritic duricrust on ridges and upper slopes, and sands and gravels in shallow depressions. *E. marginata* and *Corymbia calophylla* (Marri) dominate the forest overstorey, though low *Banksia* woodlands are found on sandy areas. The open understorey is comprised of heath plants, with *Hakea* spp., *Banksia* spp., *Styphelia tenuiflora* and *Adenanthes barbigerus* common. Sawyers Valley receives a mean annual rainfall of 1042 mm, which is mainly confined to the winter months. Climatic data are from the nearest meteorological station (Mundaring Weir, 31.96°S, 116.16°E) that has > 10 years of available data. The fuel age of the Sawyers Valley study area is approximately 6 - 7 years (Department of Parks and Wildlife; DPaW, pers. comm.).
3.3.3 Nannup

The Nannup study area (c. 220 km S of Perth, Western Australia) encompasses sample plots for *P. drouynianus* at locations within a c. 50 km radius of the Nannup town site (33.98°S, 115.77°E). The Nannup region was selected as a high emu abundance study site that contained the target large-seeded study species unavailable at the Avon valley site. Within the Nannup region, deep alluvial-type sediments are found within the forest valleys, with deeper, loamy soils found on the slopes. The forest overstorey is predominantly *E. marginata* with occasional *E. calophylla*. Understorey trees such as *Persoonia longifolia* and *P. elliptica* are found with heath-like shrubs and *X. preissii, Stirlingia latifolia* and *Leucopogon verticillatus*. Mean annual rainfall is 944 mm, and again is mostly confined to the winter months (June - August). The fire history of the areas in which plots were placed was variable, with sites having been burnt in the previous 1 - 5 years or long unburnt (ca. > 10 years since last fire).

3.3.4 Kings Park

Kings Park (31.96°S, 115.83°E) is a 267 ha remnant of mixed *Eucalyptus-Allocasuarina-Banksia* woodland (Radho-Toly et al. 2001; Crosti et al. 2007) located < 1 km from the Perth Central Business District. The understorey of the park, which is highly disturbed, is now dominated by the invasive grass, *Ehrharta calycina* (Baird 1977). Gazetted for public purposes in 1872, there are no records of emu occurrence within the park for at least 100 years. The park was selected as a no emu population study site and contains one of the four target large-seeded study species; *M. riedlei*. King's Park receives comparatively low mean annual rainfall among the study sites at 721 mm. Climate data are from the nearest meteorological station (Subiaco Wastewater Treatment Plant, 31.96°S, 115.79°E). Fire is generally excluded from the park. Although there have been wildfires in the last 10 years all sample plots were placed in areas long unburnt (ca. > 10 years since last fire).

3.3.5 Hill River Nature Reserve

The Hill River Nature Reserve (30.32°S, 115.12°E) is a large (11,000 ha) area of low woodland and heathland found ca. 200 km NNW of Perth. The Hill River study plots were located on Bassendean sands in an area of Banksia woodland with some *Eucalyptus todtiana*. The understorey consists of *Petrophile macrostachya, Jacksonia*
spp., *Xanthorrhoea preissii*, *Daviesia nudiflora* and *Acacia pulchella* (DEC 1995). The last fire in the area of the study plots occurred approximately 25 yrs ago.

### 3.4 EMU POPULATION ASSESSMENT

Counts of scats were used to provide a comparison of relative emu abundance at the Avon Valley and Sawyers Valley study sites. The scats of large ratites have been shown to be a suitable guide to abundance (Westcott 1999). To determine the number of scats at each site, twenty, $20 \times 20$ m and fifteen $20 \times 20$ m plots were installed on a random systematic basis at Avon Valley and Sawyers Valley, respectively, during February 2011. There was an initial *a priori* expectation that scats (and subsequently, emus) would be more abundant at Avon Valley in contrast to Sawyers Valley. Within the peri-urban setting, the Sawyers Valley forest persists in a mixture of rapidly expanding residential and industrial matrix. This urban expansion was expected to have displaced the emu, which can require a large home range (Davies et al. 1971). Similar pressures on other large frugivores elsewhere have been previously recorded (Corlett 2007). In contrast, the agricultural lands surrounding the extensive Avon Valley National Park provide year-round supplies of water and agricultural fodder, which has been shown to attract large numbers of emus (Caughley and Grice 1982). The purpose of the scat assessment plots was to obtain an estimate of relative emu population abundance between sites, rather than determine definitive population size. Scat density ($m^2$) from the sample plots throughout the course of the study can be seen in Figure 3.3. Plots were repeat surveyed throughout the study to account for seasonal and annual changes in the population. Plots were surveyed quarterly throughout 2011. During each survey, scats within the plot were marked so that fresh scats could be noted in subsequent counts. Owing to low deposition rates of scats per unit area, in June 2011, the plot areas were increased to $30 \times 30$ m. From this time, scat surveys were conducted ca. bi-monthly. A single emu scat assessment was also conducted at the Hill River study site during autumn 2014. At Hill River, 15 $20 \times 20$ m randomly-selected sample plots were surveyed and the number of emu scats enumerated. The scat density at Hill River during this assessment was $0.004 \pm 0.002$ scats/$m^2$ (95%CI). Emu population assessment was not required at Kings Park with no emu being observed in the park for at least 100 years. Also, as a small regional town, Nannup is untouched by major urban development and so the local emu population thrives (S. Davies *pers.*
A formal emu population assessment via scat counts was not conducted at this site.

![Figure 3.3](image-url)  
**Figure 3.3** Total emu scat density ($m^2$) at Avon Valley National Park and Sawyers Valley State Forest, southwestern Australia. Error bars are 95%CI. *Dashed line* indicates increase in scat plot assessment size from $20 \times 20$ m to $30 \times 30$ m

### 3.5 CONCLUSIONS

This chapter has described the general vegetation and geomorphology characteristics of the jarrah forests of southwestern Australia, which encapsulates three of the five key study sites (Avon Valley, Sawyers Valley and Nannup). Descriptions for the remaining sites have also been presented. The biology of the primary seed dispersal agent examined in the course of this study, the emu, as well as the key species it dispersers has also been described.

The four plant species in this study encompass a wide range of seed size, reproductive strategies and life forms but are united by a common, dominant vector of seed dispersal. They are also prominent understorey species in a range of southwestern Australian landscapes. The frugivorous dispersal strategy is not particularly common in southwestern Australian communities (where many species are serotinous) but is likely to be an important influence on population and genetic structure of the species that have propagules that may be dispersed by vertebrates (Bialozyt *et al.* 2006).

The following chapter (Chapter Four), examines the demographic parameters for each of the study species across the sites in which they occur. In particular, the population size structures, flower and fruit production, soil seed bank dynamics and recruitment
following fire were investigated to determine potential correlations between primary dispersal agent loss and demographic signals.
CHAPTER FOUR
PLANT DEMOGRAPHY

ABSTRACT

The south west of Western Australia supports a diverse and unique flora. The landscape was extensively altered after the arrival of the indigenous inhabitants around 50kybp and, more recently and intensely, by European settlers over the past 150 – 200 years. Land management policies and on-going forest clearance and fragmentation have changed fire regimes, exposed areas to invasion by exotic species and resulted in the direct and indirect decline of many faunal species. As our knowledge of ecosystem processes and linkages is incomplete, it is essential to understand the baseline condition of key species across a range of functional types within these forests to assess their current condition and likely response to global environmental change. Here the demographics and reproductive biology of four key species with differing life histories and fruit/seed sizes (as outlined in Chapter Three) are described from areas with largely intact populations of their primary seed dispersal agent, the emu (Dromaius novaehollandiae), and areas where emus are now largely absent. Little evidence was found of differences in demographic rates between study sites for the target species. Population size structures and seed/fruit production for most of the study species between sites was similar, including those for Macrozamia riedlei, where the putative primary dispersal agent had been absent from one study site for > 100 years. Where differences were observed (such as increased seed production for Podocarpus drouynianus in emu-abundant areas), improved demographic rates are most likely attributable to a favourable fire history and overall greater population size. The species exhibited principally either obligate fire-stimulated reproduction (Macrozamia, Podocarpus) or establishment. For Leucopogon nutans and Persoonia elliptica, almost no inter-fire recruitment was observed. Post-fire recruitment for these species was from soil stored seed banks that had low density of viable seed, and growth and survival of the P. elliptica recruitment cohort was poor. This chapter describes the difficulty of detecting demographic signals that might be expected to occur from the loss of a primary dispersal agent. Complex interactions between recruitment strategy following fire, local biotic and abiotic conditions obscure the potential interactions between disperser loss and demographic consequences. The following chapter (Chapter Five) explores further the a priori expectation that disperser loss can lead to a detectable
change in demographic parameters, by examining the spatial ecology of each species across high and low emu abundance sites.

4.1 INTRODUCTION

The southwest floristic region of Western Australia is a global biodiversity hotspot, with a high level of endemism and many processes that threaten its remarkable plant species diversity (Myers et al. 2000). Habitat fragmentation, invasion by exotic species, altered fire regimes, disperser decline, climate change and the interplay of these elements threatens species diversity at both local and landscape scales (Hobbs 1993; Hobbs and Kristjanson 2003). The jarrah forests, whose range extends over some hundreds of kilometres of latitude through this floristic region, contain a distinctive flora that is speciose and has been under threat since early European settlement (Abbott et al. 2003b). Extensive logging, both historically and on-going, agricultural activities and rapid urban expansion have placed pressure, directly and indirectly on the flora and fauna of these iconic forests (Abbott and Van Heurck 1988; Abbott et al. 2003a).

Species of the jarrah forests have evolved traits to enhance/cue their reproduction following the recurrent fires that have influenced their phylogenesis (Gill 1981). Resprouter species typically regenerate vegetatively after fire, regrowing from subterranean storage organs (lignotubers) or aerial buds (epicormic or apical) protected by thick bark or tightly packed leaf-bases (Gill 1981). In contrast, seeder species are killed by fire and must regenerate from a seed bank that is stored within the soil or held in the canopy (serotiny) (Gill 1981). Prior to the settlement of Australia by Aborigines, SW Australia is thought to have experienced fires of moderate to high intensity, on average every 30 - 100+ years (Enright and Thomas 2008). Conditions in SW Australia are normally conducive to fires over a 4 - 8 month period, with lightning strikes a major source of ignition during summer and early autumn, resulting in intense and widespread fires (McCaw and Hanstrum 2003). The arrival of Aborigines in the late Pleistocene instituted an anthropogenic fire regime, with a shortening of the fire interval in heavily occupied areas to 10 - 15 years (Hassell and Dodson 2003) or less. Current land management practices seek to recreate the 'natural' fire regime (Bergeron et al. 2002; Russell-Smith et al. 2003), though support for preserving biodiversity through recreating the natural pyrogenic history is equivocal (Veblen 2002; Fernandes and Botelho 2003). The ultimate goal of controlled-burning (managed fire) practices is to,
theoretically, protect life and property by reducing fuel loads and hence the risk of subsequent catastrophic wildfires. However, the efficacy of this practice is questionable (Enright and Fontaine 2014). Stable and successful populations of species within the broad "sprouter" and "seeder" regenerative life histories have a clear demographic signal that intimates long term population persistence and resilience to local and moderate disturbance, especially by fire.

With seed dispersal the only vagile component of the plant life-cycle, integral to population persistence (Cain et al. 2000), and fire the key signal for recruitment for many species in the jarrah forests, it is important to understand the potential complex interactions that may exist between seed dispersal, fire and demographic structure. Among the key demographic variables of plant populations are size structures, growth, reproductive output, spatial arrangement and genetic structure (Hutchings 1986). For seeder and resprouter species, a successful population will contain a mixture of juveniles, reproductive and old (senescent) individuals. However, soon after a disturbance for a seeder species there will be a preponderance of seedlings but few adults. Fire, and subsequent prolific seed production for those species with fire-cued reproduction, is the cue for dispersal agents, who maximise population fitness (and benefit overall population structure) by dispersing seeds so they escape the potentially deleterious effects of density-dependent mortality, conspecific inhibition and Janzen-Connell effects (Janzen 1970; Connell 1971; Nathan and Muller-Landau 2000). The typically skewed distribution of individual plant sizes in plant populations does not necessarily indicate strong intraspecific competition, but may arise from the interplay of natural senescence, herbivory and other factors such as episodic recruitment events (Hutchings 1986). These factors may impact the size class distribution of populations in different ways; for example, herbivores may select either for or against large individuals, which can substantially impact population structure skewness (Hutchings 1986). Interpreting the cause of skewed population structures requires due caution as different impacts (and their interactions), such as herbivory and local variation in abiotic conditions can produce the same population structure (Hutchings 1986).

Reproductive output is a key demographic attribute, providing an overall picture of potential reproductive capacity and important insights into a population's age structure and resilience. Reproductive output directly links to population success and seed dispersal interactions (Blendinger et al. 2011), and dispersal agents are drawn to
resource-rich areas. Typically, short-lived fire-killed species exhibit a brief primary juvenile period of between 3 - 5 years (Nield et al. 2009), with fruit production increasing approximately linearly with age (Yates et al. 2007; Yates and Ladd 2010). The relationship between seed production and age for those species within the resprouting regeneration strategy is less clear. Resprouting species may be extremely slow growing and might typically live for many hundreds, if not thousands, of years (Lamont and Wiens 2003). This extreme longevity requires a perspective shift for considering the relationship between plant age (size) and fecundity. Lamont and Wiens (2003) note that while flower production increases with age for many resprouting shrubs, the production of viable seeds and fertile cones for species found within the species-rich Western Australian northern sand plains decreases with age in very large/old individuals. Many resprouter species flower prolifically after fire (Lamont and Downes 2011) and gradually decrease flowering intensity with time since last fire. However, for other large resprouters that take longer to commence reproduction, increasing flower production may result in decreased fertile seed set as pollination events are increasingly geitonogamous. Other key demographic attributes, such as plant spatial structure, are given detailed treatment in subsequent chapters or, in the case of genetic structure, are beyond the scope of this study.

Seed banks also play a critical role in plant population dynamics (Leishman et al. 2000). For species that do not regenerate vegetatively following fire, populations recover and re-establish from seeds stored in the soil or in the canopy (Gill 1981). The storage of seeds within the soil or canopy represents an evolutionary strategy that provides a buffer against disturbance, predation, genetic drift and immigration (Leishman et al. 2000). By possessing a seed bank, plants are able to take advantage of a post-fire environment that has more available nutrients, moisture, light and decreased competition overall (Bond and Van Wilgen 1996) than during the inter-fire period. However, substantial seed loss can occur from predation, which may markedly reduce regeneration following disturbance, although loss rates can vary geographically and by season (Bond 1984; Lamont et al. 1991; Nathan and Ne’eman 2000). Seed loss within the soil is more readily predictable, and is best described by an exponential decay curve, although the percentage loss will vary by species and by year (Harper 1977; Cavers 1983; Leishman et al. 2000). Seed loss from the soil seed bank can also occur as a result of germination during the inter-fire period, or from unsuitable burial depths (too deep to receive the cue, or to emerge, after fire), and from predation, pathogen attack, and loss of viability.
Cook (1980) suggests that the majority (up to 90% in some instances) of seeds held within the soil seed bank may be lost to one or other of these causes. Where the proportion of seed or fruits removed is high, an increase in seed bank density below the canopy of fruiting trees and shrubs, particularly if they are not persistent, may be a demographic signal of disperser loss.

The loss of a primary dispersal agent can potentially disrupt key dispersal mutualisms and have deleterious demographic consequences (Bond 1994). For plants dispersed by frugivores, ingestion of seed may enhance germinability (though this effect is not uniform) and increase chances of survival through deposition into suitable microhabitats (Bradford and Westcott 2010). Unfortunately, dispersal mutualisms may be rapidly severed via direct persecution, or gradually as a consequence of habitat change, with large dispersal agents particularly vulnerable to loss (Corlett 2007). Given that seed dispersal has such an important impact on plant population dynamics (Schupp 1993; Nathan and Muller-Landau 2000; Schupp et al. 2010), the loss of key dispersal agents may have a detectable negative impact on plant demography.

The aim of this chapter is to describe the key demographic rates of the four study species identified in Chapter Three. Each of the species is compared for high emu/low emu abundance study sites and is examined in the context of the local environment and fire history. This chapter also examines the evidence for any demographic bottlenecks that may be linked to disperser decline and seeks to identify if any of the study species are particularly susceptible to a deleterious demographic shift. The overarching aim of this chapter is to quantify population structures, and recruitment, growth, survival and fecundity rates with and without fire (some species produce seeds mostly or only in the first year after fire) of the four target species. It is hypothesised that;

1. All four species require fire to promote recruitment.
2. Where emu abundance is low there will be measurable plant demographic consequences (more evident in the non-sprouter species, *L. nutans*, than in the three resprouter species), including reduced fecundity and recruitment (Wang et al. 2007).
3. The interaction of fire and an intact extant seed dispersal vector (the emu) best facilitates persistence of stable plant populations of the four key species.
4.2 MATERIALS AND METHODS

4.2.1 Population size structure

The population size structure is described separately for each study species owing to the varying size (from sub-shrub to understorey forest tree) and plant density of each species at each study site, which led to differing plot size and measurement requirements.

*Leucopogon nutans*

Population size structure for *L. nutans* was assessed at both the high emu abundance (HEA) study site (Avon Valley) and the low emu abundance (LEA) site (Sawyers Valley). Four 20 × 20 m, three 25 × 25 m and one 50 × 50 m plot(s) were established at random-sited systematic locations in Sawyers Valley during April - May 2011. In each instance an initial 20 × 20 m plot was established and expanded in 5 × 5 m increments until at least 30 individual plants were recorded. A total of 30 individuals was selected as the minimum number required for spatial pattern analysis (Chapter Five; Perry et al. 2006). Due to higher plant densities (up to 0.5 ± 0.1 individuals m\(^2\)) at Avon Valley the initial plot size was 10 × 10 m. Ultimately, there were four 10 × 10 m, four 15 × 15 m, one 20 × 20 m and one 30 × 30 m plot(s) established. Within each plot, stem diameter (ca. 2 cm from the ground), canopy height, canopy width (longest axis and perpendicular to longest axis) and plant x-y location were recorded. Following prescribed burning in spring 2011 at Sawyers Valley, four burnt plots were surveyed to quantify seedling recruitment post-fire during spring 2012.

*Persoonia elliptica*

Population size structure for *P. elliptica* was assessed at Avon Valley (HEA) and Sawyers Valley (LEA) study sites. At Sawyers Valley, eight 400 × 400 m (16 ha) random-sited systematic plots within the 900 ha study area were searched during February 2012. Stem diameter at breast height (DBH; 1.3 m), height, and maximum canopy width (and width perpendicular to this) were recorded as part of a related study in November 2010. All individuals within a 900 ha (3 × 3 km) study area at Avon Valley were recorded (*n* = 280; typical accuracy = 5 m) with a Garmin GPS. Stem diameter at breast height, tree height and canopy width were recorded for 100 of these individuals in February 2012.
Given the observed recruitment failure of *P. elliptica* within the jarrah forests of SW Australia (Abbott and Van Heurck 1988), five replicate exclosure plots were installed in areas of different burn history (autumn 2011, spring 2011 and unburnt, respectively) at Sawyers Valley to investigate the effects of fire and herbivory on seedling emergence and survival. Each 4 × 4 m exclosure plot consisted of four, 1.96 m high fence posts supporting rabbit proof fence mesh under the canopy of a randomly-selected *P. elliptica* tree. The fencing wire extended from just below the surface of the ground to a height of 1 m to exclude the assumed primary herbivores; wallabies (*Macropus irma*), kangaroos (*Macropus fuliginosus*) and rabbits. Five 4 × 4 m control (i.e. unfenced) plots were also delimited in each of the burnt and unburnt areas. The plots were erected in winter 2011 and 2012 for the autumn 2011 and spring 2011 burn areas, respectively. For the autumn 2011 burn plots, a seedling emergence assessment was conducted in winter 2012. During spring 2012, all plots were visited to check for the presence of germinants. Where present, each seedling was tagged and the height was recorded. A final census was conducted during autumn 2013 to obtain an overall estimate of seedling survival and growth rates.

*Podocarpus drouynianus*

Population size structure for *P. drouynianus* was assessed at Nannup (HEA) and Sawyers Valley (LEA). At Nannup, eight 50 × 50 m, one 40 × 40 m and one 30 × 30 m (where plant density was high; 0.14 individuals m²) plots were established in February-March 2012. Plots were located in areas prescribe burnt by the Western Australian Department of Environment and Conservation (DEC) in different seasons (autumn vs. spring) over the previous 2 years. Sample plots were established in the northern outlier population at Sawyers Valley in areas prescribe burnt by DEC in early winter (June) and early spring (September) of 2011. Two 25 × 25 m plots were located in the spring burn area and four 25 × 25 m plots in the autumn burn area. The disparity in the number and size of plots here reflects the limited size and spatial distribution of this *P. drouynianus* population. Since plots within the spring and autumn areas at Sawyers Valley were each burned by a single fire, data were aggregated into a single sample for each fire season to avoid pseudo-replication. Within each plot, x-y location of each individual was determined, and lignotuber length and width (selected as the best measure of plant size) was recorded.
Macrozamia riedlei

Population size and spatial structure for *M. riedlei* was assessed at Avon Valley (HEA), Sawyers Valley (LEA) and Kings Park (no emu presence for >100 years). Population structure was also assessed at Hill River Nature Reserve to determine the growth rate of the species. Five 50 × 50 m plots were randomly located within Kings Park in March 2012, seven 50 × 50 m and one 60 × 60 m plots were established at Sawyers Valley, and seven 50 × 50 m plots were established at Avon Valley. At Hill River, four contiguous 50 × 50 m plots were re-surveyed that had been established initially in the early 1990’s (Connell and Ladd 1993) and last remeasured in 2002 (P.G. Ladd, unpublished data).

For each individual, the trunk height (where present) was recorded in addition to the length of the longest living frond (Connell and Ladd 1993) as well as the number of fronds. Trunk height was measured from the ground surface to the location of the emergence of fronds from the plant apex. Frond length was measured from this emergence point to the tip of the leaf. The sex of each individual was determined based on the presence of old male or female cones or cone remnants (no individuals were coning at the time of the demographic survey) on or beneath the plant. Where numerous seedlings and juveniles were present beneath the crown, the adult plant was assessed as female. Beyond sex determination, individuals were classified as either a seedling, juvenile or adult to better delineate population structure. It is difficult to use size in slow-growing cycads to classify overall population structure. However, a modified demographic classification, after Snow and Walter (2007), was used with seedlings being classed as plants with no above-ground stem and a single longest-frond measurement not exceeding 25 cm. The juvenile class contained individuals which lacked an above-ground stem, had frond length of between 25 and 100 cm, and showed no indication of having reached sexual maturity. Those individuals without a trunk and with frond measurements exceeding 100 cm, but for which no determination of sex could be made, were classified as indeterminate adults. Any individual plant that had a trunk was classified as an adult, irrespective of frond length. Some individuals with frond lengths < 100 cm were able to be classified as reproductive adults based on the presence of old cones.
4.2.2 Flowering, coning and seed production

*Leucopogon nutans*

Flowering and fruiting

To determine flower production (*L. nutans* typically flowers between April - June) and flower to fruit conversion rates, five shoots on five randomly-selected flowering *L. nutans* within four study plots (total *n* = 20 plants) at Sawyers Valley were tagged in May 2011. Shoot length was measured and the number of flowers counted. Where plants had five or fewer branches, the total number of flowers on the plant was counted. The stem diameter, canopy width at widest point (and perpendicular to this) and height was recorded for each individual to ensure that flowering was assessed across a range of plant sizes. In July 2011, shoots were again measured and the number of mature and aborted fruits counted.

To gain more detailed information on flowering within and between study sites five shoots on ten randomly-selected flowering individuals within four of the study plots (*n* = 40 plants) at Avon Valley and three plots (*n* = 30 plants) at Sawyers Valley, were tagged, measured and the number of flowers counted in June 2012. Fewer plants at Sawyers Valley than at Avon Valley were tagged owing to the previous collection of 2011 flowering data at that site. The stem diameter, canopy width at widest point (and perpendicular to this) and height was recorded for each individual. In August 2012 the tagged shoots were remeasured and the number of mature and aborted fruits counted. More than 600 fruits were collected from plants within study plots (no more than 50 fruits per plant) to determine seed weight, size and potential viability. During August 2013, a fruit count was done on an additional 40 individuals at Avon Valley and 20 at Sawyers Valley. In total, the fruit production of 70 and 80 individuals from Sawyers and Avon Valley respectively was assessed across the three study years.

Seed bank dynamics

In April 2011 (and prior to 2011 seed production), 50 *L. nutans* individuals were randomly-selected at Avon Valley and Sawyers Valley, respectively for quantification of the soil seed bank beneath the plant canopy. Plants were excluded if another *L. nutans* individual was within a 2 m radius of the target plant. Stem diameter, canopy width and height were recorded for each individual. For each plant location, a soil core
(10 × 10 × 5 cm depth) was taken at 0.25 and 1.0 m from the stem along a randomly-selected radial line. Each sample was sifted using a 2 mm sieve and the number of fruits counted.

Seed viability

The viability of fresh seed from the plant canopy was determined by randomly collecting fruit from individual *L. nutans* within plots. Fruit was collected in August 2012 and stored in paper bags at 4°C until viability testing could be performed (fruits were kept for a maximum of 3 months). A cut test was performed to assess seed viability for a total of 200 fruits. A fruit was considered potentially viable if one of the five locules within the fruit contained a white embryo that appeared healthy (Allan *et al.* 2004; Ooi *et al.* 2004). The number of filled locules was recorded.

To determine the viability of seed in the soil seed bank, cut tests were performed on 20 fruits collected from the seed bank beneath each of 10 individuals at both Avon Valley and Sawyers Valley. To ensure sufficient fruits for testing, fruits were pooled across the samples taken from 0.25 and 1.0 m from each individual. In total, 400 fruits were tested. A burial experiment was also conducted to assess the potential loss of seed viability in the seed bank following one year of burial. In spring 2012, hessian bags each containing ca. 200 *L. nutans* fruits and a small quantity of river sand were buried 2 cm below the surface litter layer at three random locations at both Avon and Sawyers Valley (*n* = 6 bags in total). The bags were retrieved after 12 months and 100 fruits from each bag cut-tested to assess viability. The number of filled locules was recorded.

To determine the viability of *L. nutans* seeds contained within emu scats, 7 scats from Avon Valley and 3 from Sawyers Valley were analysed during Spring 2012. Fewer scats were collected from Sawyers Valley as the scat deposition rate at the site was much lower than at Avon Valley. Each of the scats collected had been deposited in the previous three months to ensure that seed viability within the scat would not be confounded by seed age. Within each of the scats, 20 *L. nutans* fruits were randomly selected and a cut test performed. In total, 200 fruits were tested. Seed viability was determined as described above.
Persoonia elliptica

Flowering and fruiting

*P. elliptica* flowering (typically occurring between October - February) was assessed and compared between Avon and Sawyers Valleys. In December 2011, 20 shoots (five in each cardinal direction) on ten trees at each site were tagged, measured and the number of flowers and pedicels (left after poorly developed flowers had fallen) counted (Bauer *et al.* 2001). Diameter at breast height (stem DBH), canopy width and height was recorded as described previously. In February and April 2012, the tagged shoots were remeasured and the number of mature and immature/aborted fruits counted. In winter 2013 fruit counts on an additional 10 individuals at each site were recorded to examine the potential impact of annual variability on seed production. For these counts, the number of mature fruits on 50 shoots was extrapolated for an estimate of the total number of fruits on the plant.

Seed bank dynamics

During autumn 2012, 10 *P. elliptica* individuals were randomly-selected for soil seed bank analysis at Avon Valley and Sawyers Valley, respectively. Diameter at breast height (stem DBH), canopy width at widest point and height were recorded for each individual. A $0.5 \times 0.5$ m quadrat was placed on the soil surface at 0.5, 1.5 and 3.0 m from the stem in both a northern and southern direction beneath each tree. Within each quadrat, the surface layer of litter was removed along with fresh drupes from the current crop of *P. elliptica* fruits (where present) and the soil was searched to a depth of 2 cm for soil-stored seeds. The same procedure was repeated during autumn 2013 for an additional 10 individuals at both study sites to increase the overall sample size and to compare years. Seeds collected during the 2013 estimates were stored in paper bags at 4°C until viability testing was performed (seeds were kept for no longer than 3 months).

Seed viability

Up to 20 fruits from the canopy of each of 5 randomly selected individuals were used to test seed viability. Where 20 mature fruits were not available, a minimum of 10 fruits was used. At Sawyers Valley, 20 fruits were collected from 3 individuals and 10 from an additional 2 individuals. At Avon Valley, 10 seeds were collected from each of 5
individuals. Each fruit was cut tested to determine potential seed viability. Seeds were considered to be potentially viable if they contained a white, fleshy embryo. Seed length, width and weight were recorded to provide average seed characteristics. To assess viability within the soil seed bank, 10 seeds from each of the sampled distances for 5 individuals were cut tested.

A burial experiment was also conducted to assess the potential loss of seed viability in the seed bank following one year of burial. In spring 2012, two hessian bags each containing 100 P. elliptica fruits in a matrix of dry river sand were buried 2 cm below the surface litter layer at three random locations at both Avon and Sawyers Valley (n = 6 bags in total). The bags were retrieved 12 months following burial and the fruits cut-tested to assess viability.

**Podocarpus drouynianus**

*Cone production and seed viability*

Within plots, the number of seeds on each female was counted, as was number of damaged (eaten by granivores) seeds and/or podocarpia. To examine potential seed viability, five seeds from each of 10 individuals selected at random in each plot at Nannup were collected. Fewer seeds were collected from the Nannup area plots at Milyeannup Nth, Rosa and Whichler (17, 34 and 20 in total, respectively) owing to low seed production there, and no seeds were found at the River Road East plot. At Sawyers Valley, where seed production was poor following a small prescribed burn, 38 seeds in total were collected from randomly-selected plants during autumn 2012. The weights of each seed and podocarpium were recorded. Seeds were cut in half and considered viable if a torpedo-shaped green embryo was present in the female gametophyte.

**Macrozamia riedlei**

*Cone production and seed viability*

Coning phenology and seed production of *M. riedlei* was not assessed directly during the course of this study. Fire is usually required to stimulate cone production in *M. riedlei* (though cone production may occur during inter-fire periods; Ornduff 1985; 1991; Pate 1993), but was completely absent in the years preceding and during the study.
years at three of the four *M. riedlei* study sites; Kings Park, Hill River and Avon Valley National Park. No male or female cones were observed at either of these study sites. While Sawyers Valley was subjected to prescribed burning in June and September 2011, the burns were of low intensity, exceptionally patchy and failed to initiate cone production. Here, the published literature is relied upon to cover this shortfall in data. Similarly, viability could not be determined for seeds collected within the study sites. However, the fully developed seeds of cycads (particularly within *Macrozamia*) are known to have high viability, with approximately 99% of seeds found to be viable in other studies (Terry *et al.* 2005). This viability estimate is assumed for *M. riedlei* at the study sites. A small amount of seed (*n* = 10) were opportunistically collected from forest in southwestern Australia and their weight, length and width recorded to provide an overview of general seed characteristics.

### 4.2.3. Statistical analysis

**General Model Selection**

Model selection for analysis of demographic data presented within this chapter has been done with careful consideration of current statistical methodological thinking. For most data, this involved departure from the use of typical data transformations (i.e. log-normal, square-root) to ameliorate the problems usually encountered with ecological data in various linear modelling approaches, especially count data with a preponderance of zeros. Instead, data here are mostly analysed using generalised linear models (GLMs) or general linear mixed models (GLMMs) with mixed effects where appropriate that utilise the family (link) functions to describe the error term of the model and satisfy model assumptions. This approach avoids some of the pitfalls of traditional data analysis approaches (O’Hara and Kotze 2010) and is the preferred method for analysis of non-normal ecological data with random effects (Bolker *et al.* 2009). Bolker *et al.* (2009) provide an excellent guide to the application of GLMMs for ecological data, and is followed here. All model analyses were conducted in R version 2.15.2 (R Core Team 2012) within the inbuilt generalised linear model (GLM) statistical function. GLMMs were conducted using the lme4 linear mixed-effects model package (Bates and Maechler 2009). GLM assumptions were examined visually through plots of the observed vs. fitted residuals. Where multiple models provided suitable fits, the final model selection was based on that with the lowest AIC score (Anderson *et al.* 1998), or,
for quasi-Poisson models (which cannot retain AIC estimates as log likelihood estimations are not used), F tests.

Where proportions are reported, the normal approximation method of the binomial confidence interval was used to calculate sample variance (Brown et al. 2001). Unless otherwise stated, all errors reported are 95% confidence intervals.

*Leucopogon nutans*

*Flowering and fruiting*

A GLM examined the relationship between fruit production, stem diameter, site and sampling year. Site, stem diameter and sampling year were incorporated into the model as fixed factors. The model error distribution was taken from the quasi-Poisson family to account for over dispersion in the data and to satisfy model assumptions.

*Soil seed bank dynamics*

GLMs were used to assess impact of site and distance sampled from a shrub stem on counts of seeds in the soil seed bank. Analyses were conducted on the untransformed count data, with preference given to using Poisson, quasi-Poisson and negative binomial error models instead to meet GLM assumptions (O’Hara and Kotze 2010). Models were initially constructed with a Poisson error model, with expansion to the quasi-Poisson occurring where models were found to be over dispersed (residual deviance >> residual degrees of freedom). Interactive effects were also assessed between site and distance from the stem.

*Seed viability*

Seed viability of material collected from the seed bank, canopy, retrieved from emu scats and recovered following 1 year of burial was analysed in separate GLMMs. In each instance, the models examined the relationship between seed viability as a binomial response (viable vs. not viable) against study site. The individual, shrub, scat or seed burial bag from which the seed material was obtained was included in the relevant models as a random factor.
**Persoonia elliptica**

**Flowering, fruiting and seedling survival**

A GLM was used to examine for potential impacts of study site, sampling year and stem diameter at breast height (dbh) on fruit production. The error distribution was taken from a quasi-Poisson distribution to account for data overdispersion. A GLMM was used to determine the impact of burn history and the presence of a herbivory exlosure on the survival of emerged seedlings. Burn history and exclosure presence were included in the model as fixed factors, with plot added as a random effect.

**Soil seed bank density and viability**

A GLM was used to analyse the impact of study site, distance from tree, sampling year and cardinal direction sampled on soil seed bank density. Each model element was included as a fixed factor. GLMMs were used to examine for potentially significant impacts on seed bank viability within seed sources (fresh seed from the canopy vs. soil seed bank) and between sites. For material from the soil seed bank, model structure included seed viability as a binomial response and contained study site and distance from the base of sampled tree as fixed factors. Tree was included in the model as a random effect. For seed sourced from the canopy, model structure included site as a fixed factor with tree included as a random effect. A GLMM was also used to compare seed viability between study sites for seeds recovered one year following burial. Study site was included as a fixed factor and burial bag as a random effect.

A GLM was used to examine the impact of seed source and site on overall *P. elliptica* seed viability, with seed viability as a binomial response. A term was also added to the model to determine if there was any interactive effect between seed source and site.

**Podocarpus drouynianus**

**Cone production and seed viability**

The mean number of seeds per female produced in each year/season and mean seed weight was compared using a Kruskal-Wallis rank sum test (unequal sample variance made parametric methods unsuitable). Subsequent post-hoc comparisons were conducted using a Wilcoxon rank sum test with a Bonferroni correction. Potential seed
viability was compared between autumn 2011 and spring 2010 burnt sites at Nannup using a t-test, not assuming equal variance. Female:Male sex ratios were compared for each site using chi squared analysis, with the null hypothesis assuming a 1:1 ratio (Ornduff 1985). Figures were created using the ggplot2 R package (Wickham 2009).

*Macrozamia riedlei*

Seed production and viability rates are taken from the literature owing to data paucity, so no formal statistical analysis has been conducted. Also, with only approximately 15% of potentially reproductive adults being classified as sexually mature, no formal statistical analysis of female:male sex ratios was conducted. Instead, a general description of overall demographic structure and sex ratios is provided.
4.3 RESULTS

4.3.1 *Leucopogon nutans*

*Population size structures*

The majority of *L. nutans* individuals at Sawyers Valley and Avon Valley were confined within the 5 - 15 mm stem diameter size classes with very few individuals having stem diameters > 20 mm (Figure 4.1). A few extremely large individuals (stem diameter ca. 40 mm) were observed at each of the study sites, however, these showed signs of stress and senescence such as browned leaves and low fruit production (further detail below). While there were some individuals in the < 5 mm size class, the modal size is consistent with expected size distribution for a post-fire recruiter, fire-killed small shrub species. There was no clear difference in population size structure between the two sites.

![Comparative stem size distribution of L. nutans at Avon Valley National Park (n = 707) and Sawyers Valley State Forest (n = 363); data for all plots combined within sites](image)

**Figure 4.1** Comparative stem size distribution of *L. nutans* at Avon Valley National Park (*n* = 707) and Sawyers Valley State Forest (*n* = 363); data for all plots combined within sites
Flowering and fruiting

Seed production increased with stem diameter for *L. nutans* and the production of fruits was significantly greater in 2012 than 2013 (Table 4.1). A few exceptionally large individuals had poor fruit production relative to stem diameter while a number of smaller individuals exhibited prolific fruit production (Figure 4.2).

Table 4.1 Generalised linear model parameters for the impact of site, year and stem diameter on *L. nutans* fruit production. Parameter estimates are derived from the quasi-Poisson family to account for overdispersion. Bolded t-values represent model parameters with a significant effect (*p* < 0.05)

<table>
<thead>
<tr>
<th>Effect on fruit production (SE)</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site Sawyers</td>
<td>0.273 (0.229)</td>
</tr>
<tr>
<td>Year 2012</td>
<td>1.383 (0.455)</td>
</tr>
<tr>
<td>2013</td>
<td>-0.420 (0.497)</td>
</tr>
<tr>
<td>Stem diameter</td>
<td>0.049 (0.007)</td>
</tr>
</tbody>
</table>

Model parameters:
fruits ~ site + year + stem diameter

Figure 4.2 The relationship between fruit production and stem diameter for *L. nutans* across study sites and years. No straight line model is fitted owing to the impact of year and stem diameter on fruit production
Soil seed bank dynamics

Significantly more fruits were found per soil seed bank sample close to the stem (0.25 m) of putative parent *L. nutans* shrubs in comparison to beyond the edge of the canopy at 1.0 m (Table 4.2). Almost half (49%) of the soil seed bank samples collected at 1.0 m contained no seeds, in comparison to 25% for the samples at 0.25 m.

**Table 4.2** Generalised linear model parameters for the impact of site and distance from stem on *L. nutans* soil seed bank density. Bolded \( t \)-values represent model parameters with a significant effect \( (p < 0.05) \). Fitted coefficients are scaled to the GLM log link function (quasi-Poisson)

<table>
<thead>
<tr>
<th>Effect on seed bank density (SE)</th>
<th>Site</th>
<th></th>
<th>Distance from stem (m)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sawyers</td>
<td>0.331 (0.352)</td>
<td>0.941</td>
<td></td>
</tr>
<tr>
<td>Distance from stem (m)</td>
<td>-1.89 (0.584)</td>
<td>-3.235</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Model parameters:
\( n \) fruits ~ site + distance

Seed viability

The soil seed bank at Sawyers Valley contained more fruits with viable seeds (47%) than at Avon Valley (<1%) (Table 4.3). At Avon Valley, of 200 fruits that were cut tested, only one contained a viable embryo. Although almost half the fruits sampled at Sawyers Valley contained a viable embryo, only a single locule, on average, was filled. However, for fruits retrieved one year following burial in seed bags, significantly more fruits contained at least one viable embryo at Avon Valley (38 ± 5%) in comparison to Sawyers Valley (19 ± 4%; Table 4.4). For *L. nutans* fruit retrieved from emu scats deposited in 2012 there was no difference in seed viability between sites (Table 4.4). 92% (± 4%) of fruits retrieved from scats had at least one filled locule, and many contained two. For fresh seed collected from the canopy, 90% (± 4%) contained at least one potentially viable embryo, with two embryos observed on average per fruit. There was no significant difference in fruit viability between sites for material collected from the canopy (Table 4.4).
Table 4.3 Generalised linear mixed model parameters for the impact of site on *L. nutans* seed bank fruit viability. Bolded *z*-values represent model parameters with a significant effect (*p* < 0.05). Fitted coefficients are scaled to the GLM logit link function (binomial).

<table>
<thead>
<tr>
<th>Site</th>
<th>Effect on seed viability (SE)</th>
<th>z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sawyers</td>
<td>7.159 (2.867)</td>
<td>2.497</td>
</tr>
</tbody>
</table>

Model parameters:

\[
\text{viable?} \sim \text{site + (1|shrub)}
\]

Table 4.4 Generalised linear mixed model parameters for the impact of site on *L. nutans* seed bank fruit viability following 1 year of burial (1), for those fruits retrieved from emu scats (2) and fruits collected from the canopy (3). Bolded *z*-values represent model parameters with a significant effect (*p* < 0.05). Fitted coefficients are scaled to the GLM logit link function (binomial).

<table>
<thead>
<tr>
<th>Model</th>
<th>Model Parameter</th>
<th>Effect on viability (SE)</th>
<th>z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>Site (Sawyers)</td>
<td>-0.9686 (0.1905)</td>
<td>-5.085</td>
</tr>
<tr>
<td>(2)</td>
<td>Site (Sawyers)</td>
<td>-0.696 (0.752)</td>
<td>-0.925</td>
</tr>
<tr>
<td>(3)</td>
<td>Site (Sawyers)</td>
<td>-18.83 (3584)</td>
<td>-0.05</td>
</tr>
</tbody>
</table>

Model parameters:
1. viable? ~ site + (1|bag)
2. viable? ~ site + (1|scat)
3. viable? ~ site + (1|plot/tree)

Post-fire recruitment

No seedlings were observed in any unburnt plot at either Avon or Sawyers Valley. Following prescribed burning, a total of 87 seedlings were observed across the four burnt plots. Emerged seedling density was low overall, with 0.05 (± 0.05) seedlings m\(^2\) recorded.

4.3.2 *Persoonia elliptica*

Population size structures

The majority of *P. elliptica* individuals at Avon Valley and Sawyers Valley had stem diameters of 15 - 30 cm (Figure 4.3). Most individuals at Avon Valley were contained within the 20 - 30 cm stem dbh class. Comparatively, the peak stem dbh size classes observed at Sawyers Valley were in the 15 - 25 cm range. The largest individuals were found at Sawyers Valley, with some plants having stem diameters > 40 cm. Very few
individuals were recorded at either site with stem diameters < 5 cm. No seedlings (<30 cm height) or saplings (30 – 150 cm height) were observed at the unburnt Avon Valley site, or in unburnt parts of the Sawyers Valley site. Only one seedling was recorded in the exclosure ($n = 5$) plots that were established in the unburnt area. No seedlings emerged in the control ($n = 5$) plots in the unburnt area.

![Figure 4.3](image)

**Figure 4.3** Comparative stem demography of *P. elliptica* at Avon Valley National Park ($n = 100$) and Sawyers Valley State Forest ($n = 320$)

*Flowering and fruiting*

There was a positive linear relationship between stem diameter and fruit production for *P. elliptica* (Table 4.5), although some particularly large individuals produced very few and, in one instance, no fruits (Figure 4.4). Across all canopy sizes, a number of individuals did not produce any fruit.
**Table 4.5** Generalised linear model parameters for the impact of site, year and stem diameter on *P. elliptica* fruit production. Parameter estimates are derived from the quasi-Poisson family to account for overdispersion. Bolded t-values represent model parameters with a significant effect (*p* < 0.05)

<table>
<thead>
<tr>
<th>Effect on fruit production (SE)</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Site</strong></td>
<td></td>
</tr>
<tr>
<td>Sawyers</td>
<td>0.418 (0.314)</td>
</tr>
<tr>
<td><strong>Year</strong></td>
<td></td>
</tr>
<tr>
<td>2012</td>
<td>0.014 (0.318)</td>
</tr>
<tr>
<td><strong>Stem diameter</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.052 (0.024)</td>
</tr>
</tbody>
</table>

Model parameters:
fruits ~ site + year + stem diameter

**Figure 4.4** The relationship between fruit production (*y*=25.12*stem.dbh*+18.60; df=38, \(R^2=0.07\)) and stem size for *P. elliptica* at Avon Valley and Sawyers Valley
Soil seed bank dynamics

Soil seed bank density was significantly higher at all distances from the base of the trunk at Sawyers Valley than at Avon Valley (Table 4.6; Figure 4.5). Across both sites there was a decline in the density of the seed bank with distance from the base of the tree.

Table 4.6 Generalised linear model parameters for the impact of site, year, distance from the base of the tree and cardinal direction sampled on *P. elliptica* soil seed bank density. Errors are taken from the quasi-Poisson family. Bolded t-values represent model parameters with a significant effect (*p* < 0.05)

<table>
<thead>
<tr>
<th>Effect on seed bank density (SE)</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td></td>
</tr>
<tr>
<td>Sawyers</td>
<td>0.768 (0.224)</td>
</tr>
<tr>
<td>Distance from trunk (m)</td>
<td>-0.512 (0.119)</td>
</tr>
<tr>
<td>Year</td>
<td>0.085 (0.209)</td>
</tr>
<tr>
<td>Direction from trunk</td>
<td></td>
</tr>
<tr>
<td>South</td>
<td>-0.391 (0.213)</td>
</tr>
</tbody>
</table>

Model parameters:
number of seeds ~ site + distance from trunk + year + direction

Figure 4.5 Mean number of *P. elliptica* fruit per soil seed bank sample (± 95% CI, calculated from the exponent of the natural log of the number of fruit) at varying distances from the base of the tree recorded at Avon and Sawyers Valley
Seed viability

Viability of seed stored within the soil seed bank was very low, with only 8.6% (± 3.5) of fruits containing potentially viable embryos. There was no significant difference in the proportion of potentially viable seeds between the Avon and Sawyers Valley sites or between the three distances sampled from the base of individual trees (Table 4.7). However, for seeds buried in mesh bags for one year, although low overall, viability was greater at Sawyers Valley than Avon Valley (5.6% ± 2.6%; 0.3% ± 0.7%; Table 4.7). Viability of fresh seeds from the canopy was significantly higher than for the seed bank, with 35 ± 8% of seeds potentially viable. There was no significant difference in viability of fresh seeds between sites (Table 4.7). However, when considering the seed source (canopy vs. soil) and viability, there was a significant interaction between source, study site and potential viability (Table 4.7). Seed from the soil seed bank at Sawyers Valley contained significantly more potentially viable embryos than those from Avon Valley, while seed sourced from the canopy of *P. elliptica* individuals at Avon Valley contained significantly more potentially viable embryos (Figure 4.6).

Table 4.7 Linear mixed model parameters for (1) the impact of site and distance from the base of the tree (for soil-stored seeds), (2) seed burial for 1 year, (3) site (for canopy-sourced seeds) and (4) site and seed source (canopy/soil seed bank) on *P. elliptica* seed viability. Bolded t- and z-values represent model parameters with a significant effect (p < 0.05). Fitted coefficients are scaled to the GLM logit link function (binomial).

<table>
<thead>
<tr>
<th>Model</th>
<th>Model Parameter</th>
<th>Effect on seed viability (SE)</th>
<th>t- or z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>Site (Sawyers)</td>
<td>2.75 (1.87)</td>
<td>1.471</td>
</tr>
<tr>
<td></td>
<td>Distance from trunk (m)</td>
<td>-0.132 (0.268)</td>
<td>-0.492</td>
</tr>
<tr>
<td>(2)</td>
<td>Site (Sawyers)</td>
<td>2.944 (1.044)</td>
<td>2.819</td>
</tr>
<tr>
<td>(3)</td>
<td>Site (Sawyers)</td>
<td>-1.78 (0.99)</td>
<td>-1.798</td>
</tr>
<tr>
<td>(4)</td>
<td>Site (Sawyers)</td>
<td>-1.19 (0.38)</td>
<td>-3.12</td>
</tr>
<tr>
<td></td>
<td>Source (Soil seed bank)</td>
<td>-4.62 (1.04)</td>
<td>-4.42</td>
</tr>
<tr>
<td></td>
<td>Site (Sawyers) * Source (Soil seed bank)</td>
<td>3.86 (1.10)</td>
<td>3.50</td>
</tr>
</tbody>
</table>

Model parameters:
1. viable?(binomial response) ~ site + distance from trunk + (1|tree)
2. viable?(binomial response) ~ site + (1|bag)
3. viable?(binomial response) ~ site + (1|tree)
4. viable?(binomial response) ~ site * source
Figure 4.6 Mean proportion of potentially viable seeds (±95% CI) of *P. elliptica* sourced from the soil seed bank and canopy at Avon Valley and Sawyers Valley.

*Post-fire recruitment*

*P. elliptica* exhibited post-fire recruitment, with a number of seedlings emerging in the burnt forest blocks. Following fuel reduction burning in spring 2011, 71 germinants were recorded across 30 plots. On average, 5 (± 4) seedlings emerged across both the enclosed (*n* = 5) and control (*n* = 5) plots in the area burnt in spring 2011, while only 2 (± 3) seedlings emerged in the plots (*n* = 10) established in the autumn 2011 burn area. The survival of *P. elliptica* seedlings was significantly higher in exclosed plots (Table 4.8) and in the plots that had been burnt in autumn 2011 (Figure 4.7). It should be noted that the autumn 2011 fire resulted in recruitment in winter 2011, while the spring 2011 fire led to germination in winter 2012.

Growth of seedlings in the spring 2011 burn area was 8 mm (± 4) on average. Recruits in the autumn 2011 burn area increased in height by 3 mm (± 3) on average from winter 2012 to autumn 2013.
Table 4.8 Generalised linear mixed model parameters for the impact of herbivory exlosure and burn history on survival on *P. elliptica* seedlings. Bolded z-values represent model parameters with a significant effect (*p* < 0.05)

<table>
<thead>
<tr>
<th>Effect on seedling survival (SE)</th>
<th>Effect on seedling survival (SE)</th>
<th>z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exclosure</td>
<td>2.18 (0.72)</td>
<td>2.98</td>
</tr>
<tr>
<td>Burn History</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring 11</td>
<td>-1.83 (0.64)</td>
<td>-2.84</td>
</tr>
<tr>
<td>Unburnt</td>
<td>13.31 (2399)</td>
<td>0.006</td>
</tr>
</tbody>
</table>

Model parameters:
Survival (binomial response) ~ burn history + exclosure/control + (1|plot)

Figure 4.7 Proportion of *P. elliptica* seedlings surviving as measured in autumn 2013 from control and herbivory exlosure plots established in winter 2011 and 2012 for areas burnt in autumn and spring 2011 respectively. 95% confidence intervals are calculated from the normal approximation of the binomial distribution

4.3.3 *Podocarpus drouynianus*

Population size structures

Population size structures at Nannup were all negatively skewed, with a predominance of small individuals < 50 cm mean lignotuber diameter (Figure. 4.8) and largest plant size with a mean lignotuber diameter of 350 cm. The Sawyers Valley population differed markedly in structure from the Nannup populations with an even higher proportion of small individuals and few large (> 150 cm lignotuber diameter) individuals (Figure 4.9). The largest individual at Sawyers Valley had a mean lignotuber diameter of 250 cm.
Determination of sex was only possible where plants carried reproductive structures at the time of census. There was no clear size threshold at which individuals reach reproductive stage, with a few small individuals (smallest reproductive individual had a mean lignotuber diameter of 4 cm) producing sporophylls, and no indication that males become reproductive at different size than females. Populations burnt in spring 2010 showed a much higher proportion of non-reproductive individuals (in lignotuber size classes >50 cm) than did populations burnt in autumn. The majority of individuals at spring 2011 burn sites were not reproductive and for the few plants that did have sporophylls nearly all had aborted. The ratio of female to male individuals at Nannup combined across all plots was not significantly different from 1.0 (1.02 ± 0.18; $\chi^2 = 0.05$, df = 1, p = 0.83), although three populations had female/male proportions significantly different from 1:1. River Rd (E) had a significantly greater proportion of females (1.82) ($\chi^2 = 4.08$, df = 1, p < 0.05) whereas Rosa and Milyeannup BR had significantly smaller proportions of females (0.4; $\chi^2 = 8.69$, df = 1, p < 0.05 and 0.55; $\chi^2 = 5.88$, df = 1, p <0.05 respectively). The proportion of female to male individuals at Sawyers Valley was not significantly different from 1.0 (0.95; $\chi^2 = 0.02$, df = 1, p = 0.88).
Figure 4.8 Size-class (lignotuber width) and sex distributions for *P. drouynianus* populations from the Nannup (a) River Road (autumn 2010 fire), (b) Layman, Rosa, Milyeannup North (spring 2010 fire), (c) Whicher, Sollya, Milyeannup (autumn 2011 fires), (d) Cundinup, Brockman (spring 2011 fires), and Sawyers Valley (e) autumn 2011 fire, and (f) spring 2011 fire areas, SW Australia
Cone production and seed viability

The mean number of seeds per female at each study location showed a significant difference ($\chi^2 = 73.22, p < 0.001$). Female plants in the Sollya and Milyeannup BR plots at Nannup burnt in autumn 2011 (i.e. one year since fire) produced more seeds per individual than those at River Road E burnt in autumn 2010 (2 years since fire) or at Milyeannup Nth burned in spring 2010 (1.5 years since fire). No seeds were found on plants in areas prescribe burnt during spring 2011 (6 months after fire). Differences in seed production between spring and autumn burn areas were not uniform, with moderate seed production observed in the Layman spring 2010 burn plot.

Mean seed weights between sites and burn seasons were significantly different ($\chi^2 = 149.08, p < 0.001$). Seeds sampled from areas prescribe burnt in autumn 2011 were heavier than those from areas burnt in spring 2010. Seed cut tests indicated that almost 100% of seeds sampled from areas prescribed burnt during autumn were viable. Conversely, fewer ($t = 11.0, df = 2, p < 0.01$) seeds sampled from the spring 2010 burn areas were viable (Table 4.9). Sawyers Valley plants followed the same pattern, with seeds set in the autumn, but not the spring burn area. However, seed production per female from the autumn 2011 burn at Sawyers Valley was low, and not significantly different from any season/site at Nannup. All seeds collected from Sawyers Valley were viable and had similar mean weight to those collected at Nannup.
### Table 4.9

Table 4.9 Viable seeds (%), mean seed weight (g), sex ratio (number in parentheses indicates total number of male/female individuals) and seeds per female for *P. drouynianus* sample populations from the Nannup and Sawyers Valley regions. Errors are standard error. Significant differences (p < 0.05) between sites for variables (columns) are shown by different superscript letters. *Shaded* areas indicate those plots burnt in autumn. Unshaded areas are plots burnt in spring.

<table>
<thead>
<tr>
<th>Site</th>
<th>Time since fire (yrs)</th>
<th>Seeds per female</th>
<th>Viable seeds (%)</th>
<th>Seed weight (g)</th>
<th>Female: Male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Nannup:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>River Rd (W)</td>
<td>2 (A)</td>
<td>11(^a) ± 3</td>
<td>100</td>
<td>2.19(^a) ± 0.07</td>
<td>1.80 (42)</td>
</tr>
<tr>
<td>River Rd (E)</td>
<td>2 (A)</td>
<td>1(^b) ± 1</td>
<td>-</td>
<td>-</td>
<td>1.82(^*) (48)</td>
</tr>
<tr>
<td>Layman</td>
<td>1.5 (S)</td>
<td>26(^a) ± 8</td>
<td>88</td>
<td>1.42(^bc) ± 0.08</td>
<td>1.04 (55)</td>
</tr>
<tr>
<td>Rosa</td>
<td>1.5 (S)</td>
<td>14(^a) ± 4</td>
<td>91</td>
<td>0.80(^b) ± 0.04</td>
<td>0.40(^*) (46)</td>
</tr>
<tr>
<td>Milyeannup Nth</td>
<td>1.5 (S)</td>
<td>2(^b) ± 1</td>
<td>88</td>
<td>1.14(^b) ± 0.16</td>
<td>1.35 (40)</td>
</tr>
<tr>
<td>Whichler</td>
<td>1 (A)</td>
<td>38 ± 25</td>
<td>100</td>
<td>1.49(^bc) ± 0.13</td>
<td>0.71 (29)</td>
</tr>
<tr>
<td>Sollya</td>
<td>1 (A)</td>
<td>72(^a) ± 15</td>
<td>100</td>
<td>2.23(^a) ± 0.10</td>
<td>1.27 (152)</td>
</tr>
<tr>
<td>Milyeannup BR</td>
<td>1 (A)</td>
<td>54(^a) ± 16</td>
<td>100</td>
<td>1.90(^a) ± 0.10</td>
<td>0.55(^*) (68)</td>
</tr>
<tr>
<td>Cundinup</td>
<td>0.5 (S)</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Brockman</td>
<td>0.5 (S)</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Sawyers Valley:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cole Rd (W)</td>
<td>1 (A)</td>
<td>12 ± 3</td>
<td>100</td>
<td>1.84(^a) ± 0.07</td>
<td>0.95 (43)</td>
</tr>
<tr>
<td>Cole Rd (E)</td>
<td>0.5 (S)</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

#### 4.3.4 Macrozamia riedlei

**Population size structures**

Totals of 451, 1761, 895 and 1001 individuals were measured at King's Park, Sawyers Valley, Avon Valley and Hill River, respectively. The largest individuals were found at King's Park, with numerous individuals with frond lengths > 200 cm. There was a low number of small seedlings at all sites, with peak frequency observed for large juveniles (between 25 - 50 cm frond length). Sex determination of assumed reproductive adults (frond lengths > 100 cm) proved difficult (Figure 4.10). At King's Park, only 15% of assumed adults could be accurately sexed, with 47% of these individuals being identified as female. At Sawyers Valley, 31% of potential adults could be accurately sexed, with 62% of these being female. Similarly, at Avon Valley, sex determination could be made for 34% of assumed adults, with 54% of these female. At Hill River, the sex of 44% of adults could be determined, with 46% of these female.
Overall, the growth of fronds was found to be slow during the 10 years between the successive surveys of the Hill River plots. The growth in the length of the longest frond was higher in the seedling size class and tended to decrease from the juvenile to adult classes (Figure 4.11). Adult individuals produced substantially more fronds over the course of the census period in contrast to juveniles and seedlings. Seedlings almost produced no new fronds on average during the 10 year census period (Figure 4.11).
Figure 4.10 Size class by longest frond length and sex distribution of *M. riedlei* individuals at (a) King's Park, (b) Sawyers Valley, (c) Avon Valley National Park and (d) Hill River

Figure 4.11 The recorded change in (a) longest frond length and (b) number of fronds per plant, by size class, for *M. riedlei* surveyed at Hill River Reserve, Western Australia in 2002 and then 2012. Error bars are the 95% confidence interval
Cone and seed production

No plants in the study plots (burned and unburned) produced cones or seeds during the study period.

4.3.5 General fruit and seed characteristics

The general fruit and seed characteristics of each of the study species varied substantially (Table 4.10). *M. riedlei* possess the largest seeds in terms of weight and overall size, and is some 200 times heavier than its smallest counterpart in the study, *L. nutans*.

| Table 4.10 General fruit and seed characteristics of the four target study species |
|---------------------------------|-----|----------|----------|-----|
| L. nutans | P. elliptica | P. drouynianus | M. riedlei* |
| n | 200 | 100 | 10 | 10 |
| Propagule weight (g) | 0.11 ± 0.007 | 0.39 ± 0.02 | 1.32 ± 0.16 | 22.78 ± 2.12 |
| Propagule length (mm) | 6.76 ± 0.12 | 12.92 ± 0.39 | 16.95 ± 1.21 | 44.41 ± 2.08 |
| Propagule width (mm) | 4.62 ± 0.12 | 7.01 ± 0.2 | 12.08 ± 0.88 | 28.83 ± 1.57 |

* seeds sourced opportunistically from plants in southwestern Australia outside the study areas and used in removal experiments
4.4 DISCUSSION

The aims of this chapter were to quantify the population structures, recruitment, growth, survival and fecundity rates with and without fire of the four target species for sites with high versus low emu abundance in order to identify whether demographic impacts of disperser decline could be identified. There were no substantial differences in population size structures for target species, between study sites. Both the *L. nutans* and *P. elliptica* (unburnt) populations exhibited some signs of senescence, with no seedlings or seedlings/saplings observed. Each species exhibited a dependency on fire to promote recruitment. The presence of fire either; (1) broke the physical/chemical dormancy for seeds held within the soil seed bank for the fire-killed *L. nutans* and resprouting *P. elliptica*, stimulating germination or (2) promoted coning and seed production in *P. drouynianus*. Fire-stimulated coning is also reported for *M. riedlei* (Ornduff 1991).

4.4.1 Leucopogon nutans

**Population size structures**

For *L. nutans*, as for other short-lived fire-killed species, population structure is largely determined by fire history (Cowling *et al*. 1996). Generally, the *L. nutans* populations at both Avon and Sawyers Valley had last experienced fire ca. 7 - 16 years ago. Consequently, there was only minor variation in the population size structure. With the largest individuals beginning to show signs of senescence, it is likely that the maximum age of the species is being reached and fire is required to stimulate recruitment from the soil seed bank (Dixon *et al*. 1995).

**Fruit production**

The dynamics of seed production in shrubs of Mediterranean-type ecosystems whose floras have evolved with frequent fire is well described (Keeley 1977). Seed production for fire-killed shrubs has been shown to exhibit substantial annual variability, typically linked to climatic factors (Keeley 1977). The annual variability in seed production linked to precipitation and other climatic factors is not only recorded for Mediterranean ecosystems, as similar observations have been made in more temperate floras, e.g. in Europe (Garcia *et al*. 2000). There is, however, a lag between the impact of abundant precipitation and increased fruit production, with the effects observed in the fruit crop in subsequent years. For *L. nutans* there was increased fruit production in 2012, likely
linked to above-average rainfall received in the previous year. For Western Australian shrubs within the arid zone, Davies (1976) observed variation in seed crop linked not only to rainfall but also to specific temperature and photo-period conditions. In fact, Davies (1976) notes that the seed crops of only a few shrubs are linked to patterns of total rainfall alone. Regional variations in general seed production have been widely observed, with species at the edge of their given ranges, typically exhibiting poor reproductive output overall, i.e. reduced seed production or overall decreased seed viability, again linked to climatic factors and pollen availability (García et al. 2000). *L. nutans* is at the northern-most and driest extent of its range in the Avon Valley National Park and fruit production will likely suffer in dry years or periods of extended drought. Fruit production increased in relation to stem size, which has been observed for other small fire-killed shrubs (Yates and Ladd 2010).

**Soil seed bank dynamics and viability**

The greatest rate of seed viability loss for *L. nutans* was observed at Avon Valley, with < 1% of fruits sampled from the seed bank containing a viable embryo. With canopy viability assessed as being ca. 90%, this viability loss represents a massive impediment to seedling recruitment following fire (Andersen 1989; Crawley 2000). However, Clark et al. (1999b) reminds us to be careful when assessing recruitment limitation from seed banks owing to limited inferential capabilities from typical datasets. While the drop in seed viability from the canopy to seed bank was not as marked at Sawyers Valley (ca. 90% to ca. 47%), this still represents a substantial drop in seed viability. Given that the two *L. nutans* populations are of similar age and, consequently, should have a soil seed bank of similar size and age, the clear difference in drop in seed viability between the two sites suggests that those seeds at Avon Valley may face increased seed loss pressures from pathogens and small internal seed predators (Leishman et al. 2000). Geographical variation in seed predation and loss is common (García et al. 2000). Poor viability for seeds stored within the soil seed bank is a common phenomenon, with abundant seed production inversely linked to poor seed survival and germinability (Cook 1980; Saatkamp et al. 2009). In contrast, seeds recovered from emu scats retained the viability (92%) that was evident for fresh seeds from the canopy. This suggests that the reduced avian crop possessed by the emu (Davies 2002) permits gentle processing of seed material that does not reduce viability, and this has been observed for tropical species consumed by another ratite, the southern Cassowary (*Casuarius*...
While the germination and survival of seeds deposited within the scats of many species is varied (Howe and Smallwood 1982; Cypher and Cypher 1999), the deposition of seeds within scats also may make them resistant to attack by external pathogens (Howe 1989). It may be possible that emu preferentially select the largest (and likely viable) fruits, that provide an inherent fitness benefit when deposited. However, the relationship between fruit and seed selection by frugivores based on seed phenotype within species is poor (Jordano 1995) and emu, being a generalist feeder (Dunstan et al. 2013), may not selectively forage.

Post-fire recruitment

Inter-fire recruitment was not observed for *L. nutans*, which is a trait shared with many other species that are adapted to a fairly short, recurrent fire interval (Lamont et al. 1991; Tieu et al. 2001). Obligate seeders take advantage of the removal of competition, advantageous microhabitat variation (litter sites) and nitrogen enhancement that is experienced following fire (Bond and Van Wilgen 1996). The low density of seedlings recorded in the small burnt areas following fire, coupled with the poor seedling survival usually observed for fire-killed shrubs (Nield et al. 2009), indicates that large scale fires are required to promote abundant germination and population recruitment. In the peri-urban setting, it is unlikely that *L. nutans* populations will receive such a beneficial fire regime, and the populations may decline as adults die and the soil seed bank decays.

4.4.2 *Persoonia elliptica*

*Population size structures*

The largest individuals were found at Sawyers Valley, though, being a long-lived resprouting species, it may be an inaccurate assumption that the largest species are the oldest. There was no evidence of recent recruitment of *P. elliptica* individuals in the assessed populations, with the overall demographic structure indicating on-going and long-term (possibly approaching 100 years) recruitment failure. While it has been suggested that herbivory pressure is the most likely cause for the recruitment failure (Abbott and Van Heurck 1988), it is likely that the interplay between fire and herbivory is limiting initial germination and survival (Hulme 1994). The exclosure experiment revealed that fire is necessary to cue germination of the species, with only a single seedling recorded in the unburnt plots. While this is not uncommon for species with
fire-adapted traits (Keeley 1987; Dixon et al. 1995), resprouter species typically produce fewer seeds than obligate seeders and rely on vegetative regeneration to maintain populations (Bell 2001). Therefore, *P. elliptica* is relying on comparatively fewer seeds to maintain the population. Population recruitment is unlikely for the species while significant herbivory pressure remains, with seedling survival significantly lower in unfenced plots. The slow growth of the seedlings limits transition to reproductive adult, with a number of years likely required for young individuals to develop a basal lignotuber that can survive above-ground disturbances such as fire and herbivory.

*Seed production*

It is complicated to link seed production in relation to plant size for resprouting species such as *P. elliptica*. Although seed production did increase with stem DBH, it is not clear if larger individuals would produce an overall greater viable seed crop than smaller individuals. As long-lived resprouters age, the viability of the overall seed crop can decline (despite the production of numerous fruits) as fertilisation is increasingly geitonogamous (Enright et al. 1996; Lamont and Wiens 2003). Caution must also be taken when comparing general floral phenology traits of species between different geographic locations as the general traits of resprouting have been shown to vary in different locations (Pausas et al. 2004).

*Soil seed bank dynamics and viability*

The loss of viability in seeds from the canopy (ca. 30%) to the seed bank (ca. 8%) for *P. elliptica* may also be linked to predation, pathogen attack or aging (Cook 1980). The low degree of viability within the canopy is not unusual. Seed production and viability in resprouters is typically lower than their seeder species counterparts that possess similar traits (Enright et al. 1996; Enright et al. 1998; Bellingham and Sparrow 2000). With poor fruit production observed for many *P. elliptica* individuals, seed bank limitation including poor viability (canopy seed viability was less than the ~75% reported by Abbot and Van Heurck 1988) is likely an impediment to regeneration, though this has not been considered a cause of recruitment failure in a previous assessment of the species (Abbot and Van Heurck 1988).
The decline in viable seed in the soil bank in just one year (from ~30 to 8%) suggests either or both a rapid preferential removal of viable freshly fallen seeds by granivores, and a rapid decline in viability within the soil seed bank. *P. elliptica* seems largely dependent upon the last season’s seed crop to generate new recruits. High annual variability in seed production as observed for many fire-evolved species (Keeley 1977), would make this a high risk seedling recruitment strategy. However, there was no difference in seed production for successive years. It was also found that mature trees resumed flowering in the second year after fire, so that there may be a relatively constant seed supply available through time.

*Post-fire recruitment*

Seedling recruitment was most frequent in the first winter following fire in plots that had been burned in the previous autumn or spring, but was almost absent from plots in unburned forest. Post-fire recruitment is a commonplace strategy in perennial plant species of SW Australia, and many other fire-prone environments, with recruitment timed to occur with maximum resources for early growth (increased light, moisture and nutrient availability), and maximum time for accumulation of a seed and/or bud bank before the next fire occurs (Enright *et al.* 1996). Fire has already been shown to break seed dormancy for other common and rare *Persoonia* species (Mullins *et al.* 2002; McKenna 2007). The absence of seedlings in the unburned areas reported here could be due to a lack of fire to break seed dormancy (a common requirement for many fire-adapted species; Dixon *et al.* 1995), intense herbivory pressure (Abbot and Van Heurck 1988), or the likely combination of these two factors.

4.4.3 *Podocarpus drouynianus*

*Population size structures*

The population structure of *P. drouynianus*, were all skewed to the left. There was no clear lignotuber size threshold at which males or females became reproductive (Chalwell and Ladd 2005). Though the overall sex ratio at both Nannup and Sawyers Valley was not significantly different from 1:1, the local variation observed within some populations should be seen as unsurprising, especially as quite a large number of what appeared to be adult plants did not produce sporophylls and so could not be classified. This may be related to local soil or neighbouring plant factors.
Seed production

*P. drouynianus* exhibited fire-stimulated reproduction (fsr). The phylogenetic restriction on the type of seed produced by *P. drouynianus* precludes accumulating a seed bank, so in an evolutionary sense the seeding behaviour of the species is constrained to germination when the embryo is mature. This takes about 3–4 months from when the seeds are released from the plant (Chalwell and Ladd 2005). In this species this has been synchronised to occur in the wet winter-spring when conditions for establishment are likely to be optimal. Sporophyll production is maximised 12–18 months following fire, irrespective of the season of ignition with virtually no seed production less than six months after and greater than 36 months following fire. No seeds were recorded from individuals that were burnt in spring 2011 and surveyed in autumn 6 months after fire at either Nannup or Sawyers Valley. Individuals that had long been unburnt (>10 years since the preceding fire) also produced no seeds. As with many other fsr species (Lamont and Downes 2011), *P. drouynianus* females may produce a small number of seeds in the second year following fire (Ladd and Enright 2011) and individuals in open areas such as roadsides may also sporadically cone without fire, but produce few seeds. Cessation of seed production after two seasons may be an adaptation to regrowth of the canopy and understorey that would limit pollen dispersal and resource acquisition through increased shading and reduced wind movement in the understorey. Transfer of resources to lignotuber storage in preparation for the next fire may be more advantageous than continuing sporophyll production that may not successfully set seed or produce seedlings.

The relationship of environmental cues to reproductive initiation in fsr species in not simple, but a significant impact of fire season on floral phenology has been recorded for several species exhibiting fsr in SW Australia. *Stirlingia latifolia* (Proteaceae), a common shrub of the jarrah forests, is noted to have prolific inflorescence production following summer/autumn fires, with only half the number produced following spring fires (Bowen and Pate 2004). However drought may also cue reproduction in *S. latifolia*, with inflorescence production at a site in the year following a severe drought similar to that at a site burnt in the same drought year (*P. Ladd unpublished data*). Flowering of grass trees (*Xanthorrhoea* species), is significantly influenced by fire season; *Xanthorrhoea preissii* produced only 40% as many inflorescences following spring burns compared to after autumn burns (Lamont *et al.* 2000) while *X. fulva*
produced 20% fewer flowering plants after a winter burn compared to a summer fire (Taylor et al. 1998). Both S. latifolia and X. preissii co-occur with P. drouynianus, indicating that individual species’ traits, life histories and environmental cues with some similar effects to fires may also play important roles in reproductive success. Divergent reproductive strategies may benefit individual species by limiting competition, even in a nutrient-rich post-fire environment.

Seed size is often inversely correlated with post-dispersal seed longevity, and environmental factors may further affect seed survival (Schutte et al. 2008). The smaller seed sizes observed following the spring burns is unlikely to result in greater seed longevity, rather it may reflect a depleted resource pool available for seed set following greater overstorey canopy development. Given that seeds such as those of P. drouynianus are often under significant predation pressure in the post-burn environment (Bond 1984; Ladd and Enright 2011), poor seed production, coupled with limited viability as a result of spring burning, may adversely affect recruitment of the species. Reduced seed size observed in spring burnt plants may also negatively impact potential recruitment. As the size and weight of seeds increases, so does seedling resilience to shading and competitive stress (Baker 1972; Stanton 1984). Seedlings of P. drouynianus established from the smaller seeds that are dispersed following spring burns may be less successful in the post-burn environment, having to compete with many other resprouter and seeder species (Bell 2001). The post-burn environment also varies with season of burn, with spring fires generally cooler than autumn fires, and consuming a smaller proportion of both live and dead biomass (Harrington 1993). Improved seedling recruitment may be related to the increased intensity of hot autumn fires that ashes a greater proportion of biomass and releases more resources for establishment. Nutrient and moisture availability are influenced by intensity and season of burn, fuel load and other fire characteristics (Bond and Van Wilgen 1996), so that small seeds and germinants of P. drouynianus may be disadvantaged in a less open, less nutrient-rich post-burn environment following spring fires. The spatial variability in fire temperatures encountered during prescribed burning (Hobbs and Atkins 1988) further reduce the efficacy of cool spring burns in combusting fuel and providing a suitably beneficial post-fire landscape for seedling recruitment.
4.4.4 *Macrozamia riedlei*

*Population size structures*

The largest *M. riedlei* individuals were found at Kings Park. Mature *Macrozamia* plants tend to be larger on the Swan Coastal Plain than on the lateritic soils of the Darling Range so a relationship between absolute size and age may not be directly comparable between populations on the different substrates. Most members of the Cycadaceae are very slow growing (Gilbert 1984) so it is difficult to be precise about the age structure from the size structure based on frond length. Seedlings of *M. riedlei* recruited in the Hill River population in 1989 still have only 1 or 2 fronds less than 50cm in length after over 20 years of growth (S. Connell and P.G. Ladd; unpublished data) so it is likely that many small individuals that were assumed to be potentially reproductive adults (frond length >100cm) may be over 100 years old. Despite episodic recruitment the population structure for this species generally follows a highly skewed Poisson distribution. Evidence for episodic recruitment is overwhelmed by the slow growth rate and great longevity of the plants so population spikes after fire every 15 – 20 years will not be distinguishable due to an inability to reliably age small plants.

While not able to be assessed in this study, the sex ratios within populations of *M. riedlei* have been shown to vary both spatially and temporally (Ornduff 1985). Overall, a mild male bias has been observed in some *M. riedlei* populations, although the same populations over time have been shown to move between a slightly male biased sex ratio to a 1:1 male/female ratio (Ornduff 1985; Ornduff 1991).

*Seed production*

The coning phenology of *M. riedlei* is complex, and it has been given great attention in the literature (Connell and Ladd 1993; Ladd *et al.* 1993; Ornduff 1985; Pate 1993), commencing with Baird (1939). Although fire has been shown to stimulate production of male and female cones (Ornduff 1985), coning may occur in the absence of fire, or fire may even inhibit cone production (Moreno and Oechel 1991; Pate 1993). Fire is suggested to stimulate coning through the removal of competition and the stimulation of nitrogen-fixation by Cyanobacteria (Ornduff 1991). Individual *M. riedlei* plants are unlikely to produce cones in successive years. Male cones are likely to be produced by younger plants and in greater number in comparison to their female counterparts.
(Ornduff 1985). Seed production can be substantial, with an individual female cone containing about 100 seeds and 1-3 cones appearing per female (Pate 1993; Asmussen 2009). As for other resprouters, especially cycads, it is difficult to link cone (and seed production) with a demographic measurement, with Ornduff (1991) noting that cone production cannot be linked to leaf length or number of fronds.
4.5 CONCLUSIONS

Generally, there was no evidence of different population structures between high and low emu abundance study sites. As all species have evolved in a fire-prone landscape, their current population structures and reproductive strategies are all mediated and cued by fire. Fire is required to regenerate the *L. nutans* populations and this will likely occur from a seed bank that is experiencing significant loss, at least at Avon Valley, and so recently deposited seeds within emu scats provide the likely source of regenerative material for this species. The life span of the species is limited and fire is required to promote regeneration.

The population structure of *P. elliptica* indicates widespread regeneration failure as no saplings or seedlings were recorded in the general survey and seem to accord with the ideas of extinction debt identified from urban reserves (Tilman *et al.* 1994). Regeneration failure was noted by Abbott and Van Heurk (1988) but they could not determine the reason. It is likely that herbivory is severe on seedlings that regenerate after fire. While it seems improbable that kangaroos can find all seedlings this seems to be the case and it is exacerbated by low seed viability and slow seedling growth leaving saplings available to kangaroos for a long period of time. Why herbivory pressure has increased in the last 150 or so years is not clear but it may be due to loss of dingoes and Aborigines as controls on kangaroo populations, so strategies to enhance seedling survival need to be considered to return *P. elliptica* populations to a more stable age structure.

The complex coning phenology of *P. drouynianus* and *M. riedlei* has also been highlighted. These two species that are present from two very ancient plant families have adapted to fire, which usually stimulates cone production. Seeds of the species are typically almost entirely viable and germinate readily (though viability almost disappears within two years). These two species have seen the arrival and disappearance of their once typical megafaunal dispersal agents over geological timescales (Hall and Walter 2013) and will likely rely on long distance and local dispersal agents to maintain their populations in the future.

While they are scions of ancient groups, both *Podocarpus* and *Macrozamia* are well adapted to fire that cues coning following defoliation of these resprouters. Mature seeds of the species have high viability and germinate readily (recalcitrant seeds) once they
have undergone some after-ripening following being shed from the plant. Population structures are reflections of the long life spans of the species and irregular recruitment frequency. The clumping evident in cycads, in particular, has been related to current dispersers being small and not carrying the seed far (Burbidge and Whelan 1982), the paucity of dispersers and the possibility that megafauna (now extinct) may have been important in dispersal (Snow and Walter 2007) and are now absent.

While it was hypothesised that there would be a difference in demographic attributes for each species between study sites as a result of the loss of the putative primary dispersal agent, the emu, this was not observed. It was expected that this demographic signal would be most readily observed in *L. nutans*, the short-lived seeder species. As *L. nutans* relies on fire to regenerate its populations, it is possible that dispersal limitation does not impact the demographic parameters for this species. This may also be the case for the resprouting *P. elliptica*, which was also shown to recruit, unsuccessfully, from a soil seed bank. The period over which the emu has been excluded should also be considered. At Sawyers Valley, populations of the emu have likely been in decline over the past ~60 years as a result of increasing urbanisation. For the slow-growing *P. drouynianus* and *M. riedlei* (and also, more limitedly, *P. elliptica*), this period of disperser loss may be too brief to impact plant demography. Even at King’s Park, where emus have been excluded for > 100 years, no difference was observed. It is conceivable that young *M. riedlei* seedlings and juveniles present at the time emu were first excluded may not even be reproductive yet.

It is clear that the time-frames over which a loss of dispersers may impact plant demography are beyond capture through traditional field methods for the slow-growing species of southwestern Australia and those short-lived species whose populations are regenerated by fire. The following chapter (Chapter Five) explores the spatial ecology of each target species and the link between the loss of their primary dispersal agent and life histories. Chapter Five also presents a simulation model approach to examining the conditions under which a detectable change will occur following disperser loss. Subsequent chapters will further investigate the seed dispersal vectors and predators of the target species to examine how and to what extent different agents contribute to their overall biology.
Disruption of seed dispersal mutualisms may strongly affect plant spatial structure, with more intense local aggregation one hypothesised outcome. A spatially-explicit simulation model was used to explore impacts of the loss of a key dispersal agent on plant population spatial pattern and the power to detect such changes. Simulations considered a homogeneous landscape free from potentially confounding first-order effects in which an annual plant is dispersed every year by either an active agent, or passively; in other words in an in silico system ideal for the detection of disperser-mediated shifts in spatial pattern. To provide an empirical context for the simulations, point pattern analysis was used to characterise the spatial pattern of four large-seeded species in the jarrah (*Eucalyptus marginata* Sm.) forests of southwestern Australia in relation to presence/absence of their assumed primary disperser, the emu (*Dromaius novaehollandiae* Latham). The spatial structure in species with different life histories; *Leucopogon nutans* (Ericaceae) E.Pritz, a fire-killed, short-lived seeder shrub, *Persoonia elliptica* (Proteaceae) R.Br., an epicormic resprouting tree, *Macrozamia riedlei* (Zamiaceae) (Gaudich.) C.A.Gardner, a long-lived, apical resprouting cycad, and *Podocarpus drouynianus* (Podocarpaceae) F.Muell, a long-lived, basal resprouting coniferous shrub was examined. For none of the plant species was there a detectable difference in the strength of aggregation between sites with and without emu. Model analysis confirmed the difficulties in detecting spatial change following disperser loss, with localised aggregation occurring as a result of both passive and active dispersal. It is likely that low rates of fruit removal and high seedling survival result in recruitment beneath and near parent plants, which, in turn, reveals itself as strong aggregation regardless of disperser community composition and abundance. Owing to difficulties in detecting changes in local spatial population structure, attention should be given to characterising long-distance seed dispersal shadows, rather than localised spatial patterns.
5.1 INTRODUCTION

The analysis of spatial pattern in plant communities, particularly for biodiverse tropical forests (Condit et al. 2000; Wiegand et al. 2009; Wiegand et al. 2013) and sclerophyll shrublands (Perry et al. 2008; Miller et al. 2010; Raventós et al. 2010; Perry et al. 2013a; Perry et al. 2013b) seeks to further advance our understanding of the factors that mediate species interactions in such species-rich ecosystems. At any given time a species’ spatial pattern is a static fingerprint of many complex ecological processes across a range of spatio-temporal scales. However, it is difficult to isolate how individual processes such as competition and dispersal influence species demography from observed spatial structure alone (McIntire and Fajardo 2009). Nevertheless, given that spatial pattern has a significant impact on demographic processes and rates, the description of pattern, when evaluated against strong and ecologically informed a priori hypotheses, provides useful insights into important past ecological processes and present environmental impacts.

As the only vagile component of the whole plant life cycle, seed dispersal contributes to spatial patterns across multiple scales (Rodríguez-Pérez et al. 2012b). Aggregation or clustering over relatively short distances is observed for most plant species (Fangliang et al. 1997; Condit et al. 2000; Perry et al. 2008). The spatial pattern of animal-dispersed plant species can be significantly influenced by frugivore population behaviour, environmental heterogeneity, the density of individual plants, and their interactions (Morales and Carlo 2006; Russo et al. 2006; Rodríguez-Pérez et al. 2012b). Where fruit removal rates by frugivores are high, disperser loss may have a significant impact on plant demographic rates and population spatial structure. Reported rates of successful fruit removal vary considerably. Fruit removal differs between habitat types, infructescence positions and diurnal/nocturnal periods (Denslow and Moermond 1982). Typical rates of fruit removal in most systems are 0 - 50% (Denslow and Moermond 1982), but they may be higher in some systems. Jordano and Schupp (2000) report fruit removal rates (successful removal and ingestion) of ca. 50% and 68% by seed dispersers in successive years for Prunus mahaleb, a small tree growing at mid-elevations in Spain and central and eastern Europe; total effective seed dispersal (Schupp 1993; Schupp et al. 2010), including by scatter-hoarding rodents, may be as high as 85% (Forget 1992).
The loss of frugivores in any system may have severe consequences for dispersal mutualisms, with reduced seed removal leading to the deposition of increased number of seeds below the parent plant, increased incidence of density-dependent mortality (Janzen-Connell effects; Janzen 1970; Connell 1971), reduced gene flow, reduced germination, and clumping of individuals below conspecifics (Şekercioğlu et al. 2004). The decline of seed dispersal agents through habitat destruction and direct persecution can be rapid (Corlett 2007). Şekercioğlu et al. (2004) suggest that 7 - 25% (28 - 56% on oceanic islands) of all bird species will be functionally extinct by 2100, with birds in the frugivore functional group particularly susceptible. Of greatest concern are those cases where highly specific seed dispersal mutualisms have developed and a frugivore has an irreplaceable functional role within an ecosystem (Stocker and Irvine 1983; Wenny and Levey 1998; Wotton and Kelly 2011). In some instances mutualisms have evolved to provide both dispersal and pollination functions (Muscarella and Fleming 2007), representing a ‘double-jeopardy’ for the affected plant species (Burns 2013). The disruption of such important ecological relationships will likely have negative demographic outcomes and lead to changes in the spatial structure of plant populations. There is, however, limited evidence of the effects of the loss of an irreplaceable seed dispersal agent on the spatial ecology of the plant species that depend on them.

The loss of seed dispersers may lead to more intense local aggregation as seed dispersal distances are reduced (Rodríguez-Pérez et al. 2011). However, the final pattern of established plants is not solely determined by seed dispersal, but is also influenced by microhabitat heterogeneity and patterns in germination and establishment, reinforcing spatial clustering (Enright and Lamont 1989; Lamont et al. 1993; Nathan and Muller-Landau 2000). Spatially-explicit simulation modelling allows us to examine under what circumstances the spatial signal of the loss of a dispersal agent is detectable. If recruitment is favoured in specific safe sites, such as nutrient and moisture-rich microsites in post-fire environments (Bond and Van Wilgen 1996), the impact of disperser loss on a plant species spatial pattern may be difficult to detect against environmentally-mediated clustering. Intense competition and density-dependent mortality under the crowns of conspecifics may reduce local aggregation in disperser depauperate systems (Beckman et al. 2012), while seeds dispersed in scats of large frugivores may trigger chemical or mechanical defenses facilitating resistance to density-dependent effects, with many germinants observed from single clumps (Howe 1989).
Large frugivores can remove and deposit thousands of seeds in a single scat (Howe 1989). In the jarrah forests of southwestern Australia, the emu (*Dromaius novaehollandiae* Latham) is assumed to be the sole extant large seed disperser. Other important dispersers of large-seeded species in the jarrah forests have been lost, with megafauna becoming extinct in the first few millennia after the arrival of Aborigines on the continent (Enright and Thomas 2008). Like other large frugivores, the emu, a large flightless omnivore, is especially susceptible to local population decline and loss (Cardillo *et al.* 2005; Corlett 2007). Populations of emu are threatened by habitat fragmentation, contracting home ranges and, as a declared agricultural pest in some places, direct removal (Boland 2003). Emu population decline has been ongoing over the last 100 years across some parts of its range.

Here spatially-explicit simulation modelling is used to identify the impact of key dispersal agent loss (the emu) on plant population spatial structure. The spatial patterns of the four target woody species with contrasting life histories and large to medium sized fruits/seeds are described for areas with lost/depleted vs. intact populations of the emu. It is hypothesised that for the simulation model:

1. A detectable change in spatial pattern following disperser loss will occur only where initial fruit removal rates are extremely high (ca. 100%), and in excess of empirically-determined fruit removal rates.

2. The type of seed deposition, scattered (i.e. small frugivores depositing a single or few seeds) or clumped (i.e. large frugivores such as cassowary or emu depositing hundreds of seeds in a single scat), will influence the ability to detect a change in spatial pattern following disperser loss, with a loss of scattered deposition leading to stronger change in spatial pattern (Howe 1989).

3. Even where fruit removal rates are high, reduced seed dispersal distances (expected in increasingly fragmented environments) will further inhibit the ability to detect a change in spatial pattern following the loss of frugivory.

It is hypothesised for the case-study that:

4. As aggregated patterns appear to be the norm for many perennial plant species (Condit *et al.* 2000; Perry *et al.* 2008), an aggregated spatial pattern will be the
dominant pattern for all species in the case study irrespective of dispersal agent presence.

(5) Because disperser loss can result in local-scale aggregation (Rodríguez-Pérez et al. 2012b), smaller cluster sizes and a greater number of individuals per cluster will be observed in sites where populations of the emu are reduced (i.e. aggregation will be more intense).

(6) Because a shorter generation time means they will respond more rapidly to changes in disperser activity, aggregation will be more readily observed in short-lived (fire-killed) seeder species than in long-lived resprouter species.
5.2 MATERIALS AND METHODS

5.2.1 Spatial simulation model

Model Construction

To investigate the potential impacts of dispersal agent extinction and associated reduction in dispersal kernel shape on the spatial pattern of an idealised annual plant species, a model was developed in R version 2.15.2 (R Core Team 2012), using the Spatstat package (Baddeley and Turner 2005). The model assumes complete landscape homogeneity in time and space (i.e. there is no spatial variation in establishment success or other demographic processes, nor do they vary inter-annually). The model is initiated by the creation of 100 parent plants in a 100 × 100 unit space with their location following a homogeneous Poisson process. The simulated plant species becomes reproductive in the year it is born then dies the following year (i.e. it is strictly annual). In each year, seeds are distributed either locally in the vicinity of a random proportion of parent individuals (passive dispersal), or further away (as if dispersed by a frugivore or other active dispersal agent). Each of these offspring become reproductive and may potentially disperse seeds in the following year. The proportion of active vs. passive dispersal events is determined by a pre-defined probability. Where seeds are dispersed passively, they fall in close proximity to the parent at a distance drawn from a normal distribution with mean 1 and standard deviation 0.25 (N ~ 1, 0.25), in a random direction (0 to 2π radians). In the model, the passive dispersal function represents the deposition of seed beneath the parent plant. Active dispersal represents seeds being dispersed by frugivores. The number of seeds dispersed per parent is drawn from a Poisson distribution with λ = 1 or 3 (depending on whether the model scenario is simulating scattered or clumped deposition) and dispersed in a random direction. For active dispersal, depending on the model scenario, seeds are dispersed at a distance drawn from a normal distribution with mean 10 and standard deviation 2.5, or mean 5 and standard deviation 1.25 with the latter representing a reduction in dispersal distances that may occur as a result of habitat loss and/or fragmentation. Once a total of 500 seeds have been dispersed (an arbitrary carrying capacity) the model simulation moves to the next year.

The summed log of the pair correlation function (g[r]) was used to characterise spatial pattern in each year and for each simulation. Brown et al. (2011) used a similar statistic
to described bivariate pattern and called it the cross-product function. Here the statistic is referred to as the univariate product function (UPF). For each year and in each simulation, $g(r)$ was calculated at 0.1 unit intervals, up to a distance of 20 units. The log values of $g(r)$ were summed across all distances from 0.1 – 20 units. The mean nearest-neighbour (NN) distance and Clark-Evans (CE) aggregation statistic for each year and simulation were also calculated so as not to be limited by a single spatial statistic (see Perry et al. 2006 for discussion of the utility and applicability of various spatial statistics). While some of these spatial statistics may be correlated to some degree, they each characterise important and different aspects of spatial pattern. The UPF is used as a ‘farsighted’ measure to examine spatial pattern across the whole extent of the dispersal kernel and the NN and CE statistics as a myopic descriptor of local spatial intensity. Each dispersal scenario was run for 50 simulations over 250 years in order to detect a change in spatial pattern, with the first 50 years excluded from analysis to reduce the potential influence of burn-in effects.

**Model Scenarios**

Two scenarios were used to evaluate change in spatial pattern following the loss of a seed dispersal vector. In each of these scenarios, dispersal events are caused by a vector that either results in a scattered (few seeds) or clumped (numerous seeds) deposition. Within the scattered vs. clumped dichotomy, scenarios of varying rates of initial ‘active’ fruit removal were explored: (1) high seed removal (50%) and (2) low seed removal (10%). In these scenarios, 50% or 10% of ‘active’ fruit removal occurs during the first 150 years of the simulated period, before instantaneously falling to zero in subsequent years. This abrupt disperser extinction represents the best-case scenario for detecting a post-disperser loss change in spatial pattern. In reality, rates of disperser decline may be relatively slow (Şekercioğlu et al. 2004) and population loss not absolute, making empirical detection of shifts in spatial pattern even more difficult. For each high/low fruit removal rate the effects of a reduction in the ‘active’ dispersal kernel, from $N \sim (10, 2.5)$ to $N \sim (5, 1.25)$ were also investigated. A reduction in the mean dispersal distance represents the impact of habitat loss on the dispersal capability of frugivores, as they are constrained within smaller, more isolated patches. A summary of the model scenarios and their parameterisations is presented in Table 5.1. Baseline passive and active scenarios were also generated for both scattered and clumped agents, with 100% passive or active dispersal occurring over the entire simulation period.
Table 5.1 Model parameters for each of the dispersal scenarios. Each scenario was run for 250 years and for 50 simulations. The number of seeds within each dispersal event/deposition (up to the carrying capacity of 500 points within the model world) was drawn from a random uniform distribution with the minimum and maximum values as described in \( n \) seeds per event.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Seed Deposition Type</th>
<th>( P(\text{Active Dispersal} \leq 150 \text{ yrs}) )</th>
<th>( P(\text{Active Dispersal} &gt; 150 \text{ yrs}) )</th>
<th>Dispersal distance (mean,SD)</th>
<th>( n ) seeds per event</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Active to Passive</td>
<td>Scattered</td>
<td>1</td>
<td>0</td>
<td>10,2.5</td>
<td>1</td>
</tr>
<tr>
<td>2. Active to Passive</td>
<td>Clumped</td>
<td>1</td>
<td>0</td>
<td>10,2.5</td>
<td>3</td>
</tr>
<tr>
<td>3. 50 % Active</td>
<td>Scattered</td>
<td>0.5</td>
<td>0</td>
<td>10,2.5</td>
<td>1</td>
</tr>
<tr>
<td>4. 10 % Active</td>
<td>Scattered</td>
<td>0.1</td>
<td>0</td>
<td>10,2.5</td>
<td>1</td>
</tr>
<tr>
<td>5. 50 % Active</td>
<td>Scattered</td>
<td>0.5</td>
<td>0</td>
<td>5,1.25</td>
<td>1</td>
</tr>
<tr>
<td>6. 10% Active</td>
<td>Scattered</td>
<td>0.1</td>
<td>0</td>
<td>5,1.25</td>
<td>1</td>
</tr>
<tr>
<td>7. 50 % Active</td>
<td>Clumped</td>
<td>0.5</td>
<td>0</td>
<td>10,2.5</td>
<td>3</td>
</tr>
<tr>
<td>8. 10 % Active</td>
<td>Clumped</td>
<td>0.1</td>
<td>0</td>
<td>10,2.5</td>
<td>3</td>
</tr>
</tbody>
</table>

The median, 5\(^{th}\) and 95\(^{th}\) percentiles of the UPF, NN and CE statistics calculated for selected model scenarios for the 50 simulations across the simulation period are presented. The \( bcp \) package (Erdman and Emerson 2007) in R was used to conduct a Bayesian analysis to detect potential change points in each of the spatial statistics for each of the simulations. The median, 5\(^{th}\) and 95\(^{th}\) percentiles of the posterior change probabilities are presented for selected model scenarios. In addition to this, the median posterior change probabilities are described following active dispersal loss for each model scenario and spatial statistic. Examples of point patterns produced by some of the different model scenarios are provided in Figure 5.1.
Figure 5.1 Representative spatial patterns produced by the model for (a) the plants during the final year of 100% active dispersal before (b-f) complete dispersal loss and aggregation during five successive years.
5.2.2 Case study data

Study species

The spatial pattern for the four key species (Leucopogon nutans, Persoonia elliptica, Macrozamia riedlei and Podocarpus drouynianus) was investigated across four of the study sites in the fire-prone dry sclerophyll jarrah forests of SW Australia. The recruitment of each species is linked to the timing of fire, so that populations are made up primarily of post-fire recruitment cohorts.

Further information about the study species can be found in Chapter Three.

Study sites

The study sites used for the spatial mapping of each species are those described in Chapter Three.

Spatial mapping

The size of plots used to map the spatial distribution of individuals varied across species, reflecting differences in their sizes (small shrubs to trees) and densities.

Leucopogon nutans

Four 20 × 20 m, three 25 × 25 m and one 50 × 50 m plot(s) were established at locations sited random-systematically in Sawyers Valley during April - May 2011. At each location an initial 20 × 20 m plot was established and size increased in 5 × 5 m intervals until at least 30 individual plants were recorded. Due to higher plant densities (0.5 ± 0.1 individuals/m²), initial plot size at Avon Valley was 10 × 10 m; four 10 × 10 m, four 15 × 15 m, one 20 × 20 m and one 30 × 30 m plots were established. Within each plot, plant x-y location, height and canopy width were recorded.

Persoonia elliptica

At Sawyers Valley, eight 400 × 400 m (16 ha) randomly-sited plots within the 900 ha study area were searched during February 2012. The location of each individual was recorded with a Garmin GPS (typical horizontal precision ± 5 m) along with stem diameter at breast height, height, and longest canopy width. Only three of the eight 16
ha plots contained sufficient individuals \((n = 106, 61 \text{ and } 118\) respectively) to support point pattern analysis. All individuals within a 900 ha \((3 \times 3 \text{ km})\) study area at the Avon Valley were recorded \((n = 280; \text{ horizontal precision } = 5 \text{ m})\) with a Garmin GPS. These data were collected in November 2010 as part of a related study.

**Podocarpus drouynianus**

Eight 50 × 50 m, one 40 × 40 m and one 30 × 30 m (where plant density was higher; 0.14 individuals individuals/m\(^2\)) plots were established near Nannup in February-March 2012. Three 25 × 25 m plots encompassed most of the small population at Sawyers Valley. In each plot, the x-y location of each individual of interest was determined, and lignotuber length and width (selected as the best measure of plant size) was recorded.

**Macrozamia riedlei**

Five 50 × 50 m plots were randomly located within Kings Park in March 2012, seven 50 × 50 m and one 60 × 60 m plots were established at Sawyers Valley, and seven 50 × 50 m plots were established at Avon Valley. In each plot the x-y location of each individual was determined, and the number of fronds, length of longest frond and trunk height were recorded.

**Spatial analysis**

Four null point-process models and the pair correlation function [PCF; \(g(r)\)] were used to characterise the spatial pattern of each species at each site. The first model, a homogenous Poisson process, represents complete spatial randomness (CSR, defined solely by intensity \(\lambda\)) and is the default null model. An inhomogeneous Poisson process (IPP, \(\lambda_{(x,y)}\)) was used to evaluate the presence of first-order effects. Under an IPP the location of plants is a function of an underlying gradient in intensity (e.g., reflecting first-order spatial structure in nutrient availability, topography, etc.) but assumes no inter-plant interactions. Homogenous and inhomogeneous Poisson (Thomas) cluster processes were used to assess the prevalence of second-order aggregation (Illian et al. 2008).

\(g(r)\) was calculated at 0.1 m intervals (with the exception of *P. elliptica*, where 15 m intervals were used) up to a maximum distance \((r)\) of one-quarter the length of the shortest side of each plot. Ripley’s edge (isotropic) correction, with 99% confidence
envelopes generated based on 499 simulations was used. Ripley’s $K$-function, linearised to $L(r)$, was used to examine cumulative aggregation at the intervals and distances described above. Deviation of the observed point-process from the null models was assessed by employing the Cramer-von Mises (CvM) statistic based on the PCF and visual inspection of the significance envelopes. The use of the CvM goodness-of-fit statistic avoids the inferential problems associated with the use of confidence envelopes described by Loosmore and Ford (2006) and Grabarnik et al. (2011). If the observed point-process was not adequately described by a homogeneous Poisson model, then both homogeneous and inhomogeneous Poisson and Poisson (Thomas) cluster models were fitted using minimum contrast methods (Diggle 2003). The model with the lowest CvM statistic was deemed to have the best fit. Patterns were ultimately classified as regular, random or aggregated (following Miller et al. 2010). Second-order aggregation, (homogeneous Thomas) and first and second-order aggregation (inhomogeneous Poisson) were differentiated between where appropriate. For the point processes best described by cluster models, intensity (density), cluster size and the number of individuals per cluster were derived from the model fits and compared between sites and species using Mann-Whitney $U$ tests. A Kruskal-Wallis test using post hoc Mann-Whitney tests with Bonferroni corrections was used to compare the $M. riedlei$ Poisson cluster model parameterisation. All spatial analyses were conducted using SpPack (Perry 2004) and with the R library Spatstat (Baddeley and Turner 2005).
5.3 RESULTS

5.3.1 Spatial simulation model

There were clear differences between the spatial patterns generated under the scatter and clumped deposition scenarios when simulating a complete loss in active dispersal. For all three of the spatial statistics, there was a high degree of temporal variation in the posterior change probabilities (Figure 5.2a and Table 5.2). For the spatial pattern, as characterised by the UPF, spatial aggregation increased following the complete loss of an active dispersal agent under both the scattered and clumped dispersal scenarios. However, the median posterior probability of a change in the UPF occurring following dispersal agent loss (i.e. at time = 150) was < 0.2 for both scenarios. The increase in the UPF following dispersal loss was gradual, with the system failing to reach spatial equilibrium after 100 years (generations). In contrast, both the mean NN distance and CE index rapidly decreased following dispersal agent loss and stabilised after around 10 years. This dynamic reflects increased spatial aggregation, which was detected by the change-point analysis, with median posterior change probabilities of ~ 1.0 and ~ 0.68 for the scattered and clumped scenarios, respectively (Figure 5.2b & 5.2c).

Where initial fruit removal by an active dispersal agent was 50% prior to dispersal loss, a potential change in the NN and CE statistics was more readily detected for the scattered (median NN and CE change probabilities ~ 1.00) than clumped deposition (median NN and CE change probabilities 0.46 and 0.33 respectively). There was also greater variation in the change probabilities for the clumped deposition following dispersal loss in comparison to the scattered deposition (Table 5.2). There was no obvious change in the UPF following dispersal loss where fruit removal was initially 50%, with change probabilities also highly variable (Table 5.2).

For the scenarios where initial fruit removal rates were low (10%) prior to dispersal loss, the change point analysis generally did not identify a clear breakpoint in any of the spatial statistics. However, the median probability of a change occurring following disperser loss was again greater in the scattered deposition (NN and CE statistics of 0.65 and 0.53 respectively) than the clumped deposition (NN and CE median change probabilities of 0.14).
In the scenarios where the distance of active dispersal was halved for scattered deposition, there was a lower probability of a change for each of the spatial statistics, for high and low initial rates of fruit removal (Table 5.2).
Figure 5.2 Change in pattern over the simulated period (250 years) and the Bayesian posterior change probabilities for simulated scatter- ($\lambda = 1$ seed-per-event) and clumped-dispersed ($\lambda = 3$ seeds-per-event) for baseline active to passive dispersal, with a shift from 100% active to passive dispersal during the 150th year (mean seed dispersal distance = 10, SD = 2.5). Spatial pattern was measured using (a) the median of the univariate-product function (UPF), an adaptation of a similar (though bivariate) measure described by Brown et al. (2011) for which the expected value under CSR is zero, (b) the mean nearest-neighbour (NN) distance and (c) the Clark and Evans (CE) aggregation index. Shaded areas represent the extent of the 5th and 95th percentiles of 50 model runs.
Table 5.2 The median of the Bayesian change posterior (bcp) probabilities for the calculated spatial statistics; mean nearest-neighbour distance (NN) and Clark-Evans aggregation index (CE) in the year following dispersal loss from 50 simulations over 250 years. For the univariate-product function (UPF), due to inertia in the statistic, the median bcp is calculated from the 10 years pre and post dispersal loss. See Table 5.1 for additional scenario information. Numbers in parenthesis indicate the 5th and 95th percentile. **BOLD** numbers in parentheses indicate the number of simulations in which the Bayesian change posterior probability was > 0.50 for the 10 years pre and following dispersal agent loss, respectively.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>UPF (0.00,0.46)</th>
<th>NN (0.78,1.00)</th>
<th>CE (0.62,1.00)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Active-Passive</td>
<td>0.01 (0.00,0.46) (24)</td>
<td>1.00 (0.78,1.00)</td>
<td>1.00 (0.62,1.00)</td>
</tr>
<tr>
<td></td>
<td>0.04 (0.00,0.84) (69)</td>
<td><strong>(13,84)</strong></td>
<td><strong>(13,84)</strong></td>
</tr>
<tr>
<td>2. Active-Passive</td>
<td>0.02 (0.00,0.35) (5)</td>
<td>0.73 (0.01,1.00)</td>
<td>0.63 (0.01,1.00)</td>
</tr>
<tr>
<td></td>
<td>0.04 (0.00,0.82) (24)</td>
<td><strong>(13,48)</strong></td>
<td><strong>(13,48)</strong></td>
</tr>
<tr>
<td>3. 50 % Active</td>
<td>0.01 (0.00,0.38) (19)</td>
<td>1.00 (0.67,1.00)</td>
<td>1.00 (0.70,1.00)</td>
</tr>
<tr>
<td></td>
<td>0.04 (0.00,0.76) (57)</td>
<td><strong>(8,84)</strong></td>
<td><strong>(8,89)</strong></td>
</tr>
<tr>
<td>4. 10 % Active</td>
<td>0.02 (0.00,0.60) (30)</td>
<td>0.65 (0.01,1.00)</td>
<td>0.53 (0.01,1.00)</td>
</tr>
<tr>
<td></td>
<td>0.03 (0.00,0.65) (40)</td>
<td><strong>(10,55)</strong></td>
<td><strong>(9,53)</strong></td>
</tr>
<tr>
<td>5. 50 % Active</td>
<td>0.03 (0.00,0.37) (14)</td>
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<td></td>
<td>0.05 (0.00,0.76) (47)</td>
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<td><strong>(8,71)</strong></td>
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<td>6. 10% Active</td>
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</tr>
<tr>
<td></td>
<td>0.04 (0.00,0.63) (39)</td>
<td><strong>(3,46)</strong></td>
<td><strong>(3,43)</strong></td>
</tr>
<tr>
<td>7. 50 % Active</td>
<td>0.00 (0.00,0.15) (7)</td>
<td>0.46 (0.01,1.00)</td>
<td>0.33 (0.01,1.00)</td>
</tr>
<tr>
<td></td>
<td>0.00 (0.00,0.57) (26)</td>
<td><strong>(20,41)</strong></td>
<td><strong>(10,40)</strong></td>
</tr>
<tr>
<td>8. 10 % Active</td>
<td>0.01 (0.00,0.46) (23)</td>
<td>0.14 (0.01,0.92)</td>
<td>0.14 (0.01,1.00)</td>
</tr>
<tr>
<td></td>
<td>0.01 (0.00,0.44) (23)</td>
<td><strong>(21,23)</strong></td>
<td><strong>(21,25)</strong></td>
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</tbody>
</table>

5.3.2 Case study

The locations of 5844 individuals in total (*L. nutans* n = 1086, *P. drouynianus* n = 1047, *P. elliptica* n = 565, and *M. riedlei* n = 3146) from 55 plots across four sites were measured and recorded.

Representative stem maps and respective best-fit cases for each point process can be seen in Figure 5.3. Overall, for each species, the Poisson (Thomas) Cluster process (PCP) best described (on the basis of the CvM goodness-of-fit statistics) the point pattern in the majority of plots (Figure 5.4).
Figure 5.3 Example point patterns and model fits for (a) Homogeneous Poisson (CSR), (b) Inhomogeneous Poisson (IPP), (c) Poisson (Thomas) Cluster (PCP) and (d) Inhomogeneous Poisson (Thomas) Cluster (IPCP) null models. Shaded area indicates a 99% confidence envelope based on 499 simulations. Dashed and solid lines are the predicted and observed model fits respectively. Size of the points are relative to the size of the individual plant.
Figure 5.4 Percentage of patterns best described by each point process – Homogenous Poisson (CSR), Inhomogeneous Poisson (IPP), Poisson (Thomas) Cluster (PCP) and Inhomogeneous Poisson (Thomas) Cluster (IPCP) applied for (a) *L. nutans*, (b) *P. elliptica*, (c) *P. drouynianus* and (d) *M. riedlei*

**Leucopogon nutans**

At Avon Valley, eight plots were best described by a PCP, with the other plots best described by an inhomogeneous Poisson process (a first-order model). Spatial pattern in seven of the plots at Sawyers Valley was best described by a PCP model, with one plot best described by an inhomogeneous PCP (Figure 5.4). There was no significant difference in the intensity of clusters (density, $\kappa$) or cluster size ($\sigma$) of the PCP for *L. nutans* between Avon ($\kappa = 0.06 \pm 0.03$, $\sigma = 0.5 \pm 0.34$) and Sawyers Valley ($\kappa = 0.11 \pm 0.09$, $\sigma = 0.41 \pm 0.49$). However, the median number of individuals per cluster ($\mu$) was significantly higher ($W = 4$, $p < 0.01$) at Avon Valley ($\mu = 7.46$), where the emu population was higher (Sawyers Valley $\mu = 1.70$; Table 5.3).

At both Sawyers Valley and Avon Valley the PCF and $L$ summary functions revealed aggregation up to, and at short distances (0-2 m and 0-4 m, respectively; Figure 5.5).
Persoonia elliptica

In the 900 ha plot at Avon Valley the spatial pattern of *P. elliptica* was best described by an inhomogeneous PCP model, while homogenous PCP (two plots) and IPP processes (one plot) best described the Sawyers Valley data. Median intensity, cluster size and number of individuals per cluster for Sawyers Valley were $\kappa = 0.0001$, $\sigma = 26.9$ and $\mu = 6.18$, respectively (Table 5.3).

The PCF and $L$ summary functions showed strong aggregation for all distances analysed (0-750 m) at Avon Valley. Of the three plots at Sawyers Valley, one showed strong aggregation at 0-100 m, and the remainder aggregation up to 20 m (Figure 5.6).
Figure 5.6 PCF (g(r)) and L summary functions for *P. elliptica* plots at Sawyers Valley (SV, \(n = 3\)) and Avon Valley (AV, \(n = 1\)) relative to simulated \(\alpha = 0.01\) CSR significance envelopes

*Podocarpus drouynianus*

At Nannup, seven plots were best described by PCP models, two by IPP (gradient) processes, and one by complete spatial randomness (CSR). All three plots at Sawyers Valley were best described by PCP models (Figure 5.5c). There was no significant difference between Sawyers Valley and Nannup in intensity (\(\kappa = 0.02\) and 0.02; \(W = 12, p = 0.66\)), cluster size (\(\sigma = 1.36\) and 1.45; \(W = 6, p = 0.38\)) or median number of individuals per cluster (\(\mu = 4.24\) and 1.54 ± 1.5; \(W = 17, p = 0.18\); Table 5.3).

The PCF and L summary functions were generally no different from CSR at very short distances (0-1 m) for the plots at Nannup. A single plot also showed a propensity toward CSR at all analysed distances (0-12.5 m). The three plots at Sawyers Valley showed strong aggregation at short distances (0-2 m; Figure 5.7).
Figure 5.7 PCF (g(r)) and L summary functions for *P. drouynianus* plots at Nannup (*n* = 10) and Sawyers Valley (*n* = 3) relative to simulated *α* = 0.01 CSR significance envelopes.

*Macrozamia riedlei*

All plots at Kings Park (*n* = 5), Sawyers Valley (*n* = 8) and Avon Valley (*n* = 9) were best described by a homogeneous PCP process (Figure 5.5). A Kruskal-Wallis test revealed a significant difference in cluster intensity between the three sites (*χ²*(2) = 7.14, *p* = 0.02), with Sawyers Valley having a significantly greater cluster intensity than Kings Park (*κ* = 0.006 and 0.001 respectively, *p* = 0.04). There was no significant difference in cluster size (*χ²*(2) = 5.46, *p* = 0.06) or median number of individuals per cluster (*χ²*(2) = 3.69, *p* = 0.15) between the three sites (Table 5.3).
The PCF and $L$ summary functions revealed strong aggregation across all plots at all sites (Figure 5.8). At Kings Park, aggregation was observed between 0-9 m and at Avon Valley and Sawyers Valley, 0-4 m (Figure 5.8).
Figure 5.8 PCF ($g(r)$) and $L$ summary functions for $M. riedlei$ plots at Sawyers Valley ($n = 8$), Avon Valley ($n = 7$) and Kings Park ($n = 5$) relative to simulated $\alpha = 0.01$ CSR significance envelopes.
Table 5.3 Median cluster intensity (density/m², κ), cluster size (σ) and the number of individuals per cluster (μ) for the point processes best described by Homogeneous Poisson (Thomas) cluster processes. Numbers in parentheses indicate the 5th and 95th percentile. Superscript letters (in columns) indicate a significant difference at \( p < 0.05 \).

<table>
<thead>
<tr>
<th></th>
<th>M. riedlei</th>
<th>L. nutans</th>
<th>P. elliptica</th>
<th>P. drouynianus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca. Valley</td>
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<tr>
<td>( n = 7 )</td>
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<tr>
<td>( \kappa )</td>
<td>0.003</td>
<td>0.05</td>
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<tr>
<td>(0.002,0.02)</td>
<td>(0.02,0.13)</td>
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<tr>
<td>( \sigma )</td>
<td>0.40</td>
<td>0.38</td>
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<td>(0.34,0.50)</td>
<td>(0.10,1.35)</td>
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<tr>
<td>( \mu )</td>
<td>7.8</td>
<td>7.46</td>
<td>-</td>
<td>-</td>
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<tr>
<td>(3.50,16.9)</td>
<td>(4.10,29.3)</td>
<td>-</td>
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<tr>
<td>Sawyers Valley</td>
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<tr>
<td>( n = 8 )</td>
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<td></td>
</tr>
<tr>
<td>( \kappa )</td>
<td>0.006</td>
<td>0.06</td>
<td>0.0001</td>
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<tr>
<td>(0.002,0.012)(^a)</td>
<td>(0.02,0.30)</td>
<td>(0.00002,0.0003)</td>
<td>(0.01,0.11)</td>
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<tr>
<td>( \sigma )</td>
<td>0.38</td>
<td>0.16</td>
<td>26.9</td>
<td>1.36</td>
</tr>
<tr>
<td>(0.24,0.53)</td>
<td>(0.01,1.5)</td>
<td>(12.8,33.4)</td>
<td>(0.58,1.40)</td>
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<tr>
<td>( \mu )</td>
<td>12.2</td>
<td>1.70</td>
<td>6.18</td>
<td>4.24</td>
</tr>
<tr>
<td>(5.37,23.1)</td>
<td>(0.29,3.93)</td>
<td>(2.5,28.3)</td>
<td>(3.60,5.02)</td>
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<tr>
<td>Kings Park</td>
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<tr>
<td>( \kappa )</td>
<td>0.001</td>
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<td>(0.0008,0.004)(^a)</td>
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<td>0.47</td>
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<td>(0.43,1.14)</td>
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<td>( \mu )</td>
<td>20.1</td>
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<td>(6.3,50.5)</td>
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<tr>
<td>Nannup</td>
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<tr>
<td>( \kappa )</td>
<td>-</td>
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<td>0.02</td>
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<tr>
<td>(0.006,0.03)</td>
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<td>(0.06,0.3)</td>
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<td>( \sigma )</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.45</td>
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<tr>
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<td></td>
<td>(1.45,2.97)</td>
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<tr>
<td>( \mu )</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.54</td>
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<tr>
<td>(0.89,5.76)</td>
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<td>(1.54,5.76)</td>
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</table>
5.4 DISCUSSION

Change in population spatial pattern following the loss of a dispersal agent was only detectable in the simulated data and only when initial fruit removal rates by frugivores were extremely high (100%). For more moderate rates of fruit removal, and similar to those reported in the literature, a change in spatial pattern following loss of a dispersal agent could not be consistently detected. Similarly, for the case study data, a clear spatial signal following disperser loss could not be detected. The strength of change in spatial statistic at the point of dispersal agent loss in the model varied with fruit removal rate and type of dispersal dynamic. The clearest change in pattern was observed in the simulations where 100% of seed was initially removed and deposited via scatter deposition and then the disperser was removed completely. Even then, complete extinction of the disperser does not drive the emergence of aggregation, it merely amplifies pre-existing aggregation. The selection of a sufficient spatial statistic to investigate pattern was crucial in determining whether the impact of the loss of dispersers on spatial aggregation was detected.

The model’s prediction that dispersal agent loss enhanced initial spatial aggregation is, perhaps, unsurprising given that conspecific spatial aggregation is common across many different species, life-forms and ecosystem types. (Fangliang et al. 1997; Perry et al. 2008; Miller et al. 2010; Perry et al. 2013b). Similarly, for the case-study, strong aggregation was the dominant pattern regardless of differences between sites in abundance of the putative dominant seed disperser, the emu. The loss of a key disperser has been shown in some cases to result in increased, albeit subtle, spatial aggregation (Rodríguez-Pérez et al. 2012b). Consequently, it was expected to observe a change in spatial pattern (increased aggregation) following the immediate loss of a disperser in a system in which the confounding impacts of first-order spatial effects were removed. The relatively small changes in spatial dynamics following disperser loss reported by Rodríguez-Pérez et al. (2012b) and also observed in the simulation model and empirical data present an interesting conundrum. Although the importance of seed dispersal for plant population dynamics is well-known (Clark et al. 1999a; Nathan and Muller-Landau 2000), it is likely to be very difficult to capture the consequences of disperser loss, at least in localised spatial patterns.
5.4.1 Fruit removal and spatial pattern

Where per plant fruit removal is low before disperser loss, the simulations suggest that a change in spatial pattern may be effectively undetectable. In some instances, even in the presence of abundant dispersers, fruit removal for many individual plants is zero (Carlo and Morales 2008). It is even possible that some short-lived plant species will not experience any form of active seed dispersal over their lifetime, further enhancing their local aggregation. In the case-study data it was expected that, particularly for the short-lived *L. nutans*, loss of the primary seed disperser would have driven a more strongly aggregated spatial pattern in plots where emu were less common. However this was not observed, which suggests that seed dispersal limitation may occur even where dispersers are abundant. At Avon Valley (high emu abundance) the density of *L. nutans* is much greater than at Sawyers Valley (0.4 ± 0.09 vs. 0.09 ± 0.02 individuals per m² respectively), and significantly more individuals per cluster (11.4 ± 7.3 vs. 1.9 ± 1.1 plants) were observed. Despite high emu abundances at Avon Valley, the higher density and abundant fruit production of *L. nutans* is likely resulting in a relatively lower rate of fruit removal and, consequently, a large number of individuals per cluster. Low fruit removal rates lead to the deposition of copious amounts of seed below parent plants, which, assuming seedlings survive under conspecifics, will result in strong aggregation at fine scales. *L. nutans* recruits after fires that kill adult plants, so the requirement to disperse away from the parent is not important and seeds close to the parent may be advantaged as the site is likely suitable for establishment and growth. There was also a higher density of emu scats (composed almost entirely of fruits from *L. nutans* and other Ericaceous species at Avon Valley than at Sawyers Valley. Upwards of 15 seedlings of *L. nutans* have been observed in a single emu scat at Avon Valley, potentially contributing to strong fine-scale aggregation even if long-distance dispersal has occurred.

For the three resprouter species, no impact of disperser loss on plant population spatial structure was observed. For *M. riedlei* and *P. drouynianus* there was no difference in Poisson cluster process parameters (cluster intensity, κ, cluster spread, σ and number of individuals per cluster, μ) between sites with high and low emu abundance. For *M. riedlei*, seed movement by dispersers other than emu is likely to 'fill in the gaps' even where the emu dispersal mutualism has been disrupted for a considerable period of time (e.g., > 100 yrs at Kings Park) (Burbidge and Whelan 1982). *M. riedlei* seed dispersal
events of up to 300 m from maternal plants by the Australian Raven (*Corvus coronoides*), a scatter-deposition dispersal agent, at the study sites has been recorded (Chapter Six).

### 5.4.2 Competition and spatial pattern

The absence of strong negative density-dependent effects may ameliorate or dilute the demographic impact of the loss of key dispersers. Predicting the resilience of seedlings to competition beneath the canopy of parents/con specifics is difficult (Chapman and Chapman 1995). For example, while extremely limited seedling recruitment and survival is observed under the canopy of parent trees in many tropical species (Augspurger 1984; Terborgh 2012), De Steven and Putz (1984) observed moderate survival (12%) of *Dipteryx panamensis* seedlings under the canopy of their parents. Increased crowding of heterospecifics has been shown to improve survival of seedlings and juveniles (the ‘herd protection hypothesis’) with increasing density of heterospecifics resulting in fewer interactions between hosts and species-specific pathogens and pests (Wills *et al.* 1997; Lan *et al.* 2012). Detecting interspecific effects (e.g. Janzen-Connell effects) has proved empirically difficult (Perry *et al.* 2013a). At the study sites several cohorts (inferred from the size of individuals) of *M. riedlei* under the crowns of females were observed. In some instances, up to 100 individuals, including seedlings, juveniles and assumed reproductive adults of indeterminate sex, were recorded within a 1 m radius of a single parent plant, suggesting that any density-dependent competition is relatively weak.

The reproductive biology of individual species is an important determinant in their spatial dynamics. Both *P. drouynianus* and *M. riedlei* exhibit fire-stimulated reproduction (Lamont and Downes 2011), producing large amounts of seed almost exclusively in the first 1-2 years following fire (Pate 1993; Chalwell and Ladd 2005). This massive and synchronous seed production, or ‘masting’, is a common reproductive trait among gymnosperms (Kelly and Sork 2002) and has been observed to facilitate predator satiation relative to those species that produce seed annually (Donaldson 1993). For *P. drouynianus* and *M. riedlei*, frugivore and seed predator satiation following post-fire seed production results in many seeds remaining undispersed beneath the canopy of parents (Chalwell and Ladd 2005). The competitive resilience of large-seeded and clump-dispersed species to negative density-dependent effects (Howe and Smallwood 1982; Howe 1989) may allow many of these seeds to germinate and
survive so that multiple cohorts establish under a parent plant, resulting in strong aggregation of juveniles even if not all individuals will survive to become adults.

5.4.3 Plant longevity

In the model simulations for a simulated annual plant species there was a lag of approximately 10 years before a change in spatial pattern could be detected. For long-lived and slow-growing species a detectable change in spatial pattern will likely occur only after a prolonged decoupling of the dispersal mutualism. At the sites considered, the slow growth rate and great longevity of the resprouters (Grove et al. 1980; Abbott and Van Heurck 1988; Chalwell and Ladd 2005) has likely delayed the emergence of any detectable signal in plant spatial pattern arising from disperser loss and decline. While resprouter species regenerate rapidly following disturbance (Bell 2001), they are typically slow growing as seedlings and can take many years (or decades) to reach reproductive maturity. *M. riedlei* and *P. drouynianus* are slow-growing and long-lived (Baird 1939; Chalwell and Ladd 2005) and so a relatively recent decline in emu populations coupled with the ongoing presence of other potential dispersal agents may dilute any signal of the loss of this primary dispersal vector.
5.5 CONCLUSIONS

The simulation model showed that, even under spatio-temporally homogeneous conditions, it is difficult to detect a change in spatial pattern following the loss of a key dispersal agent. The model considered dispersal in a homogenous environment, and so minimises the first-order effects (e.g., microtopography) that make disentangling the drivers of aggregation challenging (Perry et al. 2006; Law et al. 2009). In the field data, aggregation was the most common pattern for all four species, regardless of life-history (seeder/resprouter) and life-form (shrub/tree). The presence/absence of the emu as a primary dispersal vector did not significantly impact spatial pattern for any species. Rather, other dispersal vectors, habitat heterogeneity, and high rates of seedling establishment and survival under putative parents resulted in a highly aggregated pattern in most instances. Ultimately, the time required following disperser loss for a change in spatial dynamics to become evident is so extended that it may be undetectable by field methods, particularly for long-lived species. However, the physical structure of plant populations may not provide the complete picture of the impact of the loss of a dispersal agent. Molecular analysis may reveal the hidden costs associated with the loss of dispersal in terms of the removal of a diverse spatial genetic structure (Zhou and Chen 2010).

In Chapter Six, the identity of local seed dispersal agents and predators for the key study species are described. This is to further elucidate what dispersal assemblages are present and how these potentially impact on the demography of each species. Cafeteria experiments are also employed to determine visitation and removal rates for each species. Novel field (radio telemetric tagging of seeds) and analytical methods are employed to establish the dispersal distances for the key species as dispersed by the emu and other vectors.
CHAPTER SIX
SEED DISPERSAL AGENTS AND PREDATORS

ABSTRACT

Seed dispersal is a critical stage in the lifecycle of plants, allowing seeds to escape the negative density-dependent effects typically experienced beneath conspecifics and other species. Effective seed dispersal agents are those individuals, here frugivores, that can consume a large quantity of seeds and deposit them in a viable state far from the parent plant. The emu, a large ratite, is potentially the single most effective disperser of large-seeded species in the jarrah forests of southwestern Australia. This chapter describes the deployment of motion-sensitive cameras and the conduct of cafeteria experiments to identify the seed disperser assemblage and quantify seed removal rates for the four large-seeded species considered in this study. Germination experiments were also conducted to determine if passage through the emu gut enhanced germination for one of the study species, *Leucopogon nutans*, whose seeds display dormancy and are abundant within emu scats. Radio-telemetry and associated analytical methods were also employed as a trial measure to assess long distance dispersal (LDD) potential for the study species. The seed disperser assemblage was very depauperate, with few animals visiting seeds of the study species. Seed predation was low. The emu was found to consume seeds of each of the study species, with the exception of *Persoonia elliptica*. Individual emu scats contained thousands of seeds of *L. nutans*, but passage through the gut alone was not found to promote germination. Further cues, such as fire, are also required. Radio telemetry methods showed that the Australian raven (*Corvus coronoides*) may act as a LDD vector for *Macrozamia riedlei*, transporting seeds up to ~400 m from the parent plant. Nevertheless the emu remains the likely primary LDD vector for each of the study species and this is quantified in subsequent chapters using satellite telemetry and simulation modelling.
6.1 INTRODUCTION

Identifying seed dispersers and predators is of vital importance in plant ecology (Howe and Smallwood 1982). With seed dispersal (and subsequent germination) arguably the most critical component of the life cycle of a plant, it is necessary to understand the diversity in disperser and predator assemblages that are present for a given species, particularly for those species reliant on endo- and exozoochory (Levin et al. 2003). Frugivores may remove almost all the fruits of an individual species, highlighting their importance to plant demography (Denslow and Moermond 1982; Jordano 1995). Visitation and removal rates are highly dependent on both landscape- and neighbourhood-level effects and vary widely as a result of these factors (Carlo and Morales 2008). Despite the potential difficulties that these elements place on accurately establishing the presence and importance of a seed disperser and predator assemblage, assessment of their influence is necessary, particularly where dispersal vectors may contribute to long-distance dispersal (LDD; Nathan 2006). Within frugivore-dominated systems, the first step in assessing LDD potential within a population is to identify those, particularly large, vertebrate dispersers that likely act as LDD vectors. Similar attention should be given to understanding the impact of seed predators, which can have negative consequences for seed dispersal (Howe and Smallwood 1982).

Although some species have evolved in the presence of numerous dispersal agents, many large-seeded (or fruited) species rely on a single dispersal vector (Wenny 2001). As the size of a fruit or seed increases, the suite of animals that are able effectively to disperse it (as opposed to act as a predator on it) decreases (Nathan 2006). The shape of a seed or fruit is a useful indicator of the degree of disperser specialisation that the plant possesses and what dispersal vectors form part of its life history (Herrera 1992). Highly elongate fruits and seeds are consumed by many small mammalian and avian species, whereas spherical fruits and seeds are the domain of larger individuals. In the tropics, the largest fruits are often spherical, have a small fruit elongation ratio, and are dispersed by few or a single vector (Herrera 1992). The impact of ingestion and gut passage on these species may be more readily predictable and there is substantial danger in severing highly specific dispersal mutualisms via direct and indirect anthropogenic impacts.
Removal from the parent plant to escape deleterious density-dependent effects (Janzen 1970; Connell 1971) is one advantage of frugivory, while others include deposition into safe sites and a potential aid to germination received from gut chemicals. Deposition of seeds within clumps of large scats may provide a benefit as seeds have evolved to withstand intense clump competition (Howe 1989). Passage through the gut of frugivores has been shown to break chemical dormancy and aid in germination and seedling survival (Noble 1975). However, the benefit achieved via digestion is equivocal between species and endozoochorous events. For example, passage of the fruit of many tropical species through the gut of the Southern Cassowary has been shown to be both deleterious and positive (Bradford and Westcott 2010). Many plant species have evolved dispersal mutualisms with many frugivores and this diffuse evolutionary history makes it difficult to predict the effects of endozoochory on seed germination and seedling survival.

Following ingestion and deposition by frugivores, additional germination cues may be required to promote or enhance recruitment. The seeds of many species in the southwestern Australia region have evolved traits, both physical and chemical, that ensure that germination occurs under optimum conditions (Dixon et al. 1995). Physical characteristics such as hard seed coats require physical abrasions or exposure to heat in order to permit moisture access to cue germination. Chemical inhibitors may also be present, requiring the application of smoke compounds to cue germination (Dixon et al. 1995). Often physical and chemical inhibitors are present for a single species, requiring multiple events in situ to facilitate germination (Kenny 2000). Fire is a key evolutionary influence on the flora of southwestern Australia and the seeds of many species require fire to stimulate germination (Gill 1981). Heat, smoke, diurnal variation in temperatures and the onset of autumn rains are key components that lead to germination in many southwestern Australian species. The post-fire environment also creates microhabitats that are rich in nutrients, moisture and lack shading that encourage germination and enhance seedling establishment (Lamont et al. 1993).

Whether or not germination cues in addition to frugivore ingestion are necessary components for germination success may depend on the evolutionary biology of individual species. Much of the ancient flora (e.g. gymnosperms) presumably evolved in the absence of frequent fire and so the seeds of conifers and cycads may not require "modern" germination cues such as fire. However fire is generally required to stimulate
cone production in the Western Australian members of these groups (Lamont and Downes 2011), so it could be argued that the evolutionary importance of fire is already assigned through the cone development process, not after the fact (i.e. stimulating germination).

Identifying seed dispersers, estimating their visitation and fruit removal rates and determining the impact of gut passage on seed viability are vital if we are to evaluate overall seed dispersal effectiveness. Shupp (1993) initially proposed and then reviewed (Schupp et al. 2010) a framework for evaluating seed disperser effectiveness (SDE), by examining the quantity of fruits removed and the amount surviving passage (quality). This simplistic summary of Schupp’s (1993) SDE framework permits us to highlight those dispersers that are critical within a system. Considering the SDE framework, the most effective dispersal agent is one that removes a large number of fruits and can deposit seeds from them in a viable state. A vector that also contributes substantially to LDD events and that is highly effective will certainly play a key role in ecosystem dynamics.

The emu, as a large ratite with reduced avian crop, is able to consume many seeds, process them gently and then deposit them, presumably large distances from the location of consumption (Davies et al. 1971; Davies 1978). It is important then to understand how the emu (and other, more local dispersal agents) visit, consume, process and deposit large seeded species of the jarrah forests of Western Australia. As it has been identified also that the distance of dispersal from the parent plant is important, two methods of estimating seed dispersal distances – via radio telemetry (Mack and Druliner 2003) and censored tail reconstruction (CTR; Hirsch et al. 2012b) are trialled as preliminary methods for estimating LDD by the emu and other vectors, in these forests.

The aims of this chapter are to:

1. Identify the seed dispersal agents and seed predators for each of the target species.
   a. It is hypothesised that while the emu is the primary dispersal agent for each species, other species act as local seed dispersers or predators.

2. Quantify seed removal rates for the target species at each study site.
   a. It is hypothesised that seed removal rates for the target species will be highest at the sites where the emu is abundant.
(3) Quantify the seed composition, including temporal (seasonal) variation, in emu scats.
   a. It is hypothesised that there is substantial seasonal variation in the scat composition of the emu, reflecting the relative availability of their preferred food sources and,
   b. There is no significant difference in emu scat composition between the high and low emu abundance study sites.

(4) Examine the impact of passage through the emu gut on the germinability of the target species
   a. It is hypothesised that passage through the emu gut neither promotes nor inhibits germination of selected species i.e. the role of the emu is solely as a dispersal vector

(5) Assess the utility of contrasting techniques (radio telemetry and censored tail reconstruction) to examine dispersal and generate simple dispersal kernels.
6.2 MATERIALS AND METHODS

6.2.1 Detecting animals that disperse or destroy seeds

Motion-sensitive, infrared (IR) cameras (Bushnell Trophy Cam XLT) were trained on fruiting plants to determine the identity and behaviours of diurnal and nocturnal seed/fruit dispersal vectors and predators for each species. The camera was clearly trained on a single fruiting individual, and any visits to the same species in the camera background were not included in the analysis owing to difficulties in identifying dispersers/predators and their behaviours at the edge of focus. Thirty seconds of 5 megapixel footage was taken every time the infrared beam was broken with a 10 second delay between subsequent triggered events. The cameras were deployed with a moderate passive infrared setting. For each thirty seconds of footage, all species entering the frame were identified, enumerated and assigned as being diurnal or nocturnal. Length of time within the frame, animal behaviour and the number of fruiting plants within the frame were also recorded. Where dispersers or predators were observed consuming seeds or fruits, the rate of consumption was estimated. Cameras were periodically checked, batteries replaced and footage downloaded before being redeployed in a new randomly-selected location within the study areas. This ensured that local disperser and predator activities, informed by territory restrictions and preferred foraging ranges, did not unduly bias the observations (Snow and Walter 2007; Meek et al. 2014). For *P. elliptica*, once fruiting had ceased and seeds were shed onto the forest floor, the cameras were trained on the area beneath the canopy. The total number of camera hours per study species/site can be seen in Table 6.1.

<table>
<thead>
<tr>
<th></th>
<th><em>L. nutans</em></th>
<th><em>P. elliptica</em></th>
<th><em>M. riedlei</em></th>
<th><em>P. drouynianus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Avon Valley</td>
<td>4072</td>
<td>345.5</td>
<td>1397</td>
<td>…</td>
</tr>
<tr>
<td>Sawyers Valley</td>
<td>2116</td>
<td>432.5</td>
<td>1162</td>
<td>1008</td>
</tr>
<tr>
<td>Nannup</td>
<td>…</td>
<td>…</td>
<td>…</td>
<td>1152</td>
</tr>
</tbody>
</table>

Table 6.1 Total number of hours that motion-sensitive/infra-red cameras were trained on the study species at Avon Valley, Sawyers Valley and Nannup, southwestern Australia.
6.2.2 Seed removal rates

To determine the rate of seed removal and foraging preference by dispersers and predators, a seed cafeteria experiment was conducted during autumn 2013. At three randomly-selected locations at Avon Valley and Sawyers Valley a small 1 × 1 m area was cleared onto which three piles of *M. riedlei* (20 seeds), *P. elliptica* (70 fruits) and *P. drouynianus* (40 seeds) seeds were placed. Seeds were minimally handled, whilst wearing latex gloves, to limit the impact of scent transfer on foraging behaviour and seed selection (Ostfeld *et al.* 1997). The disparate number of seeds for each species reflects their relative availability at the time of the experiment. All seeds were freshly sourced from randomly chosen individuals within the respective study areas. No fresh seeds from the canopy of *L. nutans* were available at the time of the experiment. At each of the cafeteria locations a motion-sensitive, IR camera was deployed to capture the identity of diurnal and nocturnal seed dispersers and predators and assess their general foraging behaviours. Each of the cameras was set as described above. The seed piles were checked 1, 7, 19, 25 and 33 days from the initial placement of seeds. On the 19th and 25th days only the seed piles at Avon Valley and Sawyers Valley, respectively were inspected owing to logistical constraints. Seeds were considered to be 'removed' if they were consumed completely by a dispersal agent or predator. Instances in which seeds were disturbed due to indiscriminate or accidental foraging behaviour or where dispersers/predators removed the pericarp, leaving the endocarp *in situ* were not considered to be removed.

When fresh *L. nutans* fruits became available in spring 2013, a similar removal experiment was conducted. Piles of 100 *L. nutans* fruits were placed at three randomly-selected locations at Avon Valley and Sawyers Valley and co-located with motion-sensitive IR cameras. Owing to anticipated low removal rates as a result of a high density of adult *L. nutans* individuals, fruit piles were checked infrequently; 7 and 23 days following initial placement. Fruits were considered removed as described above.

6.2.3 Estimating seed dispersal distances - *M. riedlei* case study

*M. riedlei*, possessing the largest seed of the four target study species (23 ± 2 g; 4.4 × 2.9 cm), presented an opportunity for using both established and developing methods for estimating seed dispersal distances. Two different methods were used to estimate the dispersed distances of *M. riedlei* seeds - the well-established recovery of seeds
containing radio transmitters (Mack and Druliner 2003) and the emerging censored tail reconstruction (Hirsch et al. 2012b).

6.2.4 Radio telemetry

The use of varying designs of radio telemetric tags to estimate seed dispersal for species dispersed by birds is commonplace (Mack and Druliner 2003; Pons and Pausas 2007; Hirsch et al. 2012a), with the method permitting estimates of seed dispersal distances, particularly where long distance dispersal events may have occurred. A small (ca. 6 mm) hole was drilled in the apex of *M. riedlei* seeds to allow placement of the transmitters. Seeds were sourced from populations throughout southwestern Australia, as there were no local seed available at the time of the study. Two-stage radio transmitters (Advanced Telemetry Systems, Model F1040; 10 × 23 × 9 mm; 2.5 g, ca. 10% the weight of a mature *M. riedlei* seed) were inserted into the drilled cavity (Plate 6.1). The drilling of the seeds rendered them non-viable. Seeds were recovered using a folding three-element Yagi antenna and pilot testing for the recovery of tagged seeds suggested that the transmitters had a detection radius of ca. 500 m.

As a pilot trial of the tagged seeds, six telemetric tagged *M. riedlei* seeds were initially placed at the Avon Valley study site during winter 2011 beneath an assumed female *M. riedlei* individual. The plant was considered female as numerous juveniles and seedlings were located beneath the fronds. A relatively small number of seeds was used due to the high cost of the transmitters. Motion-sensitive/IR cameras were co-located at the placement site in order to capture the identity of dispersal agents and seed predators. The cameras were set to take 30 seconds of video footage, with a 10 second delay between subsequent recordings, if triggered. The tagged seeds were checked 96 hrs after placement and an attempt at recovery was made when the seeds had been removed.

Following the dispersal and successful recovery of tagged seeds during the pilot trial, the placement of telemetric tagged *M. riedlei* seeds continued throughout 2011 and 2012 across both Sawyers Valley and Avon Valley. Tagged seeds were placed as described previously and co-located with motion-sensitive/IR cameras. Seventy tagged seeds were deployed, 46 at Avon Valley and 24 at Sawyers Valley. The different number of seeds deployed at each location reflects the minimal seed disperser activity recorded at Sawyers Valley during early periods of the tagging process. Seeds were considered to be dispersed if an animal interacted with a seed that resulted in its
displacement from the initial location, even locally. The distance between the initial placement and final location of the recovered seed was determined for all individuals.

Plate 6.1 Left, fish implant two-stage radio transmitter inserted into an *M. riedlei* seed (right, red arrow). Photographs from Gerlach (2012)

6.2.5 Censored tail reconstruction

Censored Tail Reconstruction (CTR) is an analytical procedure, originally developed by Jansen *et al.* (2004) and recently evaluated by Hirsch *et al.* (2012b) for inferring the tail of seed dispersal kernels from incomplete or truncated tracking data. The evaluation by Hirsch *et al.* (2012b) revealed that CTR can accurately estimate seed dispersal kernels from truncated or incomplete tracking data, where the kernel follows a simple decay function. While the full methodological approach to CTR can be seen in Hirsch *et al.* (2012b), the procedure essentially involves collecting data on seed dispersal distances using techniques appropriate for the study system within a given search radius and note those missing (i.e. beyond the search radius). The Kaplan–Meier survivorship curve is estimated from these data, with dispersal distances as time and missing seeds as observations that are censored at the distance of the search radius (Hirsch *et al.* 2012b). Probability density functions are then fitted to the K-M curve and procedures (such as the AIC) can be used to determine best fit.

During summer 2013, 100 *M. riedlei* seeds were placed beneath three separate assumed adult female *M. riedlei* adults at Sawyers Valley. Only the Sawyers Valley study site was used owing to the limited availability of *M. riedlei* seeds and logistical constraints restricting repeated access to Avon Valley during summer 2013. The individuals were assumed to be female as described above. Each individual selected was separated by a
distance of > 100 m. At 3 and 21 days following placement, a radius of 10 m around each selected individual was searched for dispersed seeds. The search radius was selected based on the results of the radio telemetry seed dispersal experiment conducted during the previous two years, where local dispersal was contained within 10 m and where longer-distance dispersal was > 80 m from plants. Similar local dispersal distances for *M. riedlei* seeds were reported by Burbidge and Whelan (1982). During each census, the number of seeds remaining within the search radius was recorded, along with individual dispersal distances. The number of seeds extending beyond the search radius was also recorded. The sarcotesta condition of each seed was also recorded, along with an estimate of seed dispersal vector based on sarcotesta removal. No motion-sensitive/IR cameras were available during this experiment, so disperser identity is assumed from patterns of sarcotesta removal noted during the radio telemetry dispersal experiment and from Burbidge and Whelan (1982).

### 6.2.6 Emu scat seed composition

To determine the seasonal large-seed composition of emu scats, the freshest available scat was collected from each plot at each site where available. During November 2012, \( n = 6 \) and \( n = 4 \) scats were collected from Avon Valley and Sawyers Valley respectively. Scats were deposited between August 2012 and November 2012, representing spring deposition. During February 2013, \( n = 16 \) scats were collected from Avon Valley plots. Scats were deposited between November 2012 and February 2013 (summer deposition). No scats during this summer deposition period were found at Sawyers Valley. Between March and June 2013 (autumn deposition), 3 and 2 scats were collected from Avon Valley and Sawyers Valley, respectively. No scats were available to be collected during the winter months. Each scat was weighed, and placed into a beaker of warm water to dissolve the matrix. The identity and number of each large seed was recorded.

### 6.2.7 Seed germination requirements

In November 2012, seeds of *P. elliptica* and *L. nutans* were treated to determine germination requirements. Fresh seed obtained from the canopy and seed from the soil seed bank were used in the trials. Seed lots were germinated over a 10 - 16 week period in a refrigerated incubator at 17°C (Thermoline Scientific). Seeds were exposed to
normal diurnal light variation. Each of the treatments, including the control batch, consisted of five replicates of 20 seeds.

A thermal-shock treatment (100°C for 5 min applied in a dry oven) was applied to seeds from the soil seed bank and canopy obtained from each site for both *L. nutans* and *P. elliptica*. The same thermal shock treatment was also applied to *L. nutans* seeds collected from emu scats that had been deposited in spring 2012. Following the thermal shock treatment, seeds were sowed into plastic nursery punnets filled with river sand and watered with de-ionised (DI) water.

Smoke treatments applied in this study were produced by the combustion of collected *E. marginata* (jarrah) forest litter, with the smoke produced pumped into a ca. 0.2 m$^3$ chamber over a 2 hr period. *L. nutans* and *P. elliptica* seeds from the canopy and seed bank at both sites were sowed into the punnets as described above prior to being smoked. *L. nutans* seeds collected from emu scats were also treated. Following the smoke treatment, the punnets were placed in the refrigerated incubator. Smoke-treated seed lots were watered with DI water 48 hrs after treatment. Table 6.2 provides a summary of the treatments applied to each species at each site. Note that no *P. elliptica* seeds were recovered from emu scats. Seed lots were checked daily and watered with DI water as required.
Table 6.2 Summary of germination treatments conducted on each species

<table>
<thead>
<tr>
<th>L. nutans</th>
<th>Avon Valley</th>
<th>Sawyers Valley</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Heat</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Smoke</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Emu</td>
<td>×</td>
<td></td>
</tr>
<tr>
<td>Emu + Heat</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Emu + Smoke</td>
<td>×</td>
<td>×</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>P. elliptica</th>
<th>Avon Valley</th>
<th>Sawyers Valley</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Heat</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Smoke</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Emu</td>
<td>×</td>
<td></td>
</tr>
<tr>
<td>Emu + Heat</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Emu + Smoke</td>
<td>×</td>
<td>×</td>
</tr>
</tbody>
</table>

6.2.8 Statistical analysis

Detecting animals that disperse or destroy seeds

The number of visits per hour to an individual plant, for each species (per camera) was calculated. A visit was defined as the instance when an animal interacted with the fruits or seeds on the plant on which the motion-sensitive camera was trained. Visits also included the interaction with fruits or seeds by a disperser or predator beneath the canopy of the individual. Owing to visual difficulties in quantifying the number of seeds consumed in each visit, a general estimate was made as to how many seeds or fruits were consumed each visit (if any) and over what time period.

Seed removal rates

General linear mixed models were used to examine the impact of study site, species and the potential interactive effects between these on the removal of seeds during the first cafeteria experiment, with removal of seeds as determined at the final census as a binomial response. The site at which each group of seeds was located was incorporated into the models as a random effect. When comparing increasingly complex nested models, the lowest AIC score and chi-squared tests were used to select the appropriate model (Anderson et al. 1998). The general linear mixed model analysis was conducted in R version 2.15.2 (R Core Team 2012) using the 'lme4' package (Bates and Maechler 2009). For the second cafeteria experiment involving L. nutans, a general linear mixed model was also used to estimate the impact of study site on seed removal. Model construction and analysis was also conducted in R as described above.
Estimating seed dispersal distances - *M. riedlei* case study

Radio telemetry

Four dispersal kernels that are commonly used to model dispersal data were fitted to the data from the telemetric-tagged *M. riedlei* seeds in their one-dimensional form (the probability distribution function). The exponential, lognormal, Poisson and gamma functions have been previously applied to dispersal data (Dessard and Bar-Hen 2005; Hirsch *et al*. 2012b), with each representative of a simple decay function, with fewer dispersal events observed at increasing distances. The `fitdistr` function in the "MASS" package (Venables and Ripley 2002) was used within R (R Core Team 2012) to obtain the parameter estimates for each probability density function via maximum-likelihood estimation. It is noted that the `fitdistr` function defaults to the `optim` function for parameter estimation of the gamma probability density function. Kernels were fitted to the full set of dispersal data and to the data that pertained only to the Australian Raven. Similar to Hirsch *et al*. (2012b), the AIC scores were used to determine which function best fitted the observed data.

Censored tail reconstruction

As each of the seeds remained within the census radius at the completion of the experiment, there was no truncated data from which to estimate the Kaplan–Meier survivorship curve and to which univariate decay functions could subsequently be fitted. Instead, dispersal kernels were fitted as above to the seed dispersal data for the 300 seeds deployed. Additionally, dispersal kernels were also fitted to data pooled from the censored tail reconstruction field experiment and the radio telemetry experiment.
6.3 RESULTS

6.3.1 Detecting animals that disperse or destroy seeds

Cameras were deployed for a total of 11,684 hours across the three year study period. Animal visits to individual fruiting plants were generally scarce and the overall disperser community depauperate. For *L. nutans* only emus were observed to visit fruiting plants at both Avon Valley and Sawyers Valley. Camera footage revealed that birds spent ca. < 10 seconds at an individual plant before moving on. During this time, emus removed few (though indeterminate in number) seeds from the canopy and at the base of fruiting plants. Visits to fruiting *L. nutans* were relatively more frequent at Avon Valley (one visit per 100 hrs; Table 6.3) in contrast to Sawyers Valley (one visit per 500 hrs).

Emus also dispersed *M. riedlei* seeds at Avon Valley and Sawyers Valley. Similar to *L. nutans*, the visitation rate for the emu was much higher at Avon Valley (1 visit per 25 hours to simulated seeding *M. riedlei* individuals) in comparison to Sawyers Valley (1 visit per 1428 hrs). When emus visited *M. riedlei*, they tentatively pecked at seeds placed at the base of assumed female plants. This tentative pecking continued for a few minutes until most of the sarcotesta had been removed. In only a single instance, at Avon Valley, was an emu observed consuming a *M. riedlei* seed. In addition to the emu, the Australian raven was a more frequent visitor to *M. riedlei* at Avon Valley (1 visit per 25 hrs) in contrast to Sawyers Valley (1 visit per 1428 hrs). During the brief visits by the ravens (< 20 seconds), the birds would pick up a single seed with their beak and deposit it some distance away (see the *M. riedlei* case study, this chapter). The bush rat was an incidental visitor to *M. riedlei* at Avon Valley and removed a small amount of sarcotesta and minimally disturbed seed piles.

Emus were not observed to remove fruits of *P. elliptica* at either Avon Valley or Sawyers Valley. No visits were recorded to the canopy of *P. elliptica*, however, there was some evidence that fruits had been destructively consumed (and branchlets torn off individuals), likely by the red-tailed black cockatoo (*Calyptorhynchus banksii*). On the ground beneath *P. elliptica* trees the western grey kangaroo was a nocturnal consumer of fallen fruits (1 visit per 100 hrs vs. 1 visit per 500 hrs for Avon Valley and Sawyers Valley, respectively). Kangaroos were observed to remain beneath the canopy for ca. 5 minutes foraging on fallen seeds at both study sites. The invasive European rabbit was
also found to destructively consume *P. elliptica* seeds, remaining beneath individual trees for ca. 2 minutes before departing from camera vision. The rabbit was a relatively frequent visitor to Avon Valley (1 visit per 100 hrs), but was not observed at Sawyers Valley. At Sawyers Valley, a single Currawong was observed to consume a few *P. elliptica* fruits for < 10 seconds before departing.

For *P. drouynianus*, no footage was recorded of either seed dispersers or predators on seeds at any time during the study at Sawyers Valley. In contrast, at Nannup, the emu was the sole observed seed disperser, visiting a coning female once every 50 hrs. Camera footage revealed that the emu would consume only a few seeds from an individual plant (from an available crop sometimes of > 400) within ~ 15 seconds, before moving on. The emu appeared to be a clumsy feeder, with numerous seeds falling from its beak beneath the plant during the foraging process.
Table 6.3 Number of visits to fruiting/seeding species during the course of the study period in jarrah forests in southwestern Australia. The capital letter in parentheses indicates if the species is a dispersal agent (D) or predator (P). The presence of both letters suggests that the agent may act as either a disperser or predator, depending on destructive consumption of the seed/fruit. The number in parentheses represents the 95% CI.

<table>
<thead>
<tr>
<th>Species</th>
<th>L. nutans visit /h</th>
<th>M. riedlei visit /h</th>
<th>P. elliptica visit /h</th>
<th>P. drouynianus visit /h</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avon Valley</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Australian raven (D)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Corvus coronoides</em></td>
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<td>(± 0.07)</td>
<td></td>
</tr>
<tr>
<td>Bush rat (D)</td>
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<td>(± 0.001)</td>
<td></td>
</tr>
<tr>
<td><em>Rattus fuscipes</em></td>
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<td>0.04</td>
<td>(± 0.008)</td>
<td>(± 0.04)</td>
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<td>Emu (D)</td>
<td></td>
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<td></td>
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<tr>
<td>European rabbit (P)</td>
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<td></td>
<td></td>
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<tr>
<td><em>Oryctolagus cuniculus</em></td>
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<tr>
<td>Western grey kangaroo (D/P)</td>
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<td>(± 0.001)</td>
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<td>Currawong (D)</td>
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<td>0.0007</td>
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</tr>
<tr>
<td><em>Dromaius novaehollandiae</em></td>
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<td>(± 0.001)</td>
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</tr>
<tr>
<td>Western grey kangaroo (D/P)</td>
<td>0.002</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Macropus fuliginosus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nannup</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emu (D)</td>
<td>0.02</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. novaehollandiae</em></td>
<td></td>
<td></td>
<td></td>
<td>(± 0.02)</td>
</tr>
</tbody>
</table>

6.3.2 Seed removal rates

Seeds and fruits were removed by a variety of species at both study sites (Table 6.4). During the first seed removal experiment using co-located seeds of *P. drouynianus*, *P. elliptica* and *M. riedlei* at Avon Valley and Sawyers Valley, seed removal rates at the final census were higher overall at Avon Valley (Table 6.5; Figure 6.1). However, there was a significant interaction between species and study site on seed removal rates at the final census, with these rates higher at Sawyers Valley for *P. drouynianus* and *P. elliptica* (Table 6.5).
Few seeds of *P. drouynianus* were removed during the course of the seed removal experiment at Avon Valley (where the species does not occur), with 97% of seeds remaining at the final census. The few seeds that were removed at Avon Valley were taken by Australian ravens and deposited < 10 m from the seed pile. Conversely, at Sawyers Valley, only 50% of the seeds remained at the final census, with the Australian ringneck parrot and western grey kangaroos consuming seeds in close proximity to the seed piles. Ravens also removed a small number of *P. drouynianus* seeds and deposited them in close proximity (< 10 m) to the experimental piles.

Seeds of *P. elliptica* were rapidly removed from Sawyers Valley in comparison to Avon Valley. One week after placement, only ca. 20% of *P. elliptica* seeds remained, having been consumed largely by western grey kangaroos. A few seeds were incidentally removed by the Australian magpie and currawong and deposited < 5 m from the experimental pile. At the final census (33 days after placement) no *P. elliptica* seeds remained at Sawyers Valley while 40% remained at Avon Valley (Figure 6.1). *P. elliptica* seeds at Avon Valley were consumed by the western grey kangaroo and brush wallaby, with a few seeds picked up and dispersed locally by ravens and a painted button-quail (*Turnix varius*).

All *M. riedlei* seeds placed at Avon Valley had been removed by the completion of the experiment. By the 19th day of the trial all *M. riedlei* seeds at Avon Valley had been removed by ravens. For a few *M. riedlei* seeds at Avon Valley, western grey kangaroos removed the fleshy sarcotesta before they were then dispersed by ravens. In contrast, 70% of seeds remained at Sawyers Valley at the final census (Figure 6.1). Each seed remained *in situ*, following removal of the sarcotesta by the western grey kangaroo. The 30% of *M. riedlei* removed at Sawyers Valley were dispersed by ravens. The red fox and Australian magpie had incidental interaction with seeds, moving a few seeds < 50 cm from the seed piles while generally foraging.

Following one week of placement for *L. nutans* fruits, all remained at Avon Valley and 97% at Sawyers Valley. At the second and final census (23 days following placement), significantly more *L. nutans* fruits were removed at Sawyers Valley (30% remaining) and Avon Valley (70% remaining), respectively (Table 6.6). Only the emu at Avon Valley, and western brush wallaby at Sawyers Valley, were recorded as removing fruits. *Leucopogon nutans* fruit removed by species was not effectively captured on IR camera,
though it is likely that substantial fruit removal or predation was also carried out by small rodents.

**Table 6.4** Identity of species removing seeds/fruits of the four key species from cafeterias at Avon Valley (AV) and Sawyers Valley (SV), southwestern Australia

<table>
<thead>
<tr>
<th>Species</th>
<th>P. drouynianus</th>
<th>P. elliptica</th>
<th>M. riedlei</th>
<th>L. nutans</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australian magpie</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cracticus tibicen</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Australian raven</td>
<td>AV, SV</td>
<td>AV</td>
<td>AV, SV</td>
<td></td>
</tr>
<tr>
<td><em>C. coronoides</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Australian ringneck parrot</td>
<td>SV</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Barnardius zonarius</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Currawong</td>
<td>SV</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Strepera versicolor</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Emu</td>
<td></td>
<td></td>
<td></td>
<td>AV</td>
</tr>
<tr>
<td><em>D. novaehollandiae</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Painted button-quail</td>
<td>AV</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Turnix varius</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red fox</td>
<td></td>
<td></td>
<td></td>
<td>SV</td>
</tr>
<tr>
<td><em>Vulpes vulpes</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Western brush wallaby</td>
<td>AV</td>
<td></td>
<td></td>
<td>SV</td>
</tr>
<tr>
<td><em>M. irma</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Western grey kangaroo</td>
<td>SV</td>
<td>AV, SV</td>
<td>SV, AV</td>
<td></td>
</tr>
<tr>
<td><em>M. fuliginosus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 6.1 Proportion of seeds remaining for (a) *P. drouynianus*, (b) *P. elliptica*, (c) *M. riedlei* and (d) *L. nutans* during the conduct of a seed removal cafeteria experiment at Avon Valley and Sawyers Valley in southwestern Australia. Error bars indicate the 95% confidence interval calculated by the normal approximation of the binomial distribution on the proportion of seeds remaining at each census, pooled from the data at each study site.
Table 6.5 Generalised linear mixed model parameters for the impact of site, species and their interaction on the final seed removal rates at the completion of a cafeteria experiment in Avon and Sawyers Valleys, southwestern Australia. Bolded z-values represent model parameters with a significant effect ($p < 0.05$)

<table>
<thead>
<tr>
<th>Effect on seed removal (SE)</th>
<th>z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td></td>
</tr>
<tr>
<td>Sawyers</td>
<td>-5.308 (1.068)</td>
</tr>
<tr>
<td>Species</td>
<td></td>
</tr>
<tr>
<td>* P. elliptica</td>
<td>-3.794 (1.035)</td>
</tr>
<tr>
<td>* P. drouynianus</td>
<td>-7.923 (1.151)</td>
</tr>
<tr>
<td>Site * Species</td>
<td></td>
</tr>
<tr>
<td>Sawyers * P. elliptica</td>
<td>9.673 (1.304)</td>
</tr>
<tr>
<td>Sawyers * P. drouynianus</td>
<td>8.675 (1.205)</td>
</tr>
</tbody>
</table>

Model parameters:
removed?(binomial response) ~ study site * species + (1|seed pile location)

Table 6.6 Generalised linear mixed model parameters for the impact of study site on the final seed removal rates at the completion of a cafeteria experiment on *L. nutans* in Avon and Sawyers Valley, southwestern Australia. Bolded z-values represent model parameters with a significant effect ($p < 0.05$)

<table>
<thead>
<tr>
<th>Effect on seed removal (SE)</th>
<th>z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td></td>
</tr>
<tr>
<td>Sawyers</td>
<td>1.6918 (0.1834)</td>
</tr>
</tbody>
</table>

Model parameters:
removed?(binomial response) ~ study site + (1|seed pile location)

6.3.3 Emu scat deposition and seed composition

Seeds of five species dominated emu scat composition; *L. nutans*, *Styphelia tenuiflora* (Ericaceae), *Hakea* sp. (Proteaceae), *Casuarina* sp. (Casuarinaceae) and *M. riedlei*. Across all seasons of deposition, the overwhelming majority of seed material within emu scats was the fruits of *L. nutans*, with each 50g of scat containing 1027 ($\pm$ 185) fruits on average. The fruits of *S. tenuiflora*, follicles of *Hakea* sp., cones of *Casuarina* sp. and seeds of *M. riedlei* made minor contributions to scat composition, with 2 ($\pm$ 1) fruits, < 1 follicle, < 1 cone and < 1 seed, respectively found in 50g of scat. There was no significant difference in the number of fruits of *L. nutans* recovered from emu scat between spring and summer ($t = -0.30$, $p = 0.76$, df = 17; 1075 and 1158 seeds per 50g scat, respectively).
There was no significant difference between the weight of scats that were deposited during spring in comparison to those deposited during the summer (82.70g ± 16.02; 73.38g ± 14.31; $t = 2.09$, df = 19, $p = 0.41$). Too few scats were deposited during autumn monitored plots ($n = 3$ and $n = 2$ respectively; Avon Valley and Sawyers Valley) for analysis.

6.3.4 Seed germination requirements

No seeds of either *P. elliptica* or *L. nutans* across any of the treatments germinated after 10 weeks (70 days).

6.3.5 Estimating seed dispersal distances - *M. riedlei* case study

*Radio telemetry*

The recovery rate of dispersed radio-tagged *M. riedlei* seeds was very high, with 68 of the 70 placed seeds recovered. Of the 70 seeds that were placed, 49 had interacted with an animal, which included fine-scale dispersal. For 20 of the 49 events, the estimated dispersal distance was < 5 cm from initial placement, the result of incidental foraging activities. Of the 49 dispersal interactions, the majority (45%) were affected by the emu and Australian Raven (25%). The remainder of the dispersal events were carried out by the western brush wallaby (18%) and the native bush rat (6%). For a small number of dispersal events (6%), the disperser identity remained unknown. The mean dispersal distance of these 49 tagged seeds was 59 m (±37 m; 95%CI). The mean dispersal distance of the 12 seeds taken by the Australian Raven was 177 m (±63 m; 95%CI).

The final dispersal location of the tagged seeds differed markedly between disperser species. For the emu, only a single *M. riedlei* seed was ingested. This tagged seed was never recovered, however, systematic searching of the initial placement location suggests that the seed was moved > 700 m. For the rest of the dispersal interactions involving the emu, seeds were displaced < 10 m. Rather than consuming whole seeds, birds tentatively pecked at individual seeds, removing small amounts of sarcotesta. This behaviour was observed for both adult and juvenile birds.

The Australian Raven exhibited two behaviours when foraging *M. riedlei*. Ravens generally quickly removed tagged seeds and deposited them, most often, in the canopy of Grass trees (*Xanthorrhoea preissii*) or within stem hollows of dead jarrah trees. On
each of these occasions, all tagged seeds were recovered between 85 - 380 m from the initial placement point. In a few instances, birds did not remove seeds from the initial placement location, instead removing small amounts of sarcotesta, resulting in tagged seeds being displaced < 2 m. The remaining identified seed dispersal vectors; the native bush rat and western brush wallaby, also dispersed seeds only small distances (< 10 m). Seeds dispersed by the former were recovered within hollowed logs on the ground, some 9 m from the initial placement. However, the western brush wallaby completely stripped the seeds of all sarcotesta, while still depositing the seeds within 2 m of the initial placement.

For the complete dispersal data set, the best-fitting dispersal model followed a lognormal distribution with mean of log 1.51 and standard deviation of log 2.23 (Table 6.7). The dispersal kernel (Fig. 6.2a) reveals little chance of seeds being dispersed > 200 m. Conversely, for those seeds dispersed by the Australian Raven, an exponential model provided the best fit, with a rate parameter of 0.0056 (Table 6.7). Under this model, ca. 30% of seeds dispersed would travel > 300 m from the point of origin.
Figure 6.2 Dispersal kernels fitted to data collected from retrieved *M. riedlei* radio-telemetry tagged seeds at Sawyers Valley and Avon Valley National Park, southwestern Australia for (a) all dispersal agents (*n* = 49 events) and (b) the Australian Raven (*n* = 12 events).

Table 6.7 Dispersal kernel functions fitted to empirical data for all radio-tagged *M. riedlei* seeds dispersed at Sawyers Valley and Avon Valley, in southwestern Australia and for those only dispersed by the Australian Raven. The ΔAIC indicates the difference in AIC scores between the best-fitting and additional models.

<table>
<thead>
<tr>
<th>Full Data Kernel</th>
<th>Rank</th>
<th>Function</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>Lognormal</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Gamma</td>
<td>37.57</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Exponential</td>
<td>129.51</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Poisson</td>
<td>8367.08</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Australian Raven Kernel</th>
<th>Rank</th>
<th>Function</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>Exponential</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Gamma</td>
<td>2.49</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Lognormal</td>
<td>10.62</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Poisson</td>
<td>791.94</td>
</tr>
</tbody>
</table>

*Censored tail reconstruction*

At the first census three days following placement of the seeds, only 11%, 15% and 0% of seeds had been dispersed from beneath the canopy of assumed female *M. riedlei* individuals. The sarcotesta of each of the seeds had been completely removed, and each seed was found within 1 m of placement. At the final census, 21 days following deployment, each of the 300 seeds had been dispersed and the sarcotesta stripped. No seed was found further than 5 m from its initial location. The complete removal of
sarcotesta, combined with marks on the seed coat consistent with those seeds recovered following the radio telemetry experiment, suggested that either the western grey kangaroo or western brush wallaby had dispersed the seeds locally. The dispersal kernel of the 300 seeds followed a gamma distribution with shape and rate parameters of 3.02 and 3.72, respectively (Table 6.8). The model fit suggests that no seed dispersal is likely beyond 5 m (Figure 6.3a).

For the combined radio telemetry and CTR dispersal data, a lognormal distribution with mean 0.18 and standard deviation 1.30 provided the best model fit (Table 6.8). Under this model, the probability of seed dispersal beyond 20 m is minimal (Figure 6.3b).
Figure 6.3 Dispersal kernels fitted to data collected from retrieved *M. riedlei* seeds at (a) Sawyers Valley southwestern Australia as part of a censored tail reconstruction field experiment and (b) all dispersal events at Sawyers Valley and Avon Valley, southwestern Australia for both radio telemetry and censored tail reconstruction field experiments. Note different horizontal axes scaling.

Table 6.8 Dispersal kernel functions fitted to empirical data for *M. riedlei* seeds dispersed during a censored tail reconstruction (CTR) experiment at Sawyers Valley, southwestern Australia and for all dispersal data from CTR and radio telemetry experiments. The ΔAIC indicates the difference in AIC scores between the best-fitting and additional models.

<table>
<thead>
<tr>
<th>CTR Data</th>
<th>Function</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rank</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Gamma</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>Lognormal</td>
<td>24.32</td>
</tr>
<tr>
<td>3</td>
<td>Exponential</td>
<td>151.5</td>
</tr>
<tr>
<td>4</td>
<td>Poisson</td>
<td>6417.69</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>All Dispersal Data</th>
<th>Function</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rank</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Lognormal</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>Exponential</td>
<td>1182.03</td>
</tr>
<tr>
<td>3</td>
<td>Gamma</td>
<td>5335.86</td>
</tr>
<tr>
<td>4</td>
<td>Poisson</td>
<td>&gt; 10000</td>
</tr>
</tbody>
</table>

The summary statistics for each of the fitted dispersal kernels varied depending on data source (Table 6.9). The 95th and 99th percentiles of dispersal were highest for data collected from telemetric-tagged *M. riedlei* seeds, either from the entire data or from the truncated Australian Raven data. The smallest percentiles were recorded from the CTR experiment, where only local dispersal was observed. There was no clear change in median dispersal value across the data sets and fitted models.
Table 6.9 Summary statistics for *M. riedlei* seed dispersal data collected from telemetric-tagged seeds and those deployed for a censored tail reconstruction experiment in southwestern Australia. Summary statistics represent the distance dispersed in metres.

<table>
<thead>
<tr>
<th>Data</th>
<th>Mean</th>
<th>Median</th>
<th>95th percentile</th>
<th>99th percentile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radio Telemetry - All</td>
<td>59</td>
<td>1.00</td>
<td>316</td>
<td>546.4</td>
</tr>
<tr>
<td>Radio Telemetry - Ravens</td>
<td>176.75</td>
<td>159</td>
<td>371.2</td>
<td>378.24</td>
</tr>
<tr>
<td>CTR Experiment Data</td>
<td>0.81</td>
<td>0.72</td>
<td>1.64</td>
<td>1.83</td>
</tr>
<tr>
<td>Radio Telemetry &amp; CTR Data</td>
<td>9.38</td>
<td>0.75</td>
<td>3.1</td>
<td>227.35</td>
</tr>
</tbody>
</table>
6.4 DISCUSSION

Visitation and fruit removal rates for each of the target species by a depauperate assemblage of seed dispersers was generally poor and spatially variable. As predicted, visitation rates to *L. nutans*, *M. riedlei* and *P. drouynianus* by the emu were greater at the high emu abundance study sites. Over the thousands of hours during which the motion-sensitive cameras were deployed, only six potential species of dispersers and predators were observed to visit and interact with the seeds or fruits of the target species. A similarly depauperate seed disperser community was noted during the seed cafeteria experiment. Fruit removal rates varied significantly by site, by species and there were strong interactions between these elements. The emu was the only identified seed disperser for *L. nutans* during the camera trapping and was observed to consume seeds for all other study species except *P. elliptica*.

Emu scats were overwhelmingly dominated by Ericaceae seeds, notably *L. nutans*, with > 1,000 seeds (on average) within an individual scat. There was no seasonal or site effect on the seed composition of emu scats. The availability of some *L. nutans* fruit into late October/early November (fruits develop usually in August; Chapter Three) may contribute to the amount of these fruits recovered in emu scats during early summer depositions. The germination of *L. nutans* seeds from the scats proved unsuccessful, and neither passage through the emu gut, nor the addition of heat, smoke, or both these elements, promoted germination. Even in for species evolved in a fire-prone landscape, fire alone is not the sole cue required for germination. For *L. nutans* (and other species adapted to fire), variations in seasonal temperatures and the application of smoke have been shown to promote germination (Ooi *et al.* 2006). For *L. nutans*, the emu likely acts as a disperser, rather than a facilitator of germination. Both heat and smoke were also found to be ineffective in promoting the germination of *P. elliptica* (Abbott and Van Heurck 1988).

The recapture of *M. riedlei* seeds tagged with radio transmitters was a useful method for assessing seed dispersal distances. However, the radio telemetry method of seed recapture proved cumbersome and is unlikely to result in reliable estimates of long distance dispersal (LDD). In comparison, the CTR method proposed by Hirsch *et al.* (2012b) was unable to be applied to the *M. riedlei* data in the seed removal experiment as no seeds were moved beyond the 10 m search radius.
6.4.1 Detecting animals that disperse or destroy seeds, and seed removal rates

The disperser assemblage for each plant species was relatively depauperate and the number of visitations to the study species at each site was low. The visitation rate of seed dispersers observed in the jarrah forest was comparable to rates reported by Corderio and Howe (2003), who observed diurnal visits occurring between 0.08 – 0.008 times per hour for fragmented submontane forests in Tanzania. Increased visitation rates were also noted in areas of continuous submontane forest, up to 0.23 visits per hour for a rich dispersal assemblage consisting primarily of small vertebrate birds (Corderio and Howe 2003). Seed removal rates, both from the cafeteria experiments and from camera trapping on plant canopies, was relatively low in comparison to other regions. Seed removal rates by vertebrate frugivores (and seed predators) in tropical areas are well established with reports spanning 0 to ~ 100% (Denslow and Moermond 1982; Jordano 1995; Korine et al. 2000; Bleher and Böhning-Gaese 2001; Smith and McWilliams 2014). Both field studies (Smith and McWilliams 2014) and simulation models (Carlo and Morales 2008) reveal that a number of complex factors impact fruit removal and frugivore visitation, and vary temporally and spatially.

There is a strong spatial context for plant-frugivore interactions and seed dispersal (Schurr et al. 2008). Plant neighbourhood density has been shown to significantly impact visitation and fruit removal rates. Generally, increasing neighbourhood density is correlated with increased removal rates, although there is a tipping point with removal rates beginning to decline at very high densities (Sargent 1990). There is a landscape effect too, where frugivore abundance and landscape aggregation of plants can override local neighbourhood density effects. Frugivore abundance has also been shown to interact with landscape structure to impact fruit removal rates, with zero fruit removal rates observed in both high and low frugivore abundance scenarios, depending on landscape structure within a simulated landscape (Carlo and Morales 2008). Considering the jarrah forest, small (or transient) populations of emus and other dispersers, coupled with extremely high local neighbourhood density of some key study species, may have contributed to the low removal rates observed, particularly at Sawyers Valley. The landscape effect is important, with over 25% of plants in an area with high disperser abundance showing zero fruit removal. While high density stands attract numerous dispersers, comparatively low density sites were not visited (Carlo and
Morales 2008). The random placement of cameras within an aggregated landscape, therefore, may have underestimated visitation if located within low density areas. The landscape-level aggregation of plants has been shown to create inequalities in fruit removal, with a strong dichotomy between plants with very high fruit removal rates and those with zero fruit removal rates (Carlo and Morales 2008). The local spatial aggregation observed for the study species in Chapter Five, which likely scales to the landscape-level, further accounts for the limited visitation and fruit removal observed at all study sites. This landscape-level aggregation effect may depend on the type of frugivore involved in dispersal. The emu, a terrestrial ratite, would travel long distances in an aggregated landscape to find resources, leaving decreased time available for foraging and fruit removal.

Schupp et al. (2010) argue that it is fundamental to know where seed disperser assemblages fit into the overall seed dispersal effectiveness (SDE) landscape, i.e., how effective seed dispersal agents are considering the quantity and quality components initially proposed in the SDE framework (Schupp 1993). The sampled emu scats clearly reveal that the emu is a highly effective seed dispersal agent for L. nutans, at least with respect to the quantity component, with over 1,000 fruits found within individual scats. In Chapter Four, it was revealed that 90% of L. nutans seeds within scats were potentially viable (with at least one of five locule positions being filled by a healthy embryo), reflecting a high quality component under the SDE framework. Overall then, the emu should be considered a very effective seed dispersal agent. Although the rate of capture on the footage appears very low, considering the high density of plants (particularly for L. nutans, where the density at Avon Valley is much greater than at Sawyers Valley; 0.4 ± 0.09 vs. 0.09 ± 0.02 individuals per m² respectively), there is an enormous seed load being deposited into the landscape. The importance of the emu to plant population dynamics is further extended considering their propensity to consume fruit and seed material from plants whose diaspores do not possess morphologies adapted for frugivory (Calviño-Cancela et al. 2006; Calviño-Cancela et al. 2008). However, we also need to consider a spatial context and loss of viability within emu scats. Substantial loss was observed following one year, so, in the absence of stochastic processes necessary for recruitment (namely fire), much of this seed load does not contribute to population recruitment.
The general absence of fire during the study period (other than those small areas experimentally burned) has likely led to the underestimation of visitation and seed removal rates for *M. riedlei* and *P. drouynianus*, for which seed production is stimulated by fire. For *P. drouynianus*, seed production is restricted the first few years following fire (Chalwell and Ladd 2005), and no seed production is observed in long unburnt stands (> 10 years without fire). Similarly for *M. riedlei*, seeds are generally produced 12 - 18 months following fire. Reproduction may be fitful, with mature plants coning after some fires but not others (Ornduff 1985; Ornduff 1991). This fire-stimulated reproduction may be considered as a form of masting; synchronous seed production that is common in conifers and other species. The mass seed production occurring during masting events both satiates seed predators and attracts dispersers, maximising dispersal outcomes for the species (Kelly 1994). Had fires occurred prior to the course of the study, then it is probable that a greater number of emus (and other dispersal agents) would have been captured via the camera surveillance.

### 6.4.2 Seed germination requirements

The impact of ingestion by frugivores on seed viability is reported to be highly variable (Meyer and Witmer 1998; Traveset 1998; Calviño-Cancela 2004; Bradford and Westcott 2010). There is limited knowledge on the impact of ingestion of seed by the emu on germination, although recruitment from emu scats has been observed in some jarrah forest species, including *P. elliptica*, and *L. nutans* (Bell *et al.* 1983; Abbott and Van Heurck 1988). Although not observed as part of formal emu scat assessments during this study, large amounts of *M. riedlei* and *P. drouynianus* seeds have been observed in emu scats (Burbidge and Whelan 1982; Chalwell and Ladd 2005). It is unlikely that ingestion by the emu itself promotes germination. McGrath and Bass (1999) observed very poor germination (< 15% after 70 days) for a mixture of native species retrieved from emu scats collected in south eastern Australia. However, Noble (1975) noted increased germination success for the Nitre Bush (*Nitraria billardieri*), attributed to removal of the pericarp. For the Nitre Bush, it appears that ingestion and defecation is sufficient to break the dormancy of the seed. For the seeds of other species that exhibit physical dormancy (including the key species of this study), ingestion alone may not be enough, especially for those species with thick seed coats (Baskin *et al.* 2000). Species that have evolved in fire-prone landscapes, like southwestern Australia, require fire or smoke (or some combination of the two) to
promote germination. Following ingestion and excretion by frugivores, fire is required to promote germination, with frugivory useful for dispersal but not for germination.

6.4.3 Estimating seed dispersal distances - *M. riedlei* case study

Estimating seed dispersal distances, particularly long distance dispersal (LDD), and generating seed dispersal kernels are critical if we are to better understand the importance that frugivore-seed dispersal relationships play in plant population dynamics (Cain *et al.* 2000). While many methods exist to estimate LDD and seed dispersal in general, including but not limited to direct tagging with thread (Hirsh *et al.* 2012a), the use of radio isotopes (Nathan *et al.* 2003), genetic methods (Heuertz *et al.* 2003) and the use of mechanistic models (Bullock and Clarke 2000), radio telemetry has previously been used as a non-invasive method for ratites (Mack and Druliner 2003). Apart from the consumption of a single seed with radio transmitter by an emu, only the Australian raven dispersed seeds beyond the immediate vicinity (> 10 m) of parent plants. It would be erroneous to suggest that the raven is the sole LDD vector for *M. riedlei*, and for the reasons outlined above, it is likely that the emu was underrepresented in the dispersal assemblage for *M. riedlei*.

In the instances where coning occurs in the interfire period (Ornduff 1991), a dispersal assemblage remains that is capable of LDD, as the raven transports individual *M. riedlei* seeds some hundreds of metres from the parent plant. Substantial local dispersal will also occur in coning events during the interfire period as kangaroos strip seeds of their sarcotesta and deposit them *in situ*. High levels of local dispersal have been observed for *M. riedlei* (Burbidge and Whelan 1982), which may not be expected to have negative demographic consequences, as seeds that are usually deposited in clumps may have evolved resilience to density-dependent effects (Howe 1989). Clearly though, in the SDE framework (Schupp 1993; Schupp *et al.* 2010), the raven is not an effective seed dispersal agent with regard to the quantitative component of the landscape. Seed dispersal by the raven during the interfire period is ancillary and probably has a limited impact on overall *M. riedlei* population dynamics.
6.5 CONCLUSIONS

The camera trapping and seed cafeteria experiments revealed a depauperate disperser assemblage for several large-seeded species within the jarrah forests. Observed consuming the fruits of three of the target species, and noted for consuming the fruits of *P. elliptica* (Abbot and Van Heurck 1988), the emu is clearly an important LDD vectors of seeds and fruits of these and many other species. The few fruits and seeds consumed by the emu per plant before moving on to continue foraging suggests that a single emu scat contains a wealth of genetic diversity, paramount in healthy plant population structures (Jordano *et al.* 2007). Given the large number of seeds contained within the scats of emu, attention needs to be given to clarifying to what extent the emu contributes to dispersal, particularly LDD, for species within the jarrah forest. This requires an investigation in to how the emu moves through the jarrah forest and a determination of the factors that influence emu behaviour.

Chapter Seven presents a method for, and the results of, movement tracking of emus within the jarrah forests of southwestern Australia. By using Global Positioning System (GPS) technology, the trajectories of GPS tagged birds are analysed to elucidate their movement and contribution to seed dispersal under the movement ecology paradigm.
CHAPTER SEVEN
EMU MOVEMENT ECOLOGY

ABSTRACT

GPS (Global Positioning System) technology for tracking wildlife continues to evolve at a remarkable pace. As animal movement is increasingly recognised as being critical for a number of ecological processes, advanced telemetry technology permits the collection of a great volume of data at short intervals that was previously unobtainable.

Here the use of GPS telemetry to track the movements of five tagged emus (*Dromaius novaehollandiae* Latham) released within the jarrah (*Eucalyptus marginata* Sm.) forests of southwestern Australia is described and their habitat preferences investigated. Using the GPS data, the potential contribution of the emu to long distance dispersal (LDD) was investigated. The emu plays a significant role as a seed disperser for many species.

Describing the movement patterns of this species is a key requirement in refining the extent and significance of its contribution to seed dispersal, both locally and over long-distances. It was found that emus demonstrated a nuanced response to the landscape in terms of behaviour, extent of movement and habitat selection. The emu is clearly an important long distance dispersal vector, easily moving ca. 2 km (Euclidean distance from a starting point) over the course of a few hours. The value of the emu as a highly effective seed dispersal vector within increasingly fragmented habitats is diminished when a moderate amount of seeds may be deposited into areas unsuitable for recruitment. Tagged birds showed a preference for agricultural land, the forest edge and road verges; environments in which germination and recruitment of native forest species are unlikely. From a methodological perspective, 50% of GPS devices detached before 30 days of GPS locations could be collected, reflecting a need for device refinement for future studies on large ratites. Nevertheless, the data provides useful insights into the movements of the emu and potential impacts on seed dispersal within the jarrah forests.
7.1 INTRODUCTION

The movement of organisms plays a key role in ecosystem dynamics. Movement itself is both an outcome and underlying character of many ecological processes. Seed dispersal is fundamentally important for plant demography and many key ecological processes driving the dynamics of communities and ecosystems (Howe and Smallwood 1982). It is the primary process of movement during the life-cycle of plants, leading to establishment of next-generation individuals both near and far from parents (Nathan 2006).

Recent technological and affordability advances in GPS (Global Positioning System) technology have allowed researchers to gain insights into organism movement and examine the links between movement and ecosystem processes. Similarly, there have been theoretical advances in the epistemology for assessing the significance of organism movement. The movement ecology paradigm (Nathan et al. 2008a), is an inclusive framework that asks where, why, how and when organisms move. The framework also recognises the impact of external states on the internal states of the organisms, which ultimately drives movement. In presenting these questions, movement ecology requires us to have an integrative understanding of the causes of, the consequences, and the linkages between the two, of organism movement (Nathan et al. 2008a).

Given that seed dispersal is integral to plant population dynamics, including population growth and resilience, the link between the movement of frugivores and seed dispersal is paramount to having a clear understanding of plant demography. Additional to the movement ecology paradigm, Schupp (1993) and Schupp et al. (2010) present and then review a useful framework for assessing seed dispersal effectiveness (SDE). SDE investigates the quantity and quality of seed dispersal, i.e. how much seed is dispersed (qualitative) and the probability that a dispersed seed produces a new adult (quantitative). An important addition to the SDE framework by Spiegel and Nathan (2007) is the consideration of dispersal distances. Overall, seed dispersal effectiveness may be greater and has a more substantial impact on ecosystem dynamics at the metapopulation and long distance dispersal (LDD) scale, in contrast to local dispersal (Spiegel and Nathan 2007). By using GPS telemetry, the movement ecology and SDE frameworks, inferences can be made on the impact of movement and seed dispersal on plant population dynamics.
Null models of animal movements such as simple random walks, correlated random walks (CRW), biased random walks (BRW) and Lévy walks have been used to describe animal movement and provide a basis from which ecological inferences can be made (Turchin 1998). In particular, the seminal paper of Kareiva and Shigesada (1983) reveals how the net squared displacement between successive animal relocations (determined by GPS or otherwise) can be used to make meaningful inferences about animal behaviour using a CRW as a null model. Many authors have taken this approach (e.g. Bailey and Thompson 2006) and successfully applied CRW models to animal movement and explored causative departures from them. Although other models of movement have been used, in particular the BRW, Lévy walk and their subcategories, the CRW provides a useful starting point for analysing animal movement. Applying CRW models to frugivore movement provides a pathway for increased understanding of the links between movement and seed dispersal.

Seed dispersal is typically characterised through dispersal kernels, which are one-dimensional probabilistic curves that describe the likelihood of a quantity (or proportion) of seed being dispersed a given distance (Morales and Carlo 2006). To generate such kernels for frugivorous dispersal, a general model of dispersal needs to be constructed, which requires either empirical or mechanistic understanding of seed load, gut retention times and displacement velocity (movement) (Nathan et al. 2008b; Tsoar et al. 2011). These important elements, as they relate to the emu, have been dealt with in some complexity and detail in the literature: the diet of the emu has been extensively studied, and the ability of the emu to consume large amounts and variety of seed material is well known (Noble 1975; Davies 1978; Quin 1996; Davies 2002; Dunstan et al. 2013). The emu can deposit large amounts of seed in an individual scat, a common observation for large frugivores (Howe 1989; Bradford and Westcott 2010). The retention of material within the gut of the emu has also been examined. Davies (1978) reports some material passing through the gut in as little as 3 hrs, with retention times ranging between 4 and 48 hrs for material consumed at the same event. Davies (1978) also reports some material being held for > 100 days. Herd and Dawson (1984) report a mean gut retention time (GRT) of 5.5 hrs for the solid phase of fibrous material digested, and Wilson (1989) reports GRTs for the consumption of pseudoseeds of 1 - 2 days. Allometric estimations of GRT from body size (Robbins 1993) suggest a mean GRT of ca. 5 hrs. Although mean estimates of gut retention time may appear relatively short, it is the rarer events, held within the gut for sustained periods, which contribute to long distance dispersal (LDD), which is a key driver of plant population dynamics (Nathan 2006).
The emu possesses unique traits that make it a key seed dispersal agent, particularly within the jarrah forests of southwestern Australia, where up to 22% of the flora has developed vertebrate dispersal mutualisms (Willson et al. 1990). The emu is also an important non-standard dispersal agent for plants that have not evolved traits for dispersal by frugivores, as it ingests seeds of many species with various dispersal morphologies (Calviño-Cancela et al. 2006; Calviño-Cancela et al. 2008). The final component of a general model to describe seed dispersal, animal velocity/movement, has not been previously investigated in detail as it applies to the emu. Although allometric means are available to describe animal velocity (Calder 1996), system-specific empirical data is preferred where available. Davies et al. (1971) recount the visual recapture of banded emus moving through the arid and semi-arid zones in Western Australia, suggesting some birds are capable of moving many hundreds of kilometres over the course of a few months. However, this method lacks definition, with many weeks passing between observations. The movement patterns and extent of emus in arid areas may differ markedly from those in more resource-rich forest locations. While general descriptions of emu behaviour also exist (Curry 1979; Patodkar et al. 2009), no study to date has used modern and emerging technologies to elucidate the patterns of emu movement and behaviour. The use of new animal tracking technologies, particularly for other ratites, has already been invaluable in understanding individual behaviours, habitat preferences and aiding conservation management (Campbell et al. 2012). This chapter seeks to explore patterns of emu movement and the implications for seed dispersal.

The aims of this chapter are to:

1. Describe the methodology for the tagging and monitoring via GPS of captive emus released into the jarrah forests.
2. Analyse the movement trajectories of captive emus released into jarrah forest using a correlated random walk model at both
   a. Short (daily) spatiotemporal scales and,
   b. Long (whole of trajectory) spatiotemporal scales.
3. Determine the preferred habitat-type of emus from broad classifications within the jarrah forest/agricultural landscape.
4. Using the detailed movement information from (2) and habitat preference information from (3), examine the potential contribution of the emu to LDD.
7.2 MATERIALS AND METHODS

7.2.1 GPS tracking of emu movement

Emu activity was characterised by following the movements of individual birds using GPS (Global Positioning System). The design and implementation of the study was carried out in accordance with guidelines by the National Health and Medical Research Council (NHMRC; 2013). It was not feasible to capture wild birds in jarrah forest for GPS-tracking owing to their elusive behaviours, speed and resistance to anaesthetics (Dr. Tim Oldfield, pers. comm.). A pilot trial was conducted at the Clackline Free Range Emu Farm near Toodyay, Western Australia, on two captive birds from December 2012 to February 2013 to ensure the efficacy of the attachment cuff, that emu movement and behaviours were not impeded and that the cuffs did not cause injury or irritation. Birds at the farm are free to roam around large fenced paddocks and forage for food from native vegetation as well as supplementary stock feed. Captive-reared ratites have been shown to use habitat in the same manner as their wild-born counterparts (Bellis et al. 2004). GPS tracking devices were custom made by Telemetry Solutions USA following a design used on another large ratite, the Southern Cassowary (Casuarius casuarius) (Campbell et al. 2012). The total weight of the GPS-tracking unit and attachment cuff was 310 g, < 1% of the weight of the adult birds used in the study. Tracking cuffs were secured above the ankle joint (Plate 7.1) using non-UV resistant tie-wraps, designed by the manufacturers to degrade and detach within 1 year. Males on average weigh 31.5 kg and females 36.9 kg (Davies 1967). During March 2013, six birds were selected from the adult cohort at the Clackline Free Range Emu Farm for the study. The birds were transported in a custom-designed emu trailer and released into the Avon Valley National Park area in southwestern Australia, an area of typical jarrah forest. The entire tagging, transport and release process was overseen by a consultant avian veterinarian. The six birds used in the study were not sexed at the time of GPS attachment due to the difficulty in sex determination and to minimise the time taken to physically restrain the birds. Attempts were made to sex the birds via their calls (as per Curry 1979), however this was unsuccessful.

The GPS download schedule varied from short intervals (data collected every 15 minutes) to long intervals (data collected every hour) as a trade-off between definition of movement information and battery conservation. Expected battery life was approximately 18 months. The GPS tracking unit contained both a VHF transmitter for locating the birds and a UHF transmitter for data transfer. Each device contained a unique VHF frequency so that
individual birds can be tracked via the use of an antenna (a simple 3-element Yagi mounted on a vehicle).

Plate 7.1 Attachment of the cuff above the ankle joint of a released emu

7.2.2 Data analysis

General trajectory selection

The adehabitatLT package (Calenge 2006) within R version 2.15.2 (R Core Team 2012) was used to examine the parameters of the trajectories for each of the tagged birds. For each of the birds, a trajectory was built that consisted of regular, 24 hr or 15-minute time tags between relocations. Differentiation in treatment of the temporal detail did not substantially impact the overall path characteristics, which can be seen in Figure 7.1 (Results). As the main aim of the GPS tracking was to examine emu movement as it relates to potential LDD, initially selecting a daily (24hr) relocation interval of analysis is appropriate.

Walk analysis

The net squared displacement (R\textsuperscript{2}_n) was used as the path characteristic to compare the trajectories of each of the birds to a correlated random walk (CRW; Kareiva and Shigesada 1983). The net displacement is the straight-line distance between the commencement and end of a path. CRW models are typically used to examine the trajectories of animals, from
small insects (Brouwers and Newton 2010) to large aquatic and terrestrial mammals (Bergman et al. 2000; Bailey and Thompson 2006). Comparison of animal trajectories to a CRW model (via $R^2_n$) may provide useful information about directional persistence in animal movement and useful insights into general behaviour (Turchin 1998). The $R^2_n$ in a CRW is expected to grow linearly with time. The directional movement persistence assumed under the CRW is accounted for in the model based on turning angles between successive moves. As a result, the CRW assumes a unimodal and symmetric (around zero) distribution of turning angles. Step length/speed and turning angles should not be serially correlated. Both Turchin (1998) and Dray et al. (2010) suggest that this should be tested statistically. Two general approaches were taken in examining the emu trajectory data. Firstly, the emu relocations were split into 24hr ‘steps’ for a broad examination of emu movement and the applicability of a CRW model over a large scale. Secondly, the emu relocation data were analysed at hourly or 15-minute intervals, to determine the utility of the CRW at a fine spatiotemporal scale.

Correlated random walk over a large (monthly) scale

For the emu data, each relocation (or move) was defined as a 24 hr step, with the time of day from which successive steps were drawn selected from that which resulted in the longest regular path length from the available data for each bird. An autocorrelation function (ACF) in the adehabitatLT package (Calenge 2006) was used to examine the potential correlations between step-length and turning angles. A permutation approach was used to examine for autocorrelation in step lengths, up to a lag of 6 days. Although the details of the randomisation process are presented in detail in Dray et al. (2010), the basic procedure was to compute a reference value of the step length $S_L$ using the original data, then randomly permute $S_L$ values and recompute the statistic for the desired number of permutations (here, n = 999). The permutations provided a set of step length values under the null hypothesis of independent lengths. The observed step length was then compared to the set of values produced by the permutations. A similar permutation procedure was used to examine autocorrelation in turning angles, with the chord distance between successive relocations examined. The chord distances are expected to be low when successive turning angles are similar (Calenge et al. 2009; Dray et al. 2010). For both step length and turning angles, correlograms were generated from the permutations to check for any potential significant correlations. Potential autocorrelations in missing values were examined with a runs test.
using 999 replications (Calenge 2006). Significant autocorrelations in missing values within bursts of relocations are reported where identified.

Expected values of $R^2_n$ (km) for the trajectories of each bird were calculated using the equations provided by Kareiva and Shigesada (1983) and corrected in Turchin (1998; Equation 1):

**Equation 1.** Expected net-squared displacement ($R^2_n$) for a correlated random walk (Kareiva and Shigesada 1983; Turchin 1998).

\[ R^2_n = nL_2 + (2L_1^2)(c/(1-c))(n-(1-c)n/(1-c)) \]

$L_1$ = mean move length (per day, here in km)
$L_2$ = mean squared move length (per day, here in km$^2$)
$n$ = number of consecutive relocations
$c$ = mean cosine of the turning angles

95% CI intervals of the expected $R^2_n$ were also calculated from methods as described in Turchin (1998). Plots of the observed displacement against the expected displacement were visually assessed to examine how the trajectory of each emu fit the CRW model. Biased random walk (BRW) models, where $R^2_n$ increases more than expected under a CRW model were not considered as a result of initial checks of the suitability of the CRW models.

**Correlated random walk over a small (daily) scale**

GPS data from each bird was pooled for the analysis of the emu movement data recorded at a high temporal frequency (every 15 minutes and over 1 hr). Analysis was conducted as described above. Autocorrelation was calculated up to 1 hr (for the 15-minute intervals) and 4 hours (for the hourly interval data). Correlograms reporting the significance of autocorrelation in step length and turning angles are not presented, though any significant autocorrelations within the 15 minute or hourly burst data are reported.

**Nocturnal movement analysis**

Using the movement data pooled across each bird, the straight-line distance between the last evening GPS point (1830H) and the first morning GPS point (0630H) point was calculated.
The first and last GPS points taken during the day reflect the approximate sunrise and sunset times for the Avon Valley National Park during the period for which GPS data were collected. The average distance between these evening and morning fixes was calculated to provide an estimate of nocturnal movement for the emu overall.

Habitat use

The number of relocations within each habitat type were calculated to provide a proportional indication of the time spent within each area. Habitat was classified as either forest, agricultural land, edge (within 50m of forest/farm edges) or road (on or within 25m of unsealed roads). The approximate area of each habitat type within the convex hull of all GPS locations was also determined.
7.3 RESULTS

7.3.1 Emu transport and release

Five of the six emus were successfully tagged, transported to Avon Valley National Park and released. For the remaining bird, the GPS tracking device detached from the attachment cuff during transportation. Two GPS units detached ca. 2 weeks following field deployment (Emu 4 and Emu 5, see Table 7.1). These two GPS devices were retrieved from the field and movement data downloaded. Damage to the cuff and location of the find indicated that the units had detached after becoming caught on agricultural fences.

During the first few weeks, each of the birds had moved different distances from the release site (Figure 7.2). After the first week, emu 4 had moved ca. 8 km from the release site and emu 5 ca. 6 km. The other birds remained within 2 km of the release point. Over the first two weeks, each bird was observed on several occasions to ensure that the GPS cuff was not impeding movement or affecting other behaviours. As per the pilot trial, the movement of the birds showed no obvious signs of impediment and each individual was observed standing, walking, running and foraging. Each bird was also observed foraging in close proximity to wild emus found within the Avon Valley. Locating the birds using radio telemetry to download GPS data was difficult, with the last successful download of data ca. 2 months following field deployment (Table 7.1). Overall, performance of the devices was satisfactory, with the horizontal dilution of precision across all units < 2 (Table 7.1).

The movement trajectory of each bird was varied (Figure 7.2). The convex hull of the GPS points recorded for all birds was ca. 75km$^2$. Within this area, 75% of the landscape could be classified as forest (primarily jarrah forest, with small pockets of *Eucalyptus wandoo*), 19% as agricultural, 5% as forest edge and 1% as roads (Table 7.2). The trajectories also show that the birds readily moved between these distinctive habitats (Figure 7.2). There was clear evidence that the birds followed fence lines that divide the Avon Valley forest remnants and the surrounding mosaic of agricultural land. 23% of the GPS locations were recorded on roads/along fence lines or in jarrah forest within 100m of agricultural land. Generally the birds preferred to remain within the forest (41% of GPS points were recorded in the forest habitat), however, they did visit permanent water sources in neighbouring agricultural fields (Table 7.2). Four of the five tagged emus showed a general trajectory bias in their movements, favouring a north-west path. Steep slopes and deep valleys were avoided and no
bird entered the valley through which the Avon River flows (Figure 7.2). Nocturnal movement was minimal, with the mean step-length during the nocturnal period (1830H – 0630H) 13m/hr (± 6). Comparatively, the median step-length during the diurnal period was 150m/hr (± 20).

![Figure 7.1](image)

**Figure 7.1** The (a) regular daily relocations recorded for emu 2, where 24 hrs has elapsed between each point. In contrast to (b), all recorded GPS relocations, where the time-lag between each point is variable (from 10 minutes to ca. 24 hrs). The red triangles and squares indicate the start and end of the trajectories, respectively. The x- and y-axes are the eastings and northings, respectively.

**Table 7.1** Number of relocations (GPS positions) following the initial release of 5 emus into Avon Valley, Western Australia. 'NA dist' refers to the distribution of missing values during n bursts for each trajectory. The horizontal dilution of precision (HDOP) for each bird is also shown. Numbers in parentheses are the 95% CI

<table>
<thead>
<tr>
<th></th>
<th>n relocations</th>
<th>start</th>
<th>finish</th>
<th>NA dist</th>
<th>n bursts</th>
<th>HDOP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emu 1</td>
<td>374</td>
<td>27/03/2013</td>
<td>25/04/2013</td>
<td>random</td>
<td>33</td>
<td>1.7 (± 0.1)</td>
</tr>
<tr>
<td>Emu 2</td>
<td>663</td>
<td>27/03/2013</td>
<td>13/05/2013</td>
<td>random</td>
<td>60</td>
<td>1.9 (± 0.1)</td>
</tr>
<tr>
<td>Emu 3</td>
<td>611</td>
<td>27/03/2013</td>
<td>13/05/2013</td>
<td>random</td>
<td>53</td>
<td>1.9 (± 0.1)</td>
</tr>
<tr>
<td>Emu 4</td>
<td>283</td>
<td>27/03/2013</td>
<td>13/04/2013</td>
<td>random</td>
<td>20</td>
<td>1.8 (± 0.2)</td>
</tr>
<tr>
<td>Emu 5</td>
<td>199</td>
<td>27/03/2013</td>
<td>13/04/2013</td>
<td>random</td>
<td>17</td>
<td>1.7 (± 0.1)</td>
</tr>
</tbody>
</table>
Figure 7.2 Movement paths for (a) emu 1 – 30 days, (b) emu 2 – 48 days, (c) emu 3 – 48 days, (d) emu 4 – 17 days and (e) emu 5 – 17 days, in the Avon Valley National Park, southwestern Australia. The red triangles and squares indicate the start and end of the trajectories respectively.
Table 7.2 Percentage of GPS fixes recorded for emus in different habitat-types classified in Avon Valley, Western Australia. Also presented is the percentage habitat-type cover estimate calculated from the convex hull of all GPS points. Numbers in parentheses indicate 95% CI

<table>
<thead>
<tr>
<th>Habitat</th>
<th>% Habitat Cover</th>
<th>Emu 1</th>
<th>Emu 2</th>
<th>Emu 3</th>
<th>Emu 4</th>
<th>Emu 5</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>75%</td>
<td>13%</td>
<td>45%</td>
<td>54%</td>
<td>59%</td>
<td>32%</td>
<td>41% ± (16)</td>
</tr>
<tr>
<td>Agricultural</td>
<td>22%</td>
<td>67%</td>
<td>2%</td>
<td>24%</td>
<td>26%</td>
<td>10%</td>
<td>26% ± (12)</td>
</tr>
<tr>
<td>Edge</td>
<td>2%</td>
<td>19%</td>
<td>25%</td>
<td>9%</td>
<td>8%</td>
<td>52%</td>
<td>23% ± (16)</td>
</tr>
<tr>
<td>Road</td>
<td>1%</td>
<td>1%</td>
<td>28%</td>
<td>13%</td>
<td>7%</td>
<td>6%</td>
<td>10% ± (9)</td>
</tr>
<tr>
<td>Total Area</td>
<td>~ 75km²</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

7.3.2 Correlated random walk over a large (monthly) scale

Autocorrelation in step length

First- and higher-order correlations in step length were found for two of the five birds (Figure 7.3b and 7.3e), which suggests a violation of the CRW model criteria. It is possible that this reflects the arbitrary splitting of the tracking data, resulting in under-sampling of the move lengths. There was no significant autocorrelation in step length detected via the permutation process for the remaining birds.
Figure 7.3 Correlogram of step lengths [$S_L(\text{day})$] (in metres·day$^{-1}$) for (a) emu 1, (b) emu 2, (c) emu 3, (d) emu 4 and (e) emu 5, released into the Avon Valley National Park, southwestern Australia. Note the different scales for the autocorrelation values. The gray area corresponds to a 95% CI obtained by a permutation procedure (999 permutations) described in Calenge et al. (2009). The gray dotted lines are the medians of the values of the statistic computed on the permuted data. Empty circles represent non-significant autocorrelation, while the black filled squares represent significant values.

**Autocorrelation in turning angle**

One of the birds exhibited high-order autocorrelation in turning angles between relocations (Figure 7.4a; emu 1), a violation of one of the CRW assumptions. The remaining birds
showed no significant autocorrelation in turning angles. Together, these results indicate that for the five emus, only two (emu 3 and emu 4) met the requirements of the CRW model formulation.

Figure 7.4 Correlogram of successive turning angles $[T_{A}(day)]$ (in radians $^{day}$) for (a) emu 1, (b) emu 2, (c) emu 3, (d) emu 4 and (e) emu 5, released into the Avon Valley National Park, southwestern Australia. The gray area corresponds to a 95% CI obtained by a permutation procedure (999 permutations) described in Calenge et al. (2009). The gray dotted lines are the medians of the values of the statistic computed on the permuted data. Empty circles represent non-significant autocorrelation, while the black filled squares represent significant values.
**Net squared displacement**

For the majority of the birds, the net squared displacement ($R^2_n$) predicted under the CRW accorded with the observed displacement (Figure 7.5b - 7.5e). For each bird, there were periods during which $R^2_n$ did not substantially increase over time. Generally, for the first 5-10 days, the observed $R^2_n$ was lower than that predicted by the CRW model, which then increased in line with the predicted displacement of the model. The displacement of emu 1 was commonly below that predicted by the model, with only four of the relocations within the confidence error of $R^2_n$ displacement (Figure 7.5a). Emu 1 also had an observed $R^2_n$ orders of magnitude lower than the other birds.
Figure 7.5 The relationship between the net-squared displacement ($R^2_n$) (km$^2$) for a correlated random walk and the number of consecutive daily moves made for emus released into the Avon Valley, southwestern Australia. Note the different scale for consecutive moves and net displacement for (a) emu 1, (b) emu 2, (c) emu 3, (d) emu 4 and (e) emu 5. Dashed lines indicate the 95% CI of displacement, calculated following Turchin (1998)
7.3.3 Correlated random walk over a small (daily) scale

From the relocation bursts where locations were recorded every 15 minutes, the CRW model significantly under-predicted net squared displacement ($R_{n}^{2}$; Figure 7.6a). In contrast, observed $R_{n}^{2}$ for the hourly-interval (~daily) data accorded well with predictions under the CRW model (Figure 7.6b).

Though most of the steps taken within the 15 minute time period were < 100m, a number of larger steps during this period was also observed (> 300m; Figure 7.8b). The median and maximum step length noted from the 15 minute interval data were 50 m and 642 m respectively. The maximum Euclidean distance from the starting point (the square-root of the net displacement) was 1407 m (Figure 7.6a). The median and maximum step length noted from the hourly interval data were 150 m and 2172 m respectively (Figure 7.7d). The maximum Euclidean distance from the starting point from the hourly interval data was 1695 m (Figure 7.6b). The turning angles for both the 15 minute and hourly-interval data was distributed approximately around 0 radians (Figure 7.7a & 7.7b).

There were a number of significant autocorrelations in turning angle and step length (up to a lag of 1 hour) in the 15 minute and hourly-interval data. There was no significant autocorrelation in the missing values (Table 7.3).

![Figure 7.6](image)

**Figure 7.6** The relationship between the net-squared displacement ($R_{n}^{2}$) (m$^2$) for a correlated random walk and the number of consecutive daily moves made for emus released into the Avon Valley, southwestern Australia. (a) 15 minute step intervals and (b) hourly step intervals. *Dashed lines* indicate the 95% CI of displacement, calculated as per Turchin (1998)
Table 7.3 Number of bursts (from data collected at 15-minute and hourly intervals) for each emu tracked at Avon Valley, southwestern Australia. The number of bursts in which significant auto correlation was identified via a permutation test (Calenge 2006) are reported.

15-minute interval burst autocorrelations

<table>
<thead>
<tr>
<th>Emu</th>
<th>$n$ total bursts</th>
<th>$n$ bursts with auto correlated step length</th>
<th>$n$ bursts with auto correlated turning angles</th>
<th>auto correlated missing values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emu 1</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>×</td>
</tr>
<tr>
<td>Emu 2</td>
<td>7</td>
<td>1</td>
<td>2</td>
<td>×</td>
</tr>
<tr>
<td>Emu 3</td>
<td>7</td>
<td>5</td>
<td>2</td>
<td>×</td>
</tr>
<tr>
<td>Emu 4</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>×</td>
</tr>
<tr>
<td>Emu 5</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>×</td>
</tr>
<tr>
<td>Subtotal</td>
<td>25</td>
<td>10</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

Hourly interval burst autocorrelations

<table>
<thead>
<tr>
<th>Emu</th>
<th>$n$ total bursts</th>
<th>$n$ bursts with auto correlated step length</th>
<th>$n$ bursts with auto correlated turning angles</th>
<th>auto correlated missing values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emu 1</td>
<td>20</td>
<td>1</td>
<td>5</td>
<td>×</td>
</tr>
<tr>
<td>Emu 2</td>
<td>40</td>
<td>15</td>
<td>12</td>
<td>×</td>
</tr>
<tr>
<td>Emu 3</td>
<td>33</td>
<td>10</td>
<td>4</td>
<td>×</td>
</tr>
<tr>
<td>Emu 4</td>
<td>9</td>
<td>3</td>
<td>1</td>
<td>×</td>
</tr>
<tr>
<td>Emu 5</td>
<td>13</td>
<td>5</td>
<td>4</td>
<td>×</td>
</tr>
<tr>
<td>Subtotal</td>
<td>115</td>
<td>34</td>
<td>26</td>
<td></td>
</tr>
</tbody>
</table>
Figure 7.7 Distribution of (a) turning angles (in radians) and (b) step length (m) for telemetry data with 15-minute relocation intervals collected from emus released into southwestern Australia. Similarly, (c) and (d) represent the distributions of these data collected from hourly intervals.
7.4 DISCUSSION

The aim of this chapter was to describe the general utility of GPS telemetry applied to emus and to explore emu movement and link this to seed dispersal (particularly LDD; Nathan 2006) and overall seed dispersal effectiveness (Schupp 1993; Schupp et al. 2013). It is argued that, although difficult to implement and maintain, GPS telemetry is a useful method for analysing emu movement and applying movement models to emu behaviour and potential seed dispersal. Emus were capable of moving long distances (up to several kilometres) over a short time period (a week), potentially contributing to the LDD of many species. However, overall seed dispersal effectiveness may be diminished slightly, with some seed material presumable deposited within agricultural land, along roads or within the forest fringe.

7.4.1 GPS telemetry efficacy

Described here are the findings of the application of GPS telemetry to captive (semi-habituated) emus released into natural bush to better understand their movement ecology as it relates to seed dispersal of large-seeded species of jarrah forests. The use of GPS telemetry to describe the behaviours of ratites is an emerging field of investigation in animal ecology (see Campbell et al. 2012). GPS telemetry, when analysed using advanced animal movement software (Calenge 2006; Calenge et al. 2009) permits detailed investigation of fine and landscape-scale movements and the feedbacks between habitat selection and general behaviours.

Data presented in this chapter highlight the utility of GPS telemetry to elucidate the movement ecology of a large ratite, whose movement had only previously been described from traditional bird banding methods, with weeks or months passing between observations (Davies et al. 1971). While Davies et al. (1971) provide interesting insights into general emu ecology, they do not provide enough quantitative detail to be readily used in models of seed dispersal. Seed dispersal is a critical process in the lifecycle of plants and has the potential to shape the distribution and structure of populations (Levine and Murrell 2003). Moreover, the spatial patterns of seed dispersal and recruitment are increasingly recognised as paramount to plant population dynamics (Nathan and Muller-Landau 2000). Without fine-scale data on the movement of the emu, or indeed any significant dispersal agent within a system in which strong seed dispersal mutualisms exist, it is difficult to quantify the impact of the agent on dispersal.
The emu is already known to be a potentially important dispersal agent for species that have endozoochorous dispersal morphologies, as well as for others that do not have adaptations for dispersal by frugivores (Calviño-Cancela et al. 2006). The emu's generalist diet (Dunstan et al. 2013) makes it an ideal general seed disperser, and likely contributes to the population dynamic behaviour of many plant species. Although the outcome of seed passage is equivocal for fruits consumed by many ratites, with some species benefiting from ingestion while others suffer reduced seed viability, the sheer volume of material consumed makes these large birds very important for seed dispersal (Noble 1975; Bradford and Westcott 2010). Moreover, the clumped deposition of seeds within scats provides a beneficial environment for the germination and survival of new recruits (Howe and Smallwood 1982; Howe 1989).

Overall, the tagging of emus with GPS telemetry devices similar to those used by Campbell et al. (2012) for the cassowary was, at least in the short term, an effective telemetry method for collecting movement data. However, the use of this method of attachment for long term investigations on animal movement should be cautioned. Within the first month, 50% of devices were lost, with one detaching during transport and two others being removed, presumably after being caught on a fence. As devices were designed to detach following 12 months of use through UV deterioration and wear and tear, the conservative method of attachment to ensure no harm may have contributed to the early loss of these devices.

7.4.2 General movement paths and habitat use

Despite the unexpected early loss of devices and the difficulty in longer-term data collection, enough telemetry data were collected to provide some useful insights into the movements and habitat-selection by the emus. The observed trajectories for each of the released birds and the GPS tracking data generally shows a pattern of movement that is consistent with correlated random walks (Bovet and Benhamou 1988). The comparison of movement of an organism (via net displacement) to null models allows for inferences to be made about organism behaviour. Organism movement typically reflects correlated random walks where foraging and other behaviours reduce the expected mean squared displacement distance, which was observed in the data. It is important to note that while some interest has developed in the application of Lévy walks (Viswanathan and Afanasyevt 1996) to animal movement data to describe the pattern of movement (Benhamou 2007; Reynolds 2008), it is not the aim here to assess the utility of the various movement models. Seed rain pattern, the spatial fingerprint
of the seed dispersal process by frugivores, is impacted by seed dispersal distances (movement following ingestion), disperser activity and habitat structure within the landscape (Rodríguez-Pérez et al. 2012a). These data highlight the nuanced response to the landscape that individual frugivores demonstrate, and that may have an important impact on seed rain and subsequent plant population dynamics. Habitat preference by frugivores has been shown to vary with scale, with local preference given to resource-rich areas that promote foraging behaviours, though these local preferences become diluted at a landscape scale when environmental conditions (e.g. steep slopes/impassable areas) preclude or limit access (Rodríguez-Pérez et al. 2012a). The trajectories of the emus highlight the preference that the emu has for remaining within the forest and forest fringes in a dichotomous landscape split between natural bushland and agricultural areas, although the emus did spend some time foraging for fodder within the agricultural matrix.

Nevertheless, important data have been captured on the movement of emus within the jarrah forests of southwestern Australia to a level of detail that has not been described before. The movement of these birds over short time periods has been shown to be substantial and, considering their potentially large gut retention times, underscores the important role they play as a seed dispersal agent for many plant species. This likely indicates periods of local foraging, where birds travel short distances over an extended period of time and is notably different to those periods where MSD increased sharply over short time scales, when the birds were generally moving between foraging locations. This general behavioural split between local foraging and broader-scale movement is seen in the individual bird trajectories.

7.4.3 Correlated random walk

There are some difficulties in interpreting the movement of the birds released into the Avon Valley National Park that should be noted. Recent work by Nams (2013) suggests that the segmentation of continuous movement paths can have substantial impacts on CRW model interpretation. Segmentation of a continuous path into very short steps further increases the likelihood in correlation between the turning angle and step lengths of successive relocations; two parameters that should be independent under a CRW model (Turchin 1998). The rejection of a CRW model may arise as a result of bias in the movement path arising from step segmentation, rather than an underlying biological mechanism (Nams 2013). The interval between recorded relocations has been shown to be critical in determining the impact of landscape on animal movement (Thurfjell et al. 2014). The scale over which the
observations were made may result in a limited understanding of the continuing trajectories developed by each bird. The spatio-temporal scale may generally affect the utility of the CRW model, with CRW models decaying to random walk processes at large scales. The interval between successive relocations should reflect the behaviour of interest and over the time period in which it occurs (Thirfjell et al. 2014). In this chapter, movement was analysed from data collected over bursts from short time periods (ca. 6hrs) from fine-scale relocations (every 15 minutes) to longer periods (daily relocations). The short bursts revealed persistence or considerable directional bias in movement, whereas the daily steps revealed a CRW or random walk.

Without an environmental reference, organisms are thought typically to employ a searching strategy that maximises efficiency (Bartumeus et al. 2005). Correlated random walks (CRWs) have been applied to the movement of many organisms, though these are generally small (i.e. butterflies, crickets, moths etc; see Kareiva and Shigesada 1983; Brouwers and Newton 2010), and are examined over small spatial and temporal scales. For larger animals, and over larger spatio-temporal scales, using CRWs to describe movement may be rejected in favour of the scale-invariant Lèvy Walk (LW; Reynolds et al. 2013). Under a LW scenario, a trajectory may be broken up into clusters of local walks, with long biased/directional moves between these clusters. Nevertheless, CRW models provide a useful starting point for interpreting animal movement and recent research suggests that CRWs and LW may complement rather than conflict with each other (Reynolds et al. 2013).

When a CRW does not provide a suitable fit to a movement path as characterised by net squared displacement (R²ₙ), it is usually found that the CRW model has under-predicted the observed displacement (Turchin 1998). Under-prediction by a CRW is usually the result of strong autocorrelation in turning angles, with a movement path consisting of almost completely straight-line moves. In these instances, a biased random walk model (BRW) may provide an improved fit to the overall displacement (Bailey and Thompson 2006). The displacement observed under a BRW may indicate that an organism is capable of recalling experiences over large spatiotemporal scales, in contrast to being solely guided by recent events, in order to find preferred habitat or foraging areas. In contrast, the over prediction of the CRW fitted to some of the emus may reflect a degree of site fidelity – as a result of either an internal desire to remain within a given area due to the presence of preferred habitat, or physical barriers precluding additional migration. The over prediction of R²ₙ by a CRW has
been observed in other large species (Bergman et al. 2000), with site fidelity the assumed cause. Spiral paths in the Mexican bean beetle (Epilachna varivestis) in an unconstrained habitat have also resulted in $R^2_n$ over-predictions by a CRW (Turchin 1998). In this instance, the autocorrelation in the turning angles and the subsequent spiral pattern results in an effective foraging strategy, with only some a priori knowledge of the environment and available resources (Bell 1991; Bartumeus et al. 2005). The over prediction of the displacement observed for the emus may reflect a similar lack of a priori site knowledge by the birds (Bartumeus et al. 2005) where, upon release into the Avon Valley, they had to employ an optimal search and forage strategy in their new environment.

Although there are re-sampling procedures available that would likely allow the path data to fit a CRW model (Bailey and Thomson 2006 utilise a similar approach), Kareiva and Shigesada (1983), whose seminal work founded the use of the CRW $R^2_n$ model, suggest that it is useful to examine why the observed displacement did not satisfy the predicted criterion in order to provide valuable insights. Similarly, movement trajectories have been segmented into a dichotomous path, usually representing local foraging within habitat patches (which appears as either a random or systematic search strategy) combined with long, and strongly auto-correlated movements between these areas (Bailey and Thompson 2006). This segregation of path trajectories has also been translated to agent-based models of animal movements (Bialozyt et al. 2014), which accords well with field observations. Examination of the daily trajectories of the birds where high-resolution (15 minute interval) data were available revealed a very high degree of directional bias over some short temporal scales. Where over-prediction is observed here, it is possible that a fragmented landscape, consisting of highly variable habitat structure and topography, coupled with each birds’ lack of prior knowledge about the site, are the causes of this observation. The observed impact of habitat structure on the movement characteristics of the emus has important consequences for investigating the linkages between emu movement and seed dispersal.

### 7.4.4 Linking emu movement to movement ecology

The observed movement trajectories and habitat selection of the emus released into the Avon Valley are best interpreted within the movement ecology paradigm (Nathan et al. 2008a). The emus showed a disproportionally high preference for the forest edge, agricultural lands and roads as opposed to the general jarrah forest matrix. Movement ecology (Nathan et al. 2008a) provides a useful framework for asking questions about how (method of movement),
why (internal state driving the desire to move), when and where (navigation) organisms move. The internal state of an organism relates to its short-term motivations as they relate to longer-term goals such as survival and reproduction. The paradigm also presents an ‘external’ state (environmental factors) impacting organism movement. External factors of note within the Avon Valley and experienced during the course of the GPS field deployment included impassable hilly terrain, physical barriers (fences) between agricultural lands and the jarrah forest as well as considerably hot and difficult weather conditions, particularly in late March/early April 2013. It is these environmental factors that provide a limiting framework within which the emus were able to operate and, as a result, impacted the outcomes and underlying assumptions of the CRW model application.

The preference for forest edges and agricultural land may reflect the birds’ juvenile period and early adult life within the confines of the free range emu farm from which they were purchased. However, wild emus were often seen in agricultural fields during the course of the study and other wild ratites have also shown a preference towards pastures (Bellis et al. 2004). The floristic structure of the forest edge (low, open forest with sparse understorey), reflects that of the free range farm, and so movements of the birds towards these area likely reflects a degree of landscape or habitat-type fidelity. Further to this, avoidance of hilly terrain may be a result of the relatively gently undulating confines of the birds’ original habitat as well as the general preference of organisms to avoid steep terrain (Bailey 2005). Seasonality may affect movement patterns and location preferences. Most organisms normally stay within reach of available water resources. During the course of the study, there was no water available within the jarrah forest so birds were drawn to agricultural areas where permanent sources of water were readily available. Emu scats have been collected in large numbers in agricultural areas, particularly adjacent to permanent water sources (Dunstan et al. 2013). The high temperatures experienced during the field study, particularly in the first week following release, would have impacted the navigation capacity of the emus (when and where to move). Like many other organisms, emus restrict their movement to cooler parts of the day, and have been observed to take refuge beneath the canopy of trees in very hot conditions (Dawson et al. 1984). On hot days, adult emus limit their movement and seek out water sources, consuming small amounts of water either once or, occasionally, twice in a day (Dawson et al. 1984). The impact of seasonal bias on the movement of the birds considered in this study may be limited, as emus are well-adapted to high temperature environments. Efficient and low respiratory water loss and some cutaneous water loss allow
the emu to operate (forage) almost continuously over summer months (Maloney 2008), as has been observed also in cooler months (Dawson et al. 1984). Like Dawson et al. (1984), it was observed here that the movement of birds was restricted to the diurnal period, with very limited displacement occurring nocturnally. Minor movement overnight may be attributed to discontinuous sleep patterns where the birds are startled awake, defecate, and then settle a short time afterwards (Patodkar et al. 2009).

Over the relatively short temporal scale during which GPS data were collected, it is probable that the motivations for emu movement were landscape familiarisation and resource (food/water) collection. Birds were selected and transported prior to pairing, breeding and laying, so reproductive impacts on movement may be reasonably discounted. As emus are highly generalist omnivores (Davies 1978; Dawson et al. 1984; Dunstan et al. 2013), and no single preferable food resource (large, fleshy fruits) was available during the course of the field study, the foraging strategy to gather resources would likely be random, which may be an optimal search strategies (Bartumeus et al. 2005). However, birds would remain within reasonably close proximity to agricultural water sources.

7.4.5 Emu movement and seed dispersal

The movement ecology of the emus within the Avon Valley, which may be applied to other environments, could have considerable impacts on seed dispersal and consequently, recruitment and overall plant demography. The omnivorous diet of the emus, coupled with the ready consumption of seeds with dispersal morphologies not adapted for frugivory, make it an exceptional candidate as a LDD vector. For the first time, the GPS data presented in this chapter shows the remarkable capacity of the emu to travel long distances over time periods that seed material may be held within its gut. Some of the tagged birds travelled many kilometres over the course of a week. Perhaps even more interesting was the observation from the 15 minute interval data, where the birds collectively moved almost 2 km (Euclidean distance from starting point) over the course of 4 hours. Combined with knowledge of emu gut retention, these data suggest that emus are contributing to LDD of a variety of species on a daily basis, highlighting the importance of the role of this ratite within the jarrah forests.

In considering LDD events, we should not only consider ‘how far’ but also ‘where to’, in order to assess the importance or likely outcomes of LDD. Although it has been clearly shown that there is considerable scope for the emu to transport seeds long distances, the
habitats into which they are deposited may not be suitable for germination or facilitate overall recruitment success. Scat deposition within agricultural areas and along roads arguably has zero chance for establishment and successful recruitment. Similar impasses to successful plant recruitment are also noted within the edge of the forest habitat (Jules and Rathcke 1999). Not only are these areas subject to a large amount of physical disturbance, but also, key environmental factors that promote seed germination (e.g. fire) may be excluded (Russell-Smith et al. 2007) and there may be more competition from invasives (Honnay et al. 2002). As emus showed a disproportionate preference for agricultural land, it is possible that a large amount of seed material is being deposited in unsuitable sites. Schupp (1993) and Schupp et al. (2010) present and refine the concept of seed dispersal effectiveness; the overall contribution that a disperser makes to plant demography. In highly fragmented areas, although emus consume large amounts of seed, their general seed dispersal effectiveness may be quite low. Permanent water sources (such as agricultural dams and water troughs for stocks) are further facilitators for this contagious seed deposition. Physical barriers to movement (such as agricultural fences) not only direct movement but also dispersal events into areas where recruitment may be unlikely.
7.5 CONCLUSIONS

Despite the difficulty in implementing and obtaining ongoing data from the units, GPS telemetry was an effective method for investigating the movements of emus and linking this within the movement ecology paradigm to potential seed dispersal outcomes (including LDD). Movement trajectories, habitat preference and overall displacement varied between birds. It is possible that, as for other species, there is a dichotomous split between appropriate models relevant at different scales, with short periods of approximate-random foraging patterns interspersed with larger directed movement paths. Irrespective of this, there is little doubt that emus are an important LDD vector for many species within the jarrah forest, and play an important role in the demography of many species. However, landscape structure has an impact on emu movement as well as expected seed dispersal consequences.

In the following chapter, an agent-based simulation model approach uses the emu movement information to explore the impact of landscape structure on seed dispersal. Increasing forest fragmentation decreases seed dispersal distances, causes seed dispersal source areas to be revisited and may result in seed deposition in unsuitable areas (Serio-Silva and Rico-Gray 2002). A simulation model approach allows for a quantitative analysis of seed dispersal, assessed via dispersal kernels, under different landscape conditions and models of animal movement.
CHAPTER EIGHT

MODELLING SEED DISPERAL BY THE EMU

ABSTRACT

Dispersal is the only vagile component of the life cycle of plants, and as such it partially determines not only the success of individual species, but also influences broader ecosystem structure. The quantification of seed dispersal, in particular long-distance dispersal (LDD), has become a key focus of efforts to understand the complex spatial dynamics seen in many ecosystems. While the ability to characterise seed dispersal patterns for wind-dispersed species has advanced rapidly, similar efforts for animal-dispersed species have lagged behind. Large frugivores provide key dispersal and LDD service to plants, thereby play an important role in ecosystem function, yet face continued threats and are particularly susceptible to changes in landscape composition and configuration. These global trends drive a growing impetus to develop modelling tools for frugivore-generated seed dispersal capable of incorporating spatial complexity in a realistic yet tractable manner. Here a spatially-explicit agent-based model and Global Positioning System (GPS) telemetry movement data for the emu (*Dromaius novaehollandiae*) are used to estimate how landscape composition and configuration affect seed dispersal patterns. Other commonly-used generic models of animal movement to compare the capacity of simple versus complex models to capture the key interactions between frugivore movements and seed dispersal patterns in fragmented landscapes are considered. Modelling revealed a reduction in the extent of LDD events and progressively more aggregated seed rain shadows in increasingly fragmented (impassable) and disconnected habitats as the emu, like various other organisms, adheres to habitat edges (and their vicinity) and is unable to readily move between disconnected parts of the landscape. It is suggested that future work focus on the collection of fine temporal- and spatial-scale frugivore behaviour data that can better inform models of animal movement, seed dispersal and support GPS telemetry data. Also, for keystone terrestrial dispersal species, traversable habitat corridors need to be retained to facilitate dispersal, particularly LDD.
8.1 INTRODUCTION

Seed dispersal is fundamentally important for plant demography and influences community and ecosystem dynamics (Harper 1977; Howe and Smallwood 1982; Cain et al. 2000; Nathan and Muller-Landau 2000; Cousens et al. 2008). It is the primary process of movement during the life-cycle of plants, leading to establishment of next-generation individuals both near to and far away from their parents (Nathan 2006). Long distance dispersal (LDD), in which seeds are transported great distances from their parent plant in single and infrequent events, has the potential to substantially impact broad ecosystem dynamics, particularly with regard to plant invasions and range expansions under climate change (Nathan 2006).

The importance of LDD to population, community and ecosystem dynamics has motivated extensive research efforts, yet estimating and predicting the frequency and extent of LDD events is inherently difficult (Nathan et al. 2003), though new methods and emerging technologies make this task increasingly tractable. Seed dispersal is a spatial process, and its fundamental descriptor is the dispersal distance from the source (mother) plant to the establishment site. The dispersal kernel, a statistical description of the distribution of dispersal distances, is a useful quantification of seed dispersal (Cousens et al. 2008), portraying the probability of a seed dispersal event ending at a certain distance relative to the source point (see Box 15.1 in Nathan et al. 2012 for clarifications of terminology and formulations).

Seed dispersal kernels can be estimated either phenomenologically (Clark et al. 1999a) or mechanistically (Nathan et al. 2008a). The most general mechanistic model of seed dispersal requires three factors to be quantified: seed uptake by the vector, the displacement velocity of the vector while transporting seeds, and the seed passage time during this transportation (Nathan et al. 2008a). However, each of these factors varies across space in a way that cannot be predicted simply as a function of distance from the source plant. As a result, a simple mechanistic dispersal kernel approach derived from a single spatial context cannot adequately represent the complexity and variability of seed dispersal (Kremer et al. 2012, Nathan et al. 2012). In the case of frugivory the probability of an individual dispersal event occurring generally declines with increasing distance, but with relatively high variance and clumping compared to wind-generated kernels (Clark et al. 2005). The inadequacy of simple dispersal models in describing and explaining the seed dispersal patterns generated by
frugivores has been attributed to animal movement and behaviour as dynamic, complex processes controlled by internal and external factors that vary across multiple spatial scales (Westcott et al. 2005). Factors contributing to this spatial complexity include frugivore-environment and frugivore-frugivore interactions such as obstacles to movement and sites of differing attractiveness affecting movement speed and direction, and ultimately the location of seed deposition sites (Schupp et al. 2002).

Spatially complex landscape-level seed dispersal patterns are likely the rule rather than the exception, motivating the development of new methods of data analysis with which to characterise patterns of seed dispersal (Schupp et al. 2002; Kremer et al. 2012). Changing landscape structure and composition as an outcome of habitat loss and fragmentation can have significant negative impacts on seed dispersal, including a reduction in seed dispersal distances and altered seed rain composition (McConkey et al. 2012). Habitat fragmentation has particularly deleterious effects on seed dispersal by frugivores, completely disrupting dispersal mutualisms in some instances, thereby eliminating recruitment opportunities (Rodríguez-Cabal et al. 2007). While some large frugivores may move between suitable ‘stepping-stones’ in the landscape, maintaining a degree of functional connectedness (Mueller et al. 2014), terrestrial frugivores are especially susceptible to habitat fragmentation and are often unable to move between disconnected patches of habitat, with these difficulties increasing with the size of the organism (McKinney 1997). These large frugivores often involve seed dispersal mutualisms (especially with large-seeded plant species; Cramer et al. 2007) and are able to consume and deposit many seeds in a single event, making their role in ecosystem dynamics largely irreplaceable (Jordano et al. 2007; Hansen and Galetti 2009).

Current concerns over increasing habitat loss and extensive landscape fragmentation make it even more important to develop tools to incorporate and elucidate the spatial complexity of seed dispersal (Myers et al. 2000; Uriarte et al. 2007). Predicting how frugivores might respond to such changing landscapes, and how, in turn, frugivore-mediated seed dispersal patterns might be altered, requires modelling tools that capture the complex feedback mechanisms between frugivore movement, resource availability and landscape structure (Cortes and Uriarte 2013). Habitat corridors in fragmented landscapes have been shown to facilitate seed dispersal – and even if organisms do not always use the corridors per se, the linear habitat at these edges channels movement and hence dispersal (Doerr et al. 2011; Hodgson et al. 2011). Predicting the impact of fragmentation on frugivory and seed dispersal
is difficult, as both direct and indirect edge effects usually apply (Restrepo et al. 1999). Large-scale changes to landscape structure are not the only threat to seed dispersal; fine-scale (or within-remnant) habitat fragmentation effects can also negatively impact dispersal outcomes (García and Chacoff 2007).

In a recent review of the seed dispersal effectiveness (SDE) concept (Schupp 1993), Schupp et al. (2010) highlight the need to develop spatially-explicit methods to capture the typically heterogeneous nature of seed dispersal. Recently, several model frameworks have sought to address this challenge. Schurr et al. (2008) introduced a semi-mechanistic phenomenological approach that captures spatial heterogeneity in plant fecundity and in the permeability of seed passage across the landscape. Morales and Carlo (2006) show that the scale and shape of seed dispersal kernels is driven by plant spatial pattern and frugivore density, with kurtosis of the kernel increasing with plant frugivore density and the spatial aggregation of plants. Carlo and Morales (2008) also show that spatial structure in plant populations can further impact seed dispersal by (rein)forcing local variations in seed removal rates, with seed dispersal distances reduced in spatially-aggregated stands. Other models have sought to link animal behaviour with landscape heterogeneity in order to predict the emergent patterns of seed dispersal (Russo et al. 2006; Levey et al. 2008). These studies generally reveal that landscape heterogeneity reduces dispersal distances and increases seed deposition aggregation as frugivores are "held" within a suitable habitat patch long enough to deposit locally-sourced material (Russo et al. 2006; Levey et al. 2008). Recently Bialozyt et al. (2014) and Lenz et al. (2014) showed how incorporating GPS and behavioural data into spatially-explicit agent-based models can improve understanding of the seed shadows and home ranges of primates. Here, the previous approaches are built upon, incorporating GPS telemetry data for a large frugivore, the emu, into an agent-based and spatially-explicit seed dispersal model.

In this chapter, an agent-based model (Côrtes and Uriarte 2013) is used, capable of representing the effects of complex spatial dynamics and landscape heterogeneity on patterns of seed dispersal for seeds dispersed by the emu (*D. novaehollandiae*). The emu, a large ratite, is the primary dispersal agent and LDD vector for many plant species in the Australian landscape (Davies et al. 1978; Calviño-Cancela et al. 2006; Dunstan et al. 2013). Its long gut retention time (> 100 days in some instances; Davies 1978) and movements (from tens to hundreds of kilometres over time-scales of weeks to months; Davies and Bamford 2002)
make it a good candidate for examining the impact of spatially-explicit processes on seed dispersal. The relatively recent and rapid habit loss and fragmentation that has occurred across the Australian landscape, with some areas losing more than 90% of native vegetation in the last 120 years (Saunders et al. 1991), also provide an excellent context for investigating changing landscape structure and frugivore behaviour on seed dispersal. Although an agent-based approach is not unique in itself (see Bialozyt et al. 2014), the approach in this chapter incorporates real movement (GPS telemetry) data for a frugivore, alongside (rather than solely relying on) generic behavioural observations. Also illustrated is the impact of spatial structure (landscape heterogeneity) on dispersal kernels and seed shadows produced by generic dispersal agents under different models of animal movement: simple random walk, correlated random walk and a Lévy walk (Viswanathan and Afanasyev 1996). These movement models are widely used to represent animal movement and demonstrate how important frugivore data are in building effective agent-based models as movement complexity (guided by spatial variability) largely drives seed dispersal.

A spatially explicit agent-based model of frugivore movement and seed dispersal, coupled with GPS data on frugivore movement, was used to examine the following questions:

1. Does the extent (composition) and “connectedness” (configuration) of habitat fragmentation impact dispersal kernels and seed rain shadows generated by the emu?
2. Does the impact of increasingly variable landscape structure on seed dispersal vary in a predictable way for progressively complex models of animal movement?
3. What impact does frugivore behavioural response to fragmented habitat have for seed dispersal potential and, more specifically, LDD?
8.2 MATERIALS AND METHODS

8.2.1 Modelling approach

The following model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual and agent-based models (Grimm et al. 2006; Grimm et al. 2010). The agent-based model was constructed using the NetLogo modelling environment version 5.04 (Wilensky 1999), with simulations hosted in R version 2.15.2 (R Core Team 2012) using the RNetLogo package (Thiele et al. 2012).

Purpose

The purpose of the agent-based model was to investigate the impact of changes in landscape configuration and composition (i.e. increasing amounts of impassable habitat and decreasing connectedness) on the dispersal kernels derived from the emu and other generic models of animal movement (a simple random walk, correlated random walk and Lévy walk).

State variables and scales

The model contains two general types of entities: dispersal agents and habitat cells. The simulated landscape consists of 50 × 50 m habitat cells on a discretised lattice. The simulated arena comprises 101 × 101 habitat grid cells, giving a 5 × 5 km landscape, which is unbounded (represented via a vertical and horizontal toroidal wrap). Habitat cells are classified into three categories; empty (of plants) but passable (for dispersal agents), empty but impassable, and occupied by the plant species of interest and passable. Cells occupied by plants initially cover 25% of the simulated space each containing \( n \) seeds, with \( n \) drawn from a Poisson distribution (\( \lambda = 1000 \)). The plant cells are randomly distributed across the 10,201 available habitat cells. A random distribution of plant cells was selected so as not to confound changes in landscape configuration and composition with plant aggregation (this has already been shown by Morales and Carlo 2006). Depending on the model scenario, impassable habitat cells are overlayed on the world. These impassable habitat cells cannot be traversed by agents, whereas passable habitat cells may be freely traversed by model agents (Figure 8.1).
Dispersal agents are characterised by a movement model that dictates their navigation through the simulated landscape. Dispersal agent movement is characterised by step length ($S_L$, measured in cell length) and turning angle ($\beta_i$) selection per unit time ($\Delta t$). Sample traces of each of the models of animal movement considered can be seen in Figure 8.2. Simply put, dispersal agents move around the landscape, consume seeds in cells containing plants and then deposit these seeds after a gut retention time (GRT, hrs) limit has passed. Dispersal agents have a number of additional characteristics that are tracked throughout each simulation: the number of seeds consumed ($n$-seeds-consumed) from plant cells, the time since last excretion, a record of origin for each consumed seed ($x$- and $y$-coordinates adjusted from the grid cell $i$- and $j$-coordinates to account for the toroidal wrap) and the number of seeds deposited in each excretion. For each scat, the quantity of seeds contained within, and their $x$- and $y$-coordinates (both origin and location of deposition), are recorded.
Figure 8.2 Example movement paths run for 1000 model steps for (a) a simple random walk, (b) correlated random walk, (c) Lévy walk and (d) Emu walk. Red squares and stars indicate the start and end of the walks, respectively. The convex hull (CH; in grid cells) calculated for each of the walks is also shown.

Process overview and scheduling

The model runs at a temporal grain of 1 hour; this value accords to the interval of GPS data collected for the emu. Each model run simulates 1000 steps for each of the models of animal movement. Thus each simulation considers a period of 1000 h (approximately six weeks) reflecting the approximate length of the fruiting season for many species. The decision as to how far and in which direction to move at each time step is dictated by each movement model and is explained further below. Where it is present, agents detect impassable habitat at a given distance and within a selected detection radius. Impassable habitat is avoided according to decision rules that force agents to select passable habitat within a given distance of their current location. As the agents move across grid cells occupied by the plant species of interest they consume seeds that are subsequently deposited according to a pre-determined gut retention time. At each time-step a series of other processes occurs (Table 8.1 and Figure...
8.3) as described in the sub-model sections below. Note that those processes listed under 'model initialisation' occur only at the commencement of the model, not at each time step.
<table>
<thead>
<tr>
<th>Process</th>
<th>Decision description</th>
<th>Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model Initialisation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sprout plants</td>
<td>Ask ( n)-plant-grid-cells of total world grid cells to become a plant grid cell</td>
<td>( n)-plant-grid-cells ( (\lambda_{grid\ cells}) )</td>
</tr>
<tr>
<td></td>
<td>o Set ( n)-seeds per plant patch a random number from a Poisson distribution</td>
<td>( \lambda_{seeds} )</td>
</tr>
<tr>
<td>Create landscape structure</td>
<td>Seed the grid with one initial impassable grid cell.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sequentially fill the model by selecting grid cells and making them impassable.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Generate a deviate ( U(0,1) ) and if it is less than ( attract-suitable ) then</td>
<td>( attract-suitable, P(impassable) )</td>
</tr>
<tr>
<td></td>
<td><em>passable</em> patch next to an impassable patch is made impassable.</td>
<td></td>
</tr>
<tr>
<td>Create dispersal agents</td>
<td>Generate ( n)-agents, all on grid cells that are passable</td>
<td>( n)-agents</td>
</tr>
<tr>
<td></td>
<td>Set gut retention time (GRT, hrs)</td>
<td>GRT (hrs)</td>
</tr>
<tr>
<td></td>
<td>Set movement model. See sub-model section for further information on each of the</td>
<td></td>
</tr>
<tr>
<td></td>
<td>models.</td>
<td></td>
</tr>
<tr>
<td><strong>Model Run</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Move dispersal agents</td>
<td>If: grid cells in a detection-radius are impassable, move agents to a suitable</td>
<td>( Detection-radius, avoid-impassable-radius )</td>
</tr>
<tr>
<td></td>
<td>habitat patch within distance ( avoid-impassable-radius )</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Else: Move agents along turning angle ( \beta ), and along step length ( S_L )</td>
<td></td>
</tr>
<tr>
<td></td>
<td>as defined by the movement model</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Calculate real ( x )- and ( y )-coordinates of the dispersal agent from the</td>
<td></td>
</tr>
<tr>
<td></td>
<td>point of origin</td>
<td></td>
</tr>
<tr>
<td>Consume seed</td>
<td>If dispersal agent is on a plant habitat cell, consume ( p)-seeds-removed * ( \lambda_{seeds} )</td>
<td>( n)-seeds-consumed, ( p)-seeds-removed</td>
</tr>
<tr>
<td></td>
<td>Record the coordinates of the plant habitat cell that seeds are consumed from</td>
<td></td>
</tr>
<tr>
<td>Deposit seeds</td>
<td>Deposit scats containing ( n)-seeds-consumed according to distribution of mean gut</td>
<td></td>
</tr>
<tr>
<td></td>
<td>retention time (GRT, hrs).</td>
<td></td>
</tr>
</tbody>
</table>
Figure 8.3 Flow chart showing decisions made throughout the model process
Design concepts

Basic Principles: An emu movement model, derived from the GPS data presented in Chapter 7 and three well-established models of animal movement were used – a simple random walk (SRW), correlated random walk (CRW) and Lévy walk (LW) – to simulate behaviour in a lattice environment. For the emu movement model, a log-normal distribution was fitted to the hourly-interval step length emu data using maximum-likelihood estimation (MLE) within the 'fitdistrplus' package (Delignette-Muller et al. 2010) in R. The log-normal distribution of step length data was selected based on the AIC values comparing distributions fitted by MLE (log-normal, gamma, Poisson and exponential).

Emergence: The dispersal kernels and the convex hull of dispersal agent locations are emergent properties of the animal movement model and the response to impassable habitat. Each movement step follows rules describing the agent’s response to impassable habitat and the selection of suitable habitat as appropriate for each individual null model.

Plasticity: Dispersal agents alter their behaviour according to the presence of impassable habitat and their ability to detect it. Dispersal agents reduce their step length when they are within a pre-determined distance of the impassable habitat. Some organisms have been shown to substantially alter behaviour, including reducing step lengths, when close to impassable habitat or habitat edges (understorey birds - Restrepo and Gómez 1998; beetles - Young et al. 2013).

Objectives: The main objective of the dispersal agents is to consume seeds in plant grid cells, which they visit in accordance to their model of movement. Over the temporal scale of the model, there is always sufficient and locatable food. Their secondary objective is to avoid impassable habitat, taking the shortest path to minimise energy expenditure.

Sensing: Dispersal agents are sensitive to approaching the edge of impassable habitat within the extent and radius of their detection. Dispersal agents do not have a memory of the impassable habitat cells that they avoid and so may return to them as they traverse the landscape. Agents are unable to sense plant cells where they can feed
so do not preferentially move towards them. In the case of the emu, generalist feeding
behaviour (Dunstan et al. 2013) results in opportunistic foraging.

Stochasticity: There is a stochastic component inherent in all of the generic
models of animal movement (turning angle and step length). A suitable habitat cell
within a given radius from the current location is selected at random for the dispersal
agent to move to. The selection of a suitable habitat cell to move to when avoiding
habitat edges is represented as a purely stochastic process.

Collectives: For simplicity, a single dispersal agent is used in each simulation.
This avoids having to represent complex collective interactions that would arise in the
presence of multiple dispersal agents within the simulated environment and for which
there is little empirical information to support representation.

Observation: The spatial locations of the dispersal agents and the scats they
deposit (containing the amount of seeds consumed from the landscape) are recorded,
allowing accurate and precise computation of seed dispersal distances and home range
movement for each of the generic models evaluated.

Initialisation

The model is initialised as described in Table 8.1 with the parameters outlined in Table
8.2. The model first selects the 50 × 50 m cells that will become plant grid cells. These
cells are randomly selected and populated with n-seeds (a random Poisson deviate with
λ = 1000). In the base scenario, 25% of available cells contain plants. A heterogeneous
landscape is then super-imposed on the world as follows: (i) a single cell is selected at
random and deemed impassable (ii) cells adjacent to neighbours flagged as impassable
are recursively made impassable according to the attract-suitable value (which is in the
range 0-1). The world is then increasingly filled with impassable habitat cells until the
required proportion of impassable habitat is achieved (initially set at 50%). A single
dispersal agent is then randomly spawned on a suitable (passable) habitat patch. The
dispersal agent follows one of the generic models of animal movement from the
selection available: simple random walk, correlated random walk, Lévy walk or emu
model.
Table 8.2 Model parameters for each null model of animal movement for the initial (baseline) model runs

<table>
<thead>
<tr>
<th>Parameters</th>
<th>SRW</th>
<th>CRW</th>
<th>Lévy Walk</th>
<th>Emu</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>General</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Simulation length (hrs) / n steps in model</td>
<td>1000</td>
<td>1000</td>
<td>1000</td>
<td>1000</td>
</tr>
<tr>
<td>n-agents</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Habitat Cells</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n-plant-grid cells</td>
<td>2550 / 25%</td>
<td>2550 / 25%</td>
<td>2550 / 25%</td>
<td>2550 / 25%</td>
</tr>
<tr>
<td>λseeds per plant patch</td>
<td>1000</td>
<td>1000</td>
<td>1000</td>
<td>1000</td>
</tr>
<tr>
<td>P(impassable)*</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>0.25</td>
<td>0.25</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>attract-suitable</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td><strong>Dispersal Agents</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Step length (SL)</td>
<td>1-2</td>
<td>2</td>
<td>Cauchy (0,1)€</td>
<td>NOTE²</td>
</tr>
<tr>
<td>Turning angle βi</td>
<td>uniform</td>
<td>SD 180§</td>
<td>uniform</td>
<td>uniform</td>
</tr>
<tr>
<td>Gut retention (GRT,hours)¥</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>detection-dist</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>detection-radius</td>
<td>90°</td>
<td>90°</td>
<td>90°</td>
<td>90°</td>
</tr>
<tr>
<td>avoid-impassable-radius</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>p-seeds-removed</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
</tbody>
</table>

* P(impassable) various depending on the proportion of impassable habitat for a given simulation run
¥ GRT is drawn from a random exponential distribution with mean 1/rate (5 hrs)
€ Step length (in habitat cells) for the Lévy walk is drawn from a random Cauchy distribution with location and scale parameters of 0 and 1, respectively
² Step length (in habitat cells) for the Emu model is drawn from a lognormal distribution with mean 4.76 and SD 1.46 (based on model fit to the hourly emu step-length data).
§ Correlated random walk is produced in the initial model with a standard deviation of the turning angle of 180 degrees.
Gut retention time (GRT) is a key driver of dispersal dynamics and patterns (Guttal et al. 2011). Estimates of GRT reported in the literature for the emu were explored, with some incorporated into the model (Davies 1978; Herd and Dawson 1984; Wilson 1989; Table 8.3). GRT was initially set at five hrs and drawn from an exponential distribution (a special case of the gamma distribution; Guttal et al. 2011). A GRT value of five hours accords with the allometric derivation of GRT using the methods described in Robbins (1993). This GRT value was applied to all of the generic models of animal movement to facilitate comparison. Davies (1978) reports some material passing through the emu gut in as little as three hrs, with retention times varying between 4 - 48 hrs for material consumed during the same event, and extreme cases of > 100 days; it is not, however, considered a plausible estimate of GRT owing to the type of material fed, ingested and passed (marbles). Herd and Dawson (1984) report a mean GRT of 5.5 hrs for the solid phase of fibrous material digested and Wilson (1989) report GRT of the consumption of pseudo-seeds in the range of 1 - 2 days.

Table 8.3 Minimum, mean and maximum values of gut retention times (GRT) of material consumed by the emu

<table>
<thead>
<tr>
<th></th>
<th>Min GRT</th>
<th>Mean GRT</th>
<th>Max GRT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Davies 1978</td>
<td>3 hrs</td>
<td>NA</td>
<td>&gt; 100 days</td>
</tr>
<tr>
<td>Herd and Dawson (1984)</td>
<td>NA</td>
<td>5.5 ± 0.4 hrs</td>
<td>NA</td>
</tr>
<tr>
<td>Wilson (1989)†</td>
<td>4 hrs</td>
<td>1 - 2 days</td>
<td>&gt; 10 days</td>
</tr>
</tbody>
</table>

† Limited definition in GRT data. Daily census of pseudo-seeds.

Submodels

Feeding: As a dispersal agent traverses a plant patch, it arbitrarily consumes 50% of the seeds contained in that patch. Plant grid cells are 'killed' when the number of seeds contained in a patch is < 80 (c. 8% of original abundance), but the length of the model simulation period means that this rarely occurs. This reflects the rarity of frugivores locally exhausting fruit resources (Carlo and Morales 2008).

Travelling/Habitat Avoidance: While all of the habitat grid cells within an agent’s detection distance and radius are passable, agents move by selecting a suitable habitat patch based on their step-length and turning angle parameters of the animal movement model (emu, SRW, CRW, LW; see Methods: Design Concepts: Basic
Principles) examined in this particular run. If the agent detects impassable habitat within the detection distance and radius, it selects a neighbouring patch within a given radius (initially set at one cell) to which it moves. To avoid the agents becoming 'stuck' in highly heterogeneous landscapes, if an agent repeatedly (20 times) fails to move, then the radius of this selection process increases (initially set as two cells).

Defecation: The location and time of consumption for each seed is recorded. Seeds are deposited once the mean GRT is reached (drawn from an exponential distribution for each feeding bout and initially set at 5 hrs). Seeds in a given feeding event get a deposition time drawn from this distribution.

8.2.3 Model outcomes

The R package 'Spatstat' (Baddeley and Turner 2005) was used to calculate the convex hull of the coordinates that the agents visited in the simulations (as an analogue for home range). These hulls were used as the window boundary to examine the spatial deposition of seeds. Although the spatial process is neither stationary nor constrained to the convex hull (Adrian Baddeley, pers comm) the mean nearest-neighbour (NN) distance between depositions at the completion of the simulation run was calculated as a summary spatial statistic. While this statistic is myopic (only evaluates highly localised patterns), it is a useful measure for assessing spatial patterns at local scales (between patches where scats are deposited.

For each of the simulations the 'fitdistrplus' package (Delignette-Muller et al. 2010) was used in R to fit the Weibull distribution to the seed dispersal distances to generate the seed dispersal kernels. A Weibull distribution was used because it is flexible and also because its shape and scale parameters are biologically interpretable and allow a straight-forward and consistent comparison of the impact of model parameters on the dispersal kernel. The Weibull distribution also provided a good fit of seed dispersal distances in comparison to other functional forms commonly used (Clark et al. 1999a; Nathan and Muller-Landau 2000; Morales and Carlo 2006; Hirsch et al. 2012b)

8.2.4 Sensitivity analysis

The model parameters described in Table 8.2 were baseline parameters. To evaluate the importance of changes in model parameters on model outcomes, the standardised effect sizes (Nakagawa and Cuthill 2007) on model outcomes as a result of changes to
individual model parameters (using Cohen’s $d$; Cohen 1988) was examined. For the sensitivity analysis a single parameter was altered at a time, holding all others constant. The model was run with the changed parameter for 50 simulations. The standardised effect sizes in median dispersal distance, the 95th quantile (as a measure of LDD; Nathan et al. 2003) and the mean NN distance between seed (scat) depositions from the base model are presented. The parameters altered during the course of the sensitivity analysis were: the proportion of impassable habitat (from homogenous to 50% impassable), *attract-suitable* (from 0.5 in the base model to 1 - completely contiguous impassable habitat), detection distance (reduced from 10 in the base model to 5), *avoid-impassable-radius* (one cell in the base model, increased to three cells). These model parameters were varied for landscapes comprised of 0 and 50% impassable grid cells. Formal statistics were not applied to the simulated model output, instead, the relative magnitude of the effect of change in parameters was assessed (White et al. 2014).
8.3 RESULTS

8.3.1 Does the extent and “connectedness” of habitat fragmentation impact dispersal kernels and seed rain shadows generated by the emu?

The median and 95th percentile (LDD estimate) dispersal distances for the emu in a completely homogeneous landscape were 488 m (5th and 95th quantiles were 419 m and 559 m) and 1682 m (5th and 95th quantiles were 1465 m and 2129 m), respectively. The maximum seed dispersal distance across all realisations exceeded 7000 m. The mean NN distance between scat depositions was 168 m (3.28 grid cells).

Increasing the amount of impassable fragmented cells (i.e. changing landscape composition), while holding fragment configuration constant (at 50% “connectedness”) caused a sharp decline in the median and 95th percentile dispersal distances (Figures 8.4 & 8.5). The most substantial decrease in the median and 95th percentile distances occurred with a small addition (15%) of impassable habitat (Cohen’s \( d = -11.3 \) and \( d = -5.8 \) respectively). Further fragmentation (increasing abundance of impassable cells from 15% to 50%) had less of an effect on the median dispersal distances (change in \( d \) from -11.3 to -13.1) than on the 95th percentile (change in \( d \) from -5.8 to -11.1).
Figure 8.4 The median dispersal distances in a simulated homogenous (H) environment for different models of animal movement. The change in these values occurring as a result of increasingly impassable habitat (composition change; 15% - 50% impassable) and increasingly disconnected habitat (configuration change; 50% of the fragmented landscape “connected”, to a single block) are presented as Cohen’s $d$ (Cohen 1988). A negative value for $d$ indicates a decrease in the median dispersal distance estimate relative to the baseline.
Figure 8.5 The 95th percentile dispersal distances (LDD analogue) in a simulated homogenous (H) environment for different models of animal movement. The change in these values occurring as a result of increasingly impassable habitat (composition change; 15% - 50% impassable) and increasingly disconnected habitat (configuration change; 50% of the fragmented landscape “connected”, to a single block) are presented as Cohen’s $d$ (Cohen 1988). A negative value for $d$ indicates a decrease in the median dispersal distance estimate.

The change in landscape configuration (increasing attract-suitable from 0.5 to 1.0), while holding the proportion of impassable grid cells constant at 25% had less of an impact on the median and 95th percentile dispersal distances for the emu in comparison to landscape composition, up to a threshold value. The decrease in median dispersal distances relative to the baseline (measured by $d$) for the emu as the landscape became increasingly fragmented (changing attract-suitable from 1.0, 0.85, 0.65 to 0.5) was -3.3, -12.1, -12.4 and -12.5, respectively. A similarly disproportionate decrease in the 95th percentile values were observed with the imposition of a continuous block of impassable habitat (attract-suitable = 1.0; $d = -0.9$) in contrast to a minor disruption in fragment connectedness (attract-suitable = 0.85; $d = -6.1$).

The location (scale) and shape parameters of the simulated emu dispersal kernels (Fig 8.7d; 8.8d) declined as the landscape configuration became more heterogeneous.
The mean NN distance of scat depositions decreased markedly in landscapes that contained a high proportion of impassable habitat (50%; \(d = -8.4\); Figure 8.6) and disconnected fragments (attract-suitable = 0.5; \(d = -8.6\); Figure 8.6).

\[\text{Figure 8.6}\] The mean nearest-neighbour (NN) distances in a simulated homogenous environment (H) for different models of animal movement. The change in these values occurring as a result of increasingly impassable habitat (composition change; 15% - 50% impassable) and increasingly disconnected habitat (configuration change; 50% of the fragmented landscape “connected”, to a single block) are presented as Cohen’s \(d\) (Cohen 1988). A negative value for \(d\) indicates a decrease in the median dispersal distance estimate.

8.3.2 Is the impact of increasingly variable landscape structure on seed dispersal different for progressively more complex models of animal movement?

The median and 95\(^{th}\) percentile (LDD estimate) dispersal distances decreased across each of the animal movement models as the landscape became increasingly disconnected and as more impassable habitat was introduced (Figures 8.4 & 8.5). 95\(^{th}\) percentile dispersal distances in the emu-informed, LW and CRW models (\(d = -11.1\); \(d = -7.6\); \(d = -9.3\), respectively) all declined more markedly than the SRW (\(d = -6.3\)) in landscapes comprising 50% impassable habitat. The decrease in the mean NN distance between scats in increasingly impassable and disconnected impassable fragments was most notable in the emu model (Figure 8.6).
There was a marked reduction in the shape and scale of the fitted parameters in a homogenous as compared to a minimally (15%) heterogeneous/impassable landscape for all the movement models, except the SRW (Figures 8.7 & 8.8). Further increases in the proportion of impassable habitat up to 50% did not affect the shape and scale of the fitted kernels. For the Lévy walk and emu-informed model, an increasing amount of impassable habitat led to a pronounced reduction in the scale of the fitted distributions, but this was not observed for the shape parameter.

**Figure 8.7** Change in the shape and scale of the Weibull distribution of dispersal kernels fitted to models of animal movement in increasingly heterogeneous (impassable) habitat - (a) simple random walk, (b) correlated random walk, (c) Lévy walk and (d) emu movement model
Figure 8.8 Dispersal kernels produced via fitted Weibull distributions for different models of animal movement in increasingly heterogeneous (impassable) habitat: (a) simple random walk, (b) correlated random walk, (c) Lévy walk and (d) emu movement model. Note that x-axis scaling varies for each of the plots.

8.3.3 What impact does frugivore behavioural response to fragmented habitat have for seed dispersal potential and, more specifically, LDD?

Diminishing the agents’ perception of the edge of the impassable habitat by 50% (from 10 to 5 grid cells) had a limited effect on the median and 95th dispersal estimates or mean NN values. For each of the movement models, the median and 95th percentile dispersal distance standardised mean differences increased, with a range of $d$ between 0 – 2 (Figure 8.9). A similar range of small increases in the mean NN distances was also observed.

Increasing the radius over which agents could 'escape' the edge of impassable habitat by 300%, led to large increases in estimated median and 95th percentile dispersal distances for all movement models. Increasing this escape radius reduced the ‘trapping’ effect that impassable habitat edges had on agents in the models. The increase in median dispersal distance was greatest in the SRW model $d = 12$, but its magnitude decreased with increasing model complexity ($d = 10, 9.8$ and $5.8$ for the CRW, LW and emu.
Increasing the impassable habitat escape radius increased the 95th percentile dispersal distances for each model, with $d$ ranging from 5 - 7. However, this effect was similar across the models. The mean NN scat distance also decreased across all models as escape radius increased.

**Figure 8.9** The response (measured in Cohen’s $d$) of a change in the detection distance (from 10 grid cells to 5; light grey bars) and *avoid-impassable-radius* (from 1 grid cell to 3; clear bars) model parameters on the median dispersal distances, 95th percentile of dispersal distances and the nearest-neighbour (NN) distances for different models of animal movement; simple random walk (SRW), correlated random walk (CRW), Lévy walk and emu model in 50% suitable landscape.
8.4 DISCUSSION

The pioneering banding and recapture of emus by Davies et al. (1971) revealed a remarkable capacity for the birds to travel long distances over relatively short periods, and, in turn, resulted in a great deal of attention being given to the emu as a LDD vector for the seeds of many species (Calviño-Cancela et al. 2006; Calviño-Cancela et al. 2008; Dunstan et al. 2013). This chapter presents dispersal kernels for seeds dispersed by the emu within a homogenous and increasingly impassable and disconnected landscape. Median and 95th percentile dispersal distance estimates of 488 m and 1682 m highlight the important contribution that this ratite plays in seed dispersal and plant dynamics throughout its range. These values are perhaps even more remarkable considering they are, in part, derived from the most conservative gut retention time (GRT; 5 hrs) available in the literature (Herd and Dawson 1984). With some material reported to be retained within the gut for many weeks (Wilson 1989), and with the seeds of many Australian species possessing hard endocarps, likely resistant to prolonged retention, the potential for emu to be responsible for extremely long-distance dispersal further increases.

Modelling also revealed a reduction in the extent of LDD events and progressively more aggregated seed rain shadows in increasingly fragmented (impassable) and disconnected habitats as the emu adhered to habitat edges (and their vicinity), and is unable to readily move between disconnected parts of the landscape. These problems are further exacerbated when considering the extended temporal scales over which resources may be depleted in small, isolated fragments. Simulations also revealed that the response of the emu to habitat edges had a substantial impact on median and 95th percentile dispersal distances. Future work should focus on refining our knowledge of frugivore-specific responses to different types of habitat edges, especially given that these responses have been shown to be critical in other spatially-explicit models (Levey et al. 2008). Overall, the response of the emu movement model to changes in habitat structure were similar to the Lévy walk, with comparable proportionate decreases in median and LDD estimates from the homogeneous to increasingly impassable habitat. It is perhaps unsurprising that the Lévy and emu models responded similarly to increasing habitat fragmentation as both possess heavy-tailed step length distributions (a power law for the Lévy walk and a lognormal distribution for the emu model).
Cousens et al. (2010a) lament the slow rate at which landscape and general organismal behaviour have been incorporated into seed dispersal models, beyond context-specific estimates. The model, which takes a frugivore-specific (emu) and general approach in investigating the impact of landscape structure and organism responses to it, seeks to begin to redress these concerns. While landscape heterogeneity and habitat fragmentation may decrease seed dispersal distances, and hence the potential for LDD, to the author’s knowledge, there has yet to be an examination of the impact of landscape configuration and composition on dispersal outcomes in conjunction with different models of animal movement.

8.4.1 Does the extent and “connectedness” of habitat fragmentation impact dispersal kernels and seed rain shadows generated by the emu?

Landscape structure has been shown to have a considerable impact on the extent and spatial arrangement of seed dispersal (Levey et al. 2005; Levey et al. 2008; Lenz et al. 2011; Damschen et al. 2014). Recently, Trakhtenbrot et al. (2014) used a mechanistic model to examine seed dispersal by wind in hilly terrain, and found that topography influenced both median and LDD (99th percentile) estimates. Damschen et al. (2014) used an advanced mechanistic wind dispersal model to divulge how habitat structure and corridor topology affect both short- and especially long-distance dispersal of seeds by wind. Although there are far more studies of landscape fragmentation effects on animal- rather than wind-dispersed plants, modelling studies of the former group have seldom incorporated landscape structure (but see Bialozyt et al. 2014). The complex movement decisions undertaken by frugivores, encapsulated within the movement ecology paradigm (Nathan et al. 2008b), create intrinsic difficulties in modelling frugivore behaviour and seed dispersal. These challenges present an opportunity to refine existing empirical and mechanistic approaches to investigating frugivore-seed dispersal relationships.

Landscape fragmentation is well known to decrease LDD potential, and much of biological conservation and planning now gives focus to the maintenance of corridors to facilitate LDD (Pearson and Dawson 2005). The landscape constraints that were applied in the simulated world are representative of a worst-case scenario, where fragmentation results in impassable habitat edges between areas of passable landscape. Frugivore mobility has been found to be a key indicator of LDD success between isolated fragments. In the semi-arid areas of northern Australia, the emu moves readily
in a landscape heavily fragmented by pastoral activities (Davies et al. 1971). Those regions provide a different dispersal context than does the fragmentation experienced in the southern areas of Australia, where agriculture and urbanisation define the landscape matrix. The nature of the surrounding matrix in habitat fragmentation is known to be important in mediating the impacts of habitat loss and land-use change on a variety of ecological services (Ricketts 2001; Watling et al. 2011). Critically, as habitat becomes increasingly disconnected the ratio of edges to continuous/natural habitat increases, with a significant effect on frugivore behaviour (Restrepo et al. 1999).

In a homogeneous landscape, the emu movement model yielded simulated median and 95th percentile distances of 488 m and 1682 m. It is worth noting that these estimates of seed dispersal for the emu are drawn from movement data collected in a heterogeneous landscape, and may underestimate dispersal values in more uniform landscapes. The values reported are similar to those of Westcott et al. (2008) for the southern Cassowary (Casuarius casuarius), a large ratite found in tropical northern Australia, who estimated median and maximum dispersal distances of 387 m and 5212 m, respectively, for an invasive, tropical rainforest plant Annona glabra. The importance of large frugivores, particularly ratites, to seed dispersal, is well documented (Westcott et al. 2008; Mokany et al. 2014). However, it is not only the long distances over which seeds are dispersed that make them so critical for ecological function, but the quantity and quality of seeds transported. Jordano et al. (2007) suggests that within a given system, a single or limited number of large frugivores act as keystone dispersal species. In terms of the seed dispersal effectiveness framework (Schupp 1993; Schupp et al. 2010), the emu is likely the most effective dispersal agent within the majority of continental Australia. Understanding then how habitat fragmentation reduces the functionality of the emu in increasingly degraded and disconnected landscapes is paramount.

8.4.2 Is the impact of increasingly variable landscape structure on seed dispersal different for progressively complex models of animal movement?

The simulations presented in this study demonstrate how different models of animal movement respond to altered landscape composition and configuration. Typical agent-based approaches to modelling seed dispersal by frugivores either use: (i) a single model of animal movement in a single or limited landscape context (e.g., Will and Tackenberg 2008) or (ii) use behavioural information to construct dispersal models from animal movement. In the latter case, a typical approach is to classify discrete
behaviours (i.e. sleeping/foraging/travelling), with the resulting movement pattern emerging as a hybrid of random and correlated random walks (Bialozyt et al. 2014). The composite movement approach is supported by observations of captive frugivores (specifically primates) at a small scale, with movement patterns shifting from Brownian to a Lévy walk depending on behaviour, reflecting the state-space approach to analysing movement data (Sueur et al. 2011). It is, however, uncertain how these observations will apply at the landscape level and the results presented here highlight the caution required in selecting a model of movement to describe frugivore behaviour, as it can have direct impacts on seed dispersal estimates.

Through the modelling approach, it was aimed to examine seed dispersal dynamics for commonly-used generic models of animal movement in an individualistic manner and the response of dispersal dynamics to changes in landscape composition and configuration. It was hypothesised that not only increasing proportion of habitat fragmentation (composition), but decreasing landscape connectivity (configuration), would reduce the extent of LDD. In each of the movement models evaluated, increasing landscape heterogeneity resulted in a decrease in key seed dispersal parameters (the median and 95th percentile distances) and an aggregation of the seed shadows. The shape and scale of the simulated dispersal kernels reduced as the proportion of impassable habitat increased as the landscape shrunk and the proportion of fragment edges to passable habitat increased. The model revealed that landscape connectedness, not only proportion of overall impassability, substantially impacted the estimates of seed dispersal. The comparative impacts of habitat configuration and composition on dispersal has been seen in other contexts (Bond et al. 2000), but, to the author’s knowledge, has not been described for a keystone frugivore dispersal agent.

8.4.3 What impact does frugivores’ behavioural response to fragmented habitat have for seed dispersal potential and, more specifically, LDD?

In the model, greater dispersal distances were observed across all models of animal movement in less fragmented landscapes. This outcome corresponds to the findings of Levey et al. (2005), who modelled seed dispersal along corridor edges using local and simple behaviour observations for the Eastern Bluebird (Sialia sialis). In the models, once a habitat edge is detected by the agent, it searches for suitable habitat within a reduced movement radius and this effectively constrains its movement to the passable/impassable habitat interface. The sensitivity of the model to the manner in
which agents perceive and respond to the habitat edge highlights the need for robust data describing how individual frugivores respond to altered habitat types and/or impassable habitat. Will and Tackenberg (2008) call for the collection of data describing animal movement which aids the derivation of seed dispersal kernels. Frugivore response to habitat edges, both permeable and impassable, is likely to be species-specific and context-dependent. While Levey et al. (2005) has shown how small-scale edge observations can inform broader, landscape models of habitat use and seed dispersal, there is still much work to be done in examining frugivore’s edge response, particularly beyond the tropical setting. Model analysis highlights how critical the understanding of frugivore response to changes in habitat structure is for reasonable dispersal kernel estimates (see also Côrtes and Uriarte 2013). If the capacity for an organism to ‘escape’ impassable habitat edges is increased, then the median and LDD seed dispersal estimates increase and the mean NN distances between seed deposition events drop commensurately.

The model tightly constrained disperser step length once impassable habitat was detected, and the sensitivity of the agent response to habitat edges was highlighted in the reduced median and LDD estimates. Quantifying any organism’s ability to detect and respond to impassable (or low permeability) habitat edges is clearly critical for the robust estimation of LDD in landscapes of differing spatial structure. Further work is needed to consider how to effectively empirically capture the spatial awareness (and memory) of frugivores within complex landscapes.

Model capabilities and limitations

A limitation of this (and indeed, many other) agent-based models of seed dispersal is that it estimates dispersal parameters in a completely static environment. While typical patterns of animal movement are emergent properties of the landscape, the structure of the landscape is itself also an emergent property of animal movement. Although over the time-scale considered, the landscape is effectively a static canvas, future work should identify landscape-dispersal feedback mechanisms. The impact of extreme plant longevity (hundreds or thousands of years) on seed dispersal dynamics should also be considered. The impact of habitat fragmentation on seed dispersal and demography of long-lived plant species will be difficult to observe or predict. As model simulations were limited to the time-scale of fruit availability for a generic plant species for a single
fruiting season, the long-term resource (seed) depletion that may occur during extended periods of localised foraging in extremely fragmented landscapes or where desirable resources are extremely localised were not considered. Over longer temporal scales, local fruit production may decrease in small habitat remnants (Cunningham 2000), thus ultimately decreasing fruit availability and LDD potential. Finally, the model does not consider the spatial memory of frugivores, which mediates foraging strategies and detection and avoidance of habitat edges; arguably the key outcome of the model with respect to LDD estimates. Frugivore spatial memory is a key component in better understanding seed dispersal (Boyer and Walsh 2010; Corlett 2011). Unfortunately, empirically quantifying the spatial memory of a diverse frugivore assemblage is extremely challenging.
8.5 CONCLUSIONS

With habitat loss and fragmentation continuing globally (Butchart et al. 2010), agent-based models provide an opportunity to explore the feedbacks between the landscape, frugivore behaviour and seed dispersal outcomes. Future modelling efforts should focus on exploring how these persistent landscape changes alter keystone disperser species behaviour, seed dispersal dynamics and, in turn, future landscape construction. New methods in modelling movement at multiple-scales and for multiple modes of movement need to be incorporated (Benhamou 2014). Modelling has revealed the critical contribution to LDD by the emu throughout much of continental Australia. Given that the emu, and similarly large frugivores, play an essential role in negating the deleterious effects of global environmental change, urgent quantification of their contribution to seed dispersal and plant dynamics is required.

The next and final chapter (Chapter Nine) provides a final synthesis and overview of the material presented in this thesis and directions for future work.
CHAPTER NINE

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

The growth in the seed dispersal literature has been spectacular in recent years. A simple Web of Science citation search for ‘seed dispersal’ shows almost 9000 peer-reviewed works since 2000. This explosion of research is born from humble beginnings, with Darwin and his butler conducting the first reported seed dispersal experiments by placing vegetables in the bath to determine how long they would remain afloat and viable – investigating transoceanic dispersal (Quammen 2007). Since that time, there have been theoretical and technological advances that have both solved and posed a number of different ecological questions.

Detecting a demographic signal between sites of contrasting emu abundance

In this thesis, advanced technological (GPS telemetry) and analytical methods were applied to investigate the role of the emu in dispersing large-seeded species in the jarrah forests of southwestern Australia. The demography of three long-lived resprouters (Persoonia elliptica, Podocarpus drouynianus, and Macrozamia riedlei) and a short-lived, fire-killed seeder species (Leucopogan nutans) was investigated. This study into dispersal, particularly long-distance dispersal (LDD), in areas of contrasting high and low emu abundance, failed to detect a demographic signal in terms of seed production, seed viability or spatial ecology of these plant species. The absence of a detectable signal suggests that there is a long delay before the outcomes of poor dispersal on factors such as spatial pattern and genetic depression effects may be seen (Ellstrand and Elam 1993). This is further exacerbated by extreme plant longevity, seen particularly in M. riedlei and P. drouynianus, with the time since dispersal agent loss (with the emu being removed ~ 120 years prior to demographic assessment for one site) insufficient to detect a demographic shift (Angeloni et al. 2011). For M. riedlei, it may take much more than 100 years for an individual to become reproductive. The challenge of detecting a difference in demographic attributes between populations with contrasting high/low emu abundance is exacerbated by small- and large-scale biotic and abiotic differences between sites.

There was no clear spatial signal in contrasting areas of high/low emu abundance and an aggregated spatial pattern (modelled as a Thomas cluster process) was dominant for all species and at each site. A simulation model exploring dispersal agent loss in a
homogenous system, removing confounding first-order spatial effects, highlighted the
difficulty in detecting changes in spatial pattern, with the frugivore deposition process
producing aggregated patterns. Combined with low visitation and fruit removal rates
within the jarrah forests observed in Chapter Six, leading to the deposition of large
numbers of fruit and seed between the canopies of parent plants, it is unsurprising that
aggregation was the dominant pattern. The agent-based dispersal model in Chapter
Eight also showed that scats were distributed in clumps, and this was evident across
different models of animal movement: from a simple random walk, through to more
complex correlated random and Lévy walks.

Seed dispersal is not the only means by which heterozygosity is maintained within
populations as pollen dispersal is a major source of gene flow within and between
populations (Robledo-Arnuncio and Gil 2004). For *M. riedlei*, there is low genetic
difference between populations across southwestern Australia, likely owing to good
pollen dispersal and outbreeding by dioecy (Byrne and James 1991). The maintenance
of genetic diversity in ancient and disjunct populations of Cycads is variable, and
depends on factors additional to seed and pollen dispersal; including size and
connectedness of populations (Xiao *et al.* 2005). Generally, however, pollen dispersal
distances by wind can be very high – potentially up to 1000 km in some instances
(Siljamo *et al.* 2008), and long-distance pollen dispersal has been observed in the
Podocarpaceae (Salas 1983). Pollen flow then may be an effective means of
transferring genetic material between populations, particularly for wind-pollinated
species (*P. drouynianus*). Pollination by nectivorous birds has been shown to depart
from typical nearest-neighbour pollination (Krauss *et al.* 2008). Pollen dispersal
distances by insects are typically lower than wind- and other animal-dispersed species,
though this depends on the degree of pollination specialisation (Schulke and Waser
2001). In some instances, direct pollen dispersal by insects may reach distances of 160
km (Ahmed *et al.* 2009). Nevertheless, the movement of pollen allows gene movement
in the absence of seed dispersal.

**The emu as a long distance dispersal vector**

GPS tracking of emu revealed that, as proposed by Calviño-Cancela *et al.* (2006), the
emu could be an effective LDD vector, with simulation modelling using a conservative
measure of gut retention time (5 hrs) resulting in median and 95th percentile (LDD
estimate) dispersal distances of 488 m and 1682 m, respectively. Maximum dispersal
distances exceeded 7000 m. The emu also consumed a large amount of plant material (> 1000 seeds contained on average per scat for some species), potentially making it a highly effective dispersal agent within Schupp’s (1993) seed dispersal effectiveness framework. The values reported for emu were similar to those of Westcott et al. (2008) who estimated median and maximum dispersal distances of 387 m and 5212 m for another large ratite, the southern Cassowary (Casuarius casuarius), found in the tropical rainforests of northern Australia. The long distances over which the emu disperses seeds suggests that it may act as a vector supporting plant species resilience to global environmental change. However, Corlett and Westcott (2013) contend that plants may not be able to keep up with the pace of global environmental change, with species needing to move ca. 1 km yr\(^{-1}\). Plant longevity, long times required to reach maturation and anthropogenic disturbances (such as habitat fragmentation) negatively impact the velocity at which species may expand their ranges. The simulation modelling of seed dispersal by the emu (Chapter Eight) revealed that even minor changes to landscape composition and configuration has substantial deleterious impacts on median and LDD dispersal distances.

Unfortunately, the duration over which the emus could be tracked (a maximum of 3 months, after which re-location proved unsuccessful) has limited the inferences that can be drawn regarding dispersal and LDD potential. The emu is known to show seasonal variation in movement patterns and behaviour (Dawson et al. 1984), and the tracking data cannot explore this. High resource availability in spring, coinciding with the commencement of fruiting of many large-seeded species, may result in reduced emu movement and subsequent potential seed dispersal distances. Lower resource availability in the warmer summer periods, which is when emus were tracked during the course of this study, have been seen to result in relatively larger-scale movements, particularly within semi-arid environments (Davies et al. 1971). However, in periods of poor resource availability in the jarrah forest, movement may be reduced as emus confine themselves to the agricultural matrix, where there is a ready supply of fodder and permanent water sources. The absence of fire in the study sites during the course of the study is also unfortunate. Fire stimulates the cone and seed production of many species in the jarrah forest (including M. riedlei and P. drouynianus), resulting in a localised flush of resources, which would undoubtedly influence movement and behaviour. In addition, the emus tracked in the study were captive-reared and this may have influenced movement within a natural forested habitat. However, Bellis et al.
(2004) showed that another captive-reared smaller ratite, the greater rhea (*Rhea americana*), used an agricultural/natural landscape matrix similarly to its wild-born counterparts.

**Long distance dispersal and responding to global environmental change**

Pollen cannot produce colonisation so dispersal, particularly LDD, has an important role to play in the accommodation of plants to global environmental change. In contrast to pollen dispersal, LDD of seeds by vertebrates (fish, birds, bats elephants etc.) ranges between 5 – 20 km (see Table 1 in Kremer *et al.* 2012). The potential physical range expansion afforded by LDD during climatic shifts is one response mechanism to climate change. However, climate change itself goes beyond a simplistic spatial shift of suitable climate envelopes (Kremer *et al.* 2012), involving complex change to climatic and other biotic conditions. The physical shift in populations also needs to be accompanied by relatively rapid genotypic adaptations (Williams and Jackson 2007). In this sense, the plant response to climatic change requires both a genetic and physical response, and there is emerging evidence that gene flow may occur over spatial scales beyond expected habitat shifts, and within a single generation for long-lived forest trees (Kremer *et al.* 2012).

The most recent evidence suggests that LDD is required to facilitate range expansions to combat adverse effects of climate change and other global environmental change on species survival (Corlett and Westcott 2013). The capacity of individual species to extend their ranges will depend on their dispersal morphologies, the dispersal mutualisms in which they function (diversity and abundance of dispersal agents) and the capacity of the disperser to move throughout the landscape. Emerging research suggests that habitat connectivity is a primary factor impacting the capacity of species to expand their ranges, with habitat corridors and ‘stepping-stones’ necessary to facilitate the movement of seeds (Saura *et al.* 2014). The successful utilisation of these stepping-stone patches depends on structure of the fragmented matrix and the ability of the dispersal agent to move through or over it. Large terrestrial frugivores are the least likely to be able to move between habitat fragments that are connected by a highly degraded or impassable matrix. In addition to this, these large frugivores are most likely to be lost through direct or indirect persecution in fragmented systems (McKinney 1997). Unfortunately, these large frugivores also represent the most effective dispersal agents (Schupp 1993; Schupp *et al.* 2010); capable of traversing...
large distances (at least in continuous habitat), consuming large amounts of seeds, and depositing these in a viable state within large clumps (Howe 1989).

**Future research directions**

Despite the huge proportion of species that rely on some form of animal-mediated dispersal (up to 75% in tropical forests, > 60% in temperate communities and dominant beyond the wet continental forests; Howe and Smallwood 1982), recent advances in modelling seed dispersal remain focused on those species transported by wind (see Nathan et al. 2011b; Heydel et al. 2014; Snell 2014; Trakhtenbrot et al. 2014). It is possible that the difficulties in modelling the complicated decisions that frugivores make and the uncertain impacts of spatially complex landscapes has resulted in this disparity in the literature. However, even mechanistic models of wind dispersal now reveal the impact that variations in landscape structure and geography can have on estimated seed dispersal kernels (Trakhtenbrot et al. 2014).

There is little doubt that spatially-explicit, agent-based models of seed dispersal by frugivores provide an immense opportunity for better understanding long distance dispersal and its importance in plants’ responses to global environmental change. The model of Bialozyt et al. (2014) is an excellent recent example of the use of animal behavioural and movement data to build a seed dispersal model and builds on previous animal-mediated seed dispersal models (see Morales and Carlo 2006; Carlo and Morales 2008; Will and Tackenberg 2008; Cousens et al. 2010a). The challenge faced by researchers investigating animal-mediated seed dispersal is to incorporate the extensive model elements in these works into future efforts. Further research needs to focus on the collection of animal movement data at both fine and broad spatial and temporal scales in order to capture the scale-dependent facets of animal movement that impact seed dispersal. Rapidly-evolving Global Positioning System (GPS) technology, combined with detailed activity and behavioural data are essential if we are to disentangle frugivore movement and seed dispersal in complicated landscapes (Mueller et al. 2014). Some difficult aspects of frugivore behaviour, especially memory, should also be considered (Corlett 2011).

Typically when LDD is examined, questions are asked about how much seed material is moved and how far? To a lesser extent, consideration is given to where (and in what spatial arrangement) seeds are deposited. In order to close the seed dispersal loop
(Wang and Smith 2002), more attention needs to be given to seed fate following LDD. Post-dispersal survival of seeds to reproductive adult is a critical component of models that attempt to predict range expansions by LDD (Nathan et al. 2011a). Improved understanding of seed persistence within different habitats (Long et al. 2014) provides some assistance in elucidating the fate of seeds following deposition.

The abundance and distribution of plants has been traditionally dichotomously split along seed-limited and establishment-limited lines, where the availability of seeds or the presence of suitable microhabitats prevents or promotes establishment (Clark et al. 2007). Climate change may open up new niches and remove the establishment limitation likely preventing range expansion (Lavergne et al. 2010). Another fundamental consideration is that the areas into which species move must experience the stochastic biotic processes that drive plant population dynamics under current conditions, especially for the fire-adapted Australian flora. With much of the Australian flora adapted to recurrent fire, which stimulates germination and recruitment, some plants may fail to expand their ranges where they are process-limited (namely fire), in addition to seed- and establishment-limited. Rapid loss of seed viability following deposition (which was observed for L. nutans and P. elliptica in this thesis) may further impede potential range expansions if the required biotic conditions are not met, especially if frugivore ingestion does not promote germination. Future research should focus on the biotic processes that are present within areas where species may seek refuge and how these will be affected as a result of global environmental change.

Conclusions

Assessing LDD is notoriously difficult, though recent technological and analytical advances have made the process less problematic. Given these developments, perhaps the most pertinent question to ask is not can we effectively estimate LDD, but why? Global environmental change, which includes climate change and associated anthropogenically-driven processes are already severely impacting populations of many plant species. For species whose seeds are dispersed by frugivores and for whom pollen transfer between populations is limited, LDD is the only means of (1) transferring genes into new regions/maintaining genetic diversity and (2) colonising new suitable habitats. Research needs to focus on how effectively species may be able to colonise new ranges, including improved vector-specific understanding of how organisms move within and between degraded and disconnected landscapes.
The emu, whose range extends throughout continental Australia, will play a key role in determining how many Australian plant species will respond to global environmental change. Its diverse diet, remarkable movement potential and resistance to direct and indirect persecution make it a key LDD vector. This study provides the basis for further work into the role of the emu as a dispersal vector within the diversity of changing landscape types throughout Australia.
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