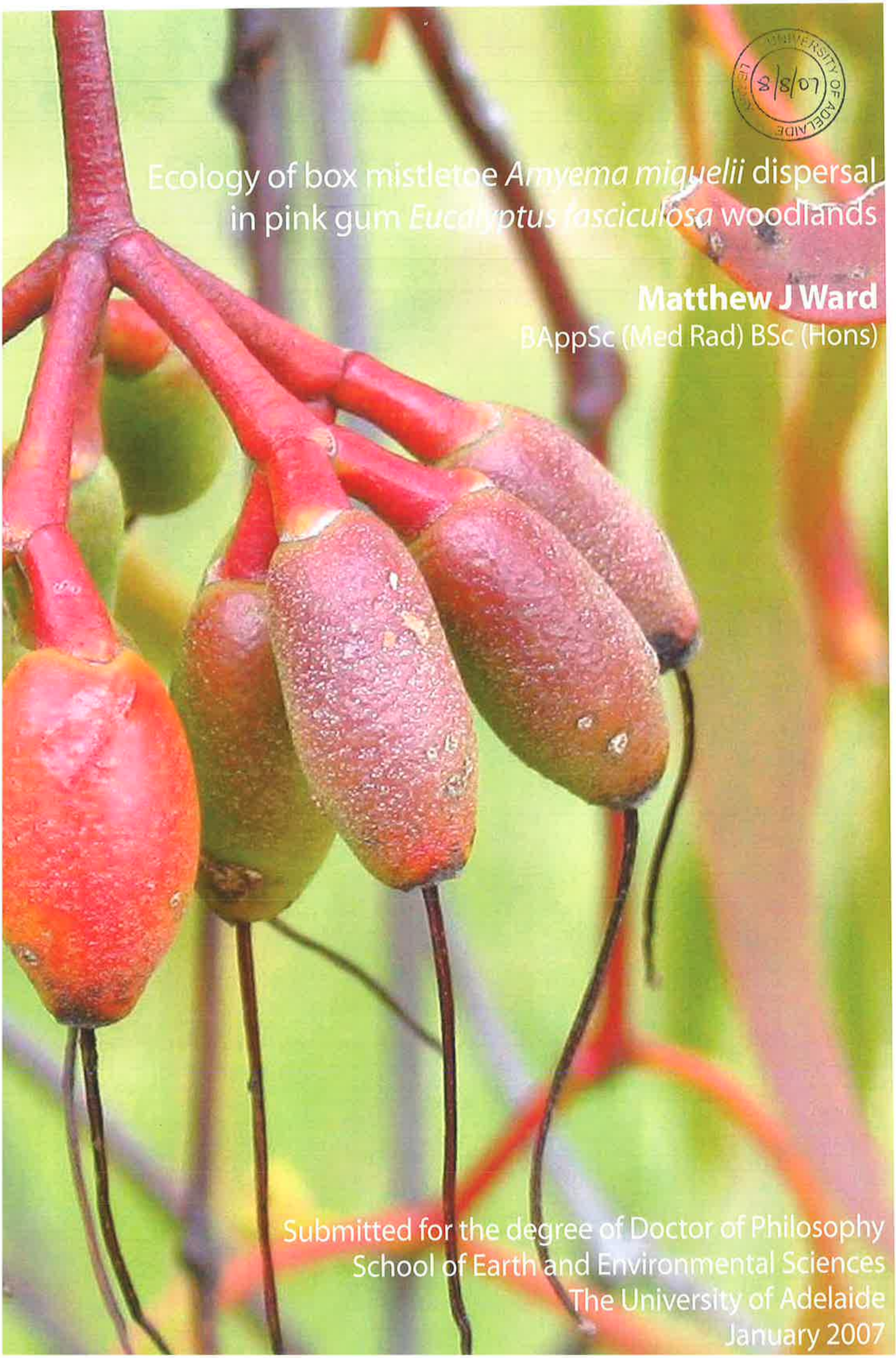

Ecology of box mistletoe *Amyema miquelii* dispersal in pink gum *Eucalyptus fasciculosa* woodlands

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CHAPTER 5: After dispersal: establishment and recruitment of box mistletoe *Amyema miquelii* in a pink gum *Eucalyptus fasciculosa* woodland.

CHAPTER 6: General Discussion.

DEDICATION

This thesis is dedicated to my nephew, Sam Roberts. Sam spent the last 22 months of his life in the Adelaide Women's and Children's Hospital fighting a rare genetic condition, Niemann's Pick Disease. Sam showed immense courage and brought joy to many. Sam passed away peacefully April 19th, 2005.

www.cycle4sam.com

ABSTRACT

The proliferation of box mistletoe *Amyema miquelii* in eucalypt woodlands of south-eastern Australia may have resulted from the suppression of canopy fires, a reduction in herbivory by possums, and through environmental change, an improvement in conditions for mistletoe dispersal and establishment. In the Mount Lofty Ranges (MLR), South Australia, box mistletoe is often seen in high numbers in pink gum *Eucalyptus fasciculosa* woodlands. The following dissertation investigated box mistletoe dispersal and establishment by Mistletoebirds *Dicaeum hirundinaceum* in a pink gum woodland. The broad aims of the study were to advance our theoretical knowledge of mistletoe dispersal ecology, to understand why pink gum woodlands are more susceptible to mistletoe infection, and to increase the amount of ecological information available to land managers.

A survey of box mistletoe and its *Eucalyptus* hosts in reserves of the MLR region revealed that almost a third of all pink gums were infected with box mistletoe. Individual pink gums with less foliage cover surrounding their canopy were more likely to host box mistletoe, suggesting canopy access for Mistletoebirds may influence the susceptibility of pink gums to mistletoe infection. Woodland type was more influential than fragmentation and edge effects in determining mistletoe presence, indicating a variation in host specificity across *Eucalyptus* species. The results of this survey indicated that further examination was required on Mistletoebird behaviour and mistletoe establishment success.

Two aspects of Mistletoebird ecology were examined: the influence of their movement patterns on the spatial dynamics of mistletoe dispersal, and their foraging behaviour. Mistletoebirds had home ranges of around 20 ha, and used small core areas (1 ha) of high mistletoe infestation more frequently than areas with lower mistletoe abundance. Modelling of mistletoe seed shadows indicated that the majority of mistletoe seeds (approx. 70%) would be deposited within 100 m of a parent plant. Consistent with this, seed rain modelling showed that mistletoe seed rain was aggregated, with birds dispersing large amounts of seed (> 66 000 / ha) in areas with higher mistletoe infestation levels. This indicated that the movements of

mistletoe dispersers promote mistletoe aggregation not only at the scale of an individual tree, but also at a landscape scale. From a management perspective, the results indicated that the removal of mistletoes from single trees may have only short-term results, as reinfection from neighbouring host trees is likely.

The attractiveness of pink gums to Mistletoebirds was a function of tree size, mistletoe crop size and tree access. Mistletoebirds preferred to forage in taller trees with a larger mistletoe crop size and which had greater canopy access, and Mistletoebirds most often alighted on dead pink gum when visiting a tree. The results support the notion that woodland dieback may improve conditions for mistletoe dispersal by allowing favourable habitat for Mistletoebirds, by increasing canopy access and by providing more perch sites. Dieback will also reduce mistletoe establishment, however, through a loss of suitable live host branches.

The high frequency of box mistletoe infection in pink gum woodlands could also be explained by differences in establishment of box mistletoe between eucalypt species. A mistletoe establishment experiment demonstrated that establishment was significantly higher on pink gums than on *E. porosa* and *E. camaldulensis*, and that mistletoes established on pink gums were larger and had a greater number of leaves. The differences probably lay in underlying differences in host physical and chemical defences, and subsequent relative success of mistletoes to establish a functional haustorium.

The dispersal syndrome of box mistletoe as described in this study is suitable and perhaps facilitated in the contemporary fragmented environment in a number of ways. These include an ability to concentrate their feeding and breeding activities in small areas of remnant vegetation, greater manoeuvrability between trees isolated by clearing, and easier access to the canopies and perch sites of individual trees in deteriorated woodlands. Priority research stemming from this study should include studies into the underlying causes of pink gum dieback, an experiment to test whether canopy dieback directly results in more frequent visitation by Mistletoebirds, an examination of Mistletoebird movements in areas with low mistletoe abundance, and continued monitoring of mistletoe abundance and tree condition as established in this dissertation.

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Thesis

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Personal

When researching potential PhD projects, I considered many locations and supervisors. In the end, the decision to return to South Australia and supervision under David Paton was an easy one. His commitment to research in order to achieve better conservation outcomes for South Australia has been the inspiration not only for this thesis but also the career I currently find myself in. DCP has been open minded, supportive and always good for a laugh. He has a pretty good grip on ecology too. Cheers.

Thanks to my family. Through their support my parents have provided me with many opportunities, and my siblings and their families have provided me with much laughter, perspective and sanity.

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Thanks to Aldinga Holiday Park for caravan accommodation. David Paton and Wendy Telfer read and gave constructive criticism on the chapter. Thanks to the Friends of Aldinga Scrub Conservation Park for being understanding about the number of trees with various colours of flagging tape around them.

Chapter 5

Amy Lees, Wendy Telfer and Judy Ward assisted in deploying seeds and/or checking seeds through the experiment. Colin Bailey assisted in the collection of mistletoe fruit, and provided outstanding assistance in placing ladders, locating mistletoes young and old, tagging mistletoes and providing valuable advice. Joel Allen provided valuable assistance with data entry. Wendy Telfer and David Paton read and improved earlier versions of the manuscript. Thanks to the Friends of Aldinga Scrub for being understanding about flagging tape around trees.

Images such as this, of a dead pink gum hosting many mistletoes, provided inspiration to conduct my PhD research.

CHAPTER 1

GENERAL INTRODUCTION

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Introduction

The academic in me would suggest that this thesis grew from an interest in theoretical issues surrounding seed dispersal, and unanswered questions relating to the evolution of host-parasite interactions. In fact, the initial impetus for the following research was a concern for the declining condition of *Eucalyptus* (eucalypt) trees in south-eastern Australia, and a broad interest in plant-animal interactions. Natural history observations are, however, an intuitive starting point for ecological research, and a concern for the wellbeing of the natural environment a worthy inspiration.

In temperate regions of Australia, eucalypts lining roadsides, isolated paddock trees, and natural stands of trees demonstrate a variety of signs of poor condition, including the browning of leaves, the loss of large amounts of foliage, the death of outer branches and often complete mortality. This deterioration in condition has been attributed to a range of factors including exotic pathogens, insect attack, drought and agricultural pollution (Landsberg and Wylie 1983; Reid and Landsberg 2000; Yates *et al.* 2000; Jurkis 2005). These trees can also be heavily laden with mistletoes, whose parasitic life form and noticeable habit make them an obvious target when attributing blame for the dieback of eucalypts.

A good bird watcher, however, will tell you that bird abundance and diversity is generally higher in areas where mistletoe occurs. Indeed, studies have supported this, and mistletoes are considered keystone resources for biodiversity (Watson 2001; 2002). Thus, mistletoes provide an intriguing paradox - mistletoes are likely to stress trees, yet moderate levels may be beneficial for biodiversity. It was this conundrum which initially drove me to conduct my PhD research on mistletoes.

Through the naivety which naturally accompanies the initial stages of research projects, I envisaged that my PhD would determine exactly why mistletoes are so prolific in some eucalypt woodlands, and would provide lucid direction for the management of mistletoes in eucalypt woodlands. A review of the recent literature, however, revealed that many basic yet important questions regarding mistletoe ecology remained unanswered. How far can mistletoe seeds be dispersed? What trees do dispersers prefer to visit? What percentage of seeds are dispersed to suitable locations? Can we predict how quickly mistletoes will spread?

On further consideration, I realised that answers to these questions would not only fill important gaps in our knowledge of the ecology of mistletoes, but would also provide important information which could be considered in an applied context. Therefore, I undertook a PhD research program which aimed to gain a better understanding of the patterns of mistletoe dispersal in both an Australian and international context.

The following dissertation begins with a background and literature review of 'directed' seed dispersal, mistletoe ecology, and the management issues surrounding the proliferation of mistletoes and host condition. The thesis then comprises four data chapters and a discussion chapter. All chapters that present original data (Chapters 2-5) are written in a style appropriate for publication in a scientific journal, and Chapters 2 and 3 have already been published or accepted for publication. Each chapter can, therefore, be read both as an individual contribution to knowledge, and as part of a collective that makes a substantial contribution. Therefore, individual chapters contain detailed literature reviews and some information is unavoidably repeated in the methods and discussions of the chapters.

Where possible, I have tried to preserve a logical progression of ideas as one advances through the chapters. In addition, each chapter is preceded by a preamble that briefly describes the content of the chapter and presents information on the publication status of the chapters at the time of thesis submission (where applicable). All literature cited in this thesis is displayed in a separate section at the end of the thesis.

Directed seed dispersal

The acquisition of space is critical to the growth and maturation of many plant species. Unlike animals, plants are not motile, and they must therefore develop mechanisms by which their seeds can be dispersed and established in a new site. The manner in which plants disperse their seeds, and the implications of these for ecology, biogeography and evolution, has been the subject of continued research and discussion (van der Pijl 1969; Howe and Smallwood 1982; Howe 1986; Murray 1986a; Nathan and Muller-Landau 2000).

The wide variety of mechanisms by which seeds are dispersed encompass both abiotic and biotic means (van der Pijl 1969). Abiotic dispersal includes the dispersal of spores, fruits and seeds using wind and water currents (Burrows 1986; Murray 1986b), as well as the role fire plays in the release of seeds of some plants (Whelan 1986). Biotic seed dispersal is best reflected in animal mediated seed dispersal, including dispersal by invertebrates, fish, reptiles, mammals and birds (van der Pijl 1969; Murray 1986a). The dispersal of seeds by birds is most often seen in a wide variety of plants which develop fleshy fruits, which are consumed by birds and often disseminated in a condition suitable for germination (Snow 1971).

Three non-exclusive hypotheses could explain the advantages of seed dispersal, and there is much evidence for and against each advantage (Howe and Smallwood 1982). The 'Escape Hypothesis' suggests that seeds dispersed away from the parent plant will enjoy greater recruitment success through decreased density- or distance-dependent mortality (Janzen 1970). The 'Colonisation Hypothesis' acknowledges the variable nature of environments, and presumes that the aim of a parent plant is to disperse seeds widely in space and time to allow the colonisation of uncompetitive environments. The 'Directed Dispersal Hypothesis' assumes that seed dispersal adaptations ensure seeds are dispersed directly to sites suitable for establishment.

Directed dispersal can be demonstrated when dispersal agents take seeds to non-random places that are suitable for seedling establishment (Howe and Smallwood 1982). Critical to directed dispersal is the fact that seeds dispersed to particular locations should have greater establishment success than if they were dispersed to random locations – to be demonstrated this requires information on the substrate to which seeds are dispersed, and the establishment success of these seeds relative to seed dispersed to random sites.

For example, Davidson and Morton (1981b; 1981a) demonstrated that seeds of some chenopod plants are harvested by ants and returned to ant mounds, where they enjoy higher nutrient availability and have greater establishment success than seeds not dispersed to ant mounds. Also, Wenny and Levey (1998) demonstrated that by favouring canopy gaps for song perches, bellbirds *Procnias tricarunculata* deposited more seed in canopy gaps where seedling survival was higher because of fewer fungal pathogens in such gaps.

A broader component of seed dispersal is the spatial arrangement of seeds around the maternal plant. Processes such as predation, germination, competition, and growth of seedlings will vary depending on the location of seeds, thereby influencing recruitment patterns and the spatial pattern of parent plants (Nathan *et al.* 2000). The spatial arrangement of seeds can be described in terms of the 'seed shadow' of a plant and patterns of 'seed rain'. The 'seed shadow' of a plant is the spatial distribution of seeds dispersed around a parent plant (Janzen 1971), and 'seed rain' is the distribution of seeds within the habitat occupied by the plant population (Alcantara *et al.* 2000), a combination of the seed shadows of all plants.

Estimating the spatial arrangement of seeds which are dispersed by animals has been a challenge for ecologist for many years. Seed shadows have been measured and estimated using a number of techniques, each with advantages and disadvantages. Techniques have included direct observations of dispersers (Fragoso 1997; Gomez 2003), seed traps (Nathan *et al.* 2000), the measurement of seedling density (Hoppes 1988), the use of tracers such as small pieces of metal or fluorescent microspheres (Mack 1995; Levey and Sargent 2000) and extrapolating genetic links between plants and their parents (Dow and Ashley 1996 as cited in Levey and Sargent 2000). With the advent of radio-telemetry technology to track the movements of animals, predictive models of seed shadows have been produced from the accurate documentation of detailed movement paths (e.g. Murray 1988; Holbrook and Smith 2000; Westcott and Graham 2000).

The following dissertation aims to gain a better understanding of the directed dispersal of mistletoe seeds, and the resulting influence on the distribution and spread of mature mistletoe plants. It does so by investigating the foraging and defaecation behaviour of a disperser to determine the 'direct' part of mistletoe seed dispersal - that is, how and where seeds are dispersed, and the establishment success of these seeds on different final locales. Also, the spatial arrangement of seeds around parent plants is predicted by describing the movements of its primary disperser.

Mistletoes and directed seed dispersal

Mistletoes are plants of two major flowering plant families, the Loranthaceae and the Viscaceae, which show some degree of parasitism or dependence on a host plant – as either a root parasite, or more often a stem epiparasite (Barlow 1983; Calder 1983). All are shrubby and use the xylem sap of their host to provide water, mineral nutrients and heterotrophic carbon (Raven 1983; Reid and Yan 2000). With a few exceptions, the fruits of mistletoes are almost exclusively disseminated by birds.

The dispersal of mistletoes falls under the directed dispersal strategy, because seeds are dispersed directly to non-random locations - the small branches of potential host trees. It is perhaps the most striking example of directed dispersal (Howe 1986), as seeds must be firmly deposited on suitable host branches in order to survive, and seeds that land on the ground, on dead branches or on an unsuitable host, are wasted (Godschalk 1983b). Directed dispersal is unusual in plants dispersed by vertebrates, because plants can exert so little control over the behaviour of the fruit-eating animal and therefore where their seeds will be dispersed (Wheelwright and Orians 1982). Mistletoes, however, have overcome this problem and indirectly exert considerable control over the microenvironment to which birds will disperse their fruit.

They do this by producing fruits with a succulent, sticky viscid pulp which surrounds a soft seed (Kuijt 1969; Reid 1986). The viscous pulp provides a nutritious reward for avian dispersal agents (Bhatnagar and Johri 1983; Godschalk 1983a), and the sticky nature of the pulp means the disperser must wipe either its cloaca or beak on the branch of a potential host in order to rid itself of the seed (Davidar 1983; Reid 1989), hence transferring the seed to a potentially suitable location. Furthermore, some specialised mistletoe dispersers, such as the flowerpeckers (Dicaeidae), have simple alimentary tracts with wide intestinal lumen and a small gizzard, promoting short gut passage times and minimising any damage to the seeds (Desselberger 1931; Keast 1958; McKey 1975; Walsberg 1975; Richardson and Wooller 1988; Murphy *et al.* 1993). Dispersed seeds are, therefore, in a suitable condition for germination and establishment. This extraordinary example of coevolution between a plant and its disperser (Reid 1991) ensures that mistletoe seeds are directly deposited on the small branches of potential host trees.

As outlined in the previous section, directed seed dispersal can only be confirmed when it is proven that seeds that are dispersed to particular microsites have greater establishment success than seeds that are dispersed randomly. This has been established in many mistletoes systems, with seeds that are dispersed onto the small branches of host trees having higher establishment success than seeds that are dispersed to branches which are either too thick or senesced (Liddy 1983; Reid 1989; Sargent 1995; Yan and Reid 1995; Norton and Ladley 1998). Seeds must not only be dispersed to branches of suitable size, however, they must also be dispersed to the branches of compatible hosts.

Mistletoe host compatibility describes how susceptible a potential host is to infection and mistletoe infectivity (Yan 1993a), or the ability of a seed to establish to maturity on a host branch. Mistletoe seeds which are on incompatible hosts will still form a haustorium, which may penetrate through the host bark and reach the xylem, yet fail to form a functional connection with the host tissues (Yan 1990; 1993b). This may result from incompatible water potentials (Calder 1983), the growth of abnormal host tissue around the haustorium (Yan 1990), host chemical defences (Frei and Dodson 1972 as cited in *Clay et al.* 1985) or genetic incompatibility (Clay *et al.* 1985). The deposition of seeds on compatible hosts is therefore an important part of mistletoe directed dispersal.

The probability that seeds are dispersed to the branches of compatible hosts are increased by the feeding behaviour of most mistletoe seed dispersers. For example, the specialist disperser Phainopepla *Phainopepla nitens* preferentially perches in previously infected hosts trees, increasing the probability that desert mistletoe *Phoradendron californicum* seeds are lodged in a site suitable for establishment (Larson 1996; Aukema and Martinez del Rio 2002). The Chilean Mockingbird *Mimus thenca* perches and deposits seeds primarily on previously parasitised cacti, and the feeding behaviour of the Swallow-tanager *Tersina viridis viridis* in Brazil results in high concentrations of the mistletoe *Psittacanthus robustus* on the preferred host plants (Monteiro *et al.* 1992). This pattern of behaviour not only increases the probability that mistletoe seeds will be deposited on compatible hosts, it also leads to an aggregated distribution of mistletoes, with individual trees hosting large numbers of mistletoes. This is maintained through a positive feedback cycle, with more mistletoes increasing visitation by mistletoe dispersers, and hence greater seed rain (Aukema and Martinez del Rio 2002).

Host selection by birds is, therefore, a critical behavioural factor in the directed dispersal of mistletoes that maximises the chances of mistletoe seeds being deposited in suitable host trees. Furthermore, it can help to explain the prevalence of mistletoes among host species and infection levels among individuals of one host species (Lopez de Buen and Ornelas 1999) and patterns of mistletoe distribution at local scales (Aukema 2004).

The spatial distribution of mistletoe seeds around parent plants, however, has not been comprehensively assessed. The seed shadow of a mistletoe plant comprises not only a host selection component, but also the location of the disperser when it defaecates or regurgitates the seed relative to the parent mistletoe. This requires information on the movement patterns, gut passage times (GPTs) and the average visitation time to individual mistletoe plants. Research on mistletoe dispersal systems has described these components of seed shadow in varying detail, however no research has taken the extra step of quantifying seed shadow or the spatial component of mistletoe dispersal.

For example, the flight distance and perch times of phainopeplas were quantified in describing the spatial patterns of dispersal of *Phoradendron californicum*, however the seed shadow was not estimated (Aukema and Martinez del Rio 2002). Also, although GPTs and the mean distance of immediate post-feeding flights away from mistletoe plants of several barbet *Pogoniulus* species in South Africa were documented, Godschalk (1985) concluded only that seed dispersal apparently occurs 'not far from the parent plant'. A logical step in our understanding of mistletoe dispersal systems would therefore be to attempt to quantify the spatial components of seed dispersal.

Mistletoe dispersal in Australia

Birds are also the main dispersal vector of stem-parasitic mistletoes in Australia (Blakely 1922; Keast 1958; Barlow 1981; Liddy 1983; Reid 1986; 1990; Yan 1993c). The Mistletoebird *Dicaeum hirundinaceum* and Painted Honeyeater *Grantiella picta* are almost entirely dependent on mistletoe fruits, and the Spiny-cheeked Honeyeater *Acanthagenys rufogularis* regularly feeds on mistletoe fruit. However it is the Mistletoebird, a small 10 g member of the mistletoe specialist flowerpecker family Dicaeidae, which is the most widespread and specialised of the mistletoe dispersers. The taxonomy, morphology, biogeography, breeding biology, distribution and diet of Mistletoebirds has been well discussed and recently comprehensively reviewed (Keast 1958; Reid 1997a; Simpson 1997; Higgins *et al.* 2006).

Mistletoebirds are specialist dispersers of mistletoe fruit. Their diet consists almost exclusively of mistletoe fruit (Liddy 1982; Reid 1986; Simpson 1997; Higgins *et al.* 2006), they have a specialised alimentary tract which minimises damage to the seed (Richardson and Wooller 1988; Murphy *et al.* 1993), and their defaecation behaviour ensures a large percentage of defaecated seeds are dispersed directly to the branch of a potential host (Reid 1989).

The only rigorous description of mistletoe dispersal by Mistletoebirds was made in an arid acacia woodland in South Australia (Reid 1984). This was achieved through a direct comparison of disperser efficiency (proportion of seeds dispersed to a safe site), and disperser effectiveness (proportion of seedlings that a particular seed vector is responsible for disseminating), between Mistletoebirds and spiny-cheeked honeyeaters (Reid 1984; 1989). By making observations of defaecation behaviour and following the fate of disseminated seeds, it was shown that Mistletoebirds dispersed more seeds to suitable branches for infections than spiny-cheeked honeyeaters. These branches, however, were often dead, the wrong species or too thick to permit seedling establishment, with seed dispersal to live branches being a rare event (Reid 1989). Nevertheless, the gentle treatment of seeds in the Mistletoebird's gut ensured seeds had consistently higher germination percentages than seeds defecaeted by Spiny-cheeked Honeyeaters (Reid 1989).

As with other mistletoe systems, little is known about the spatial arrangement of mistletoe seed dispersal in Australia, primarily because little is known of the movements of Mistletoebirds. Although larger seasonal movements across parts of Australia have been described (Blakers *et al.* 1984; Schodde and Tidemann 1986; Simpson 1997; Higgins *et al.* 2006), the detailed movement patterns of Mistletoebirds at a local and landscape scale are poorly described. The most detailed information on small scale Mistletoebird movements are based on occasional observations of only three colour banded birds (Reid 1997a) from the same arid woodland, which suggested birds had large territories with a maximum diameter of 660 m and an area of 13-25 ha (Reid 1997a). Thus, the local scale movements of Mistletoebirds, and the implications on mistletoe seed dispersal, are the least known aspect of mistletoe ecology in Australia.

Hence, Reid (1997a) concluded that further studies were required on the movements of Mistletoebirds, which would allow a quantitative estimation of the 'seed shadow' of mistletoe plants and a detailed description of the spatial dynamics of mistletoe dispersal. Spatial information on where mistletoe seeds are dispersed to will also allow predictions on where and how mistletoe is likely to spread across a landscape. Such information would be useful for ecologists and land managers interested in the proliferation of mistletoe in eucalypt woodlands of south eastern Australia, which have been linked to tree decline. The Mistletoebird is the primary disperser of mistletoe in these woodlands, and further research on the spatial dynamics of mistletoe dispersal is, therefore, justified.

Mistletoe proliferation

In temperate eucalypt woodlands, it is generally accepted that box mistletoe *Amyema miquelii* has increased in abundance as a result of broad landscape changes since European settlement. In pre-European landscapes, mistletoe abundance was limited by a series of evolutionary and environmental filters relating to host specificity, pollination, dispersal, infection, environmental habitat quality, predation, and disturbance events (Norton and Reid 1997). European settlement, however, has caused changes to these filters, in particular changes to habitat quality, predation and disturbance events.

In response to these changes, mistletoe abundances have apparently increased in south eastern Australia. For example, the wide-spread tree clearance and habitat fragmentation and grazing induced suppression of natural tree regeneration since 1900, has coincided with apparent increases in mistletoe populations, particularly box mistletoe, drooping mistletoe *A. pendulum* and wire-leaf mistletoe *A. preissii* (Reid 1997b; Lavorel *et al.* 1999; Reid and Yan 2000). Simulation models have supported this trend, showing that intermediate levels of tree clearing and habitat fragmentation increase the abundance and spread of mistletoe (Lavorel *et al.* 1999).

Also, mistletoes are more sensitive to fire than their eucalypt hosts. Fire kills mistletoes and post-fire dispersal and re-invasion have to occur over long distances (Gill 1981). Large-scale fire suppression has therefore coincided with apparent increases in mistletoe infestations (May 1941; Reid 1997b). Lastly, a reduction in the density of brushtail possums *Trichosurus vulpecula* in many parts of south-east Australia, which are known to consume mistletoe leaves, is also thought to be a contributing factor in the apparent increase in mistletoe infestation levels (Reid 1997b).

The significant damage sometimes caused to host trees by heavy mistletoe infestations is, to an extent, a natural component of the forest and woodland ecosystems in which they occur (Reid *et al.* 1995). However in Australia, many problem mistletoe infestations threaten the maintenance of remnant farm trees and trees in conservation reserves.

Since the early 1900s, the pruning of branches carrying mistletoe, or pruning of the mistletoe itself, has been the primary mistletoe control technique (Fagg 1997), and in some cases it has been shown to be effective in maintaining or restoring tree health. For example, the survival of Blakely's red gum *E. blakelyi* was significantly greater for trees with all mistletoe pruned than for untreated trees, and an increase in host foliage and radial growth was attributable to mistletoe removal (Reid *et al.* 1994). Given mistletoe is a keystone resource for biodiversity across the world (Watson 2001; 2002), however, all pruning should coincide with appropriate monitoring of tree condition. Furthermore, pruning is costly, logistically difficult, may lead to a significant loss of a tree's foliage, and it is only a short-term measure.

A better understanding of the effectiveness of different mistletoe pruning strategies could be gained through modelling the likely spread of mistletoes within theoretical landscapes. For example, Lavorel *et al.* (1999) demonstrated that the spread of mistletoe was likely to be greater in a fragmented landscape. This work was based on empirical mistletoe demographic data from arid acacia woodlands, and made assumptions about host tree selection behaviour and the movements of Mistletoebirds. A next step in the management of mistletoes in eucalypt woodlands, therefore, is to provide more accurate information on Mistletoebird movements and behaviour which would then be available for the development of more accurate models of mistletoe spread.

The following dissertation sets out to understand the patterns of mistletoe dispersal in a woodland with particularly high abundances of box mistletoe in the Mount Lofty Ranges (MLR), South Australia. It does so by identifying particular eucalypt species which suffer from heavy mistletoe infestations and by testing mistletoe establishment success and recruitment rates on different eucalypt species. It also describes host tree selection behaviour of Mistletoebirds, and by documenting Mistletoebirds movements, models mistletoe seed shadow and seed rain.

Study objectives

In summary, the preceding discussion noted:

1) that mistletoe dispersal is a classic example of directed dispersal, with comprehensive knowledge that mistletoe dispersers, primarily birds, deposit seeds onto the small branches of potential host trees;
2) a lack of knowledge of the influence of mistletoe disperser movements on mistletoe seed shadow and patterns of seed rain;
3) an understanding of the influences of host tree selection in a variety of mistletoe systems, yet a lack of quantitative data on host tree selection and foraging behaviour of Mistletoebirds in Australia; and
4) an understanding of components of mistletoe dispersal ecology in arid systems of Australia, yet an urgent need for research into host and mistletoe population dynamics and mistletoe dispersal in eucalypt woodlands where heavy mistletoe infestations may be a factor in tree decline.

Therefore, this project will examine the spatial dynamics of mistletoe dispersal by Mistletoebirds in eucalypt woodlands in South Australia. It will aim to:

1) investigate the habitat and host attributes which contribute to varying levels of mistletoe infestations in the Mount Lofty Ranges, South Australia;
2) document the local movements of Mistletoebirds and model mistletoe seed shadow and seed rain;
3) describe the host tree selection behaviour of Mistletoebirds, and document detailed behavioural patterns whilst foraging for mistletoe fruit; and
4) test and determine the establishment success of box mistletoe *A. miquelii* on different eucalypt species, and document natural recruitment and mortality on pink gums.

A flow chart representing the flow of ideas between research chapters, and the transfer of data from one chapter to another, is given in Fig 1.1.

Study location

Within South Australia, box mistletoe can occur in high densities on a variety of eucalypt species and in a variety of geographic locations. In the Flinders Ranges, for example, box mistletoe occurs on mallee eucalypts such as *Eucalyptus socialis.* Also, box mistletoe occurs in such high densities on blue gum *E. leucoxylon* in the picturesque hills of the Clare Valley (Ben Kahn 1993), that a 'mistletoe action group' was established. In parts of the South East, proliferations have seemingly contributed to dieback on large numbers of sandhill stringybarks *E. arenaceae* (pers. obs.).

A study of the spatial ecology of mistletoe dispersal and the link with mistletoe proliferations could, therefore, have occurred in one or numerous sites across South Australia, particularly if the studies of various aspects of mistletoe dispersal were to be replicated. However, a comprehensive study of mistletoe ecology needed to cover the salient stages of dispersal – where dispersers move, how they behave when disseminating fruit, where they deposit seeds and what happens to these seeds after they have been deposited. In the context of a modern PhD program with strict timelines, this would have been logistically impossible over numerous study sites.

I decided to focus my research at Aldinga Scrub Conservation Park (Aldinga Scrub hereafter) within the southern Mount Lofty Ranges (MLR hereafter), which has large numbers of healthy fruiting box mistletoe. My decision was justified the first day Daniel Rogers, Colin Bailey and Tina Bentz prompted me to start trapping Mistletoebirds – I caught 6 Mistletoebirds in an afternoon of trapping. In hindsight, Aldinga Scrub was an excellent choice of study site.

Accordingly, three chapters of the following dissertation were conducted in Aldinga Scrub. These included documentation of Mistletoebird movements, the foraging behaviour of Mistletoebirds and monitoring and experimental studies of mistletoe recruitment and establishment. By conducting research on all these elements of mistletoe dispersal within the one study site, I have gained a detailed appreciation of the parameters of mistletoe dispersal within a fragment of eucalypt woodland typical of those across temperate Australia.

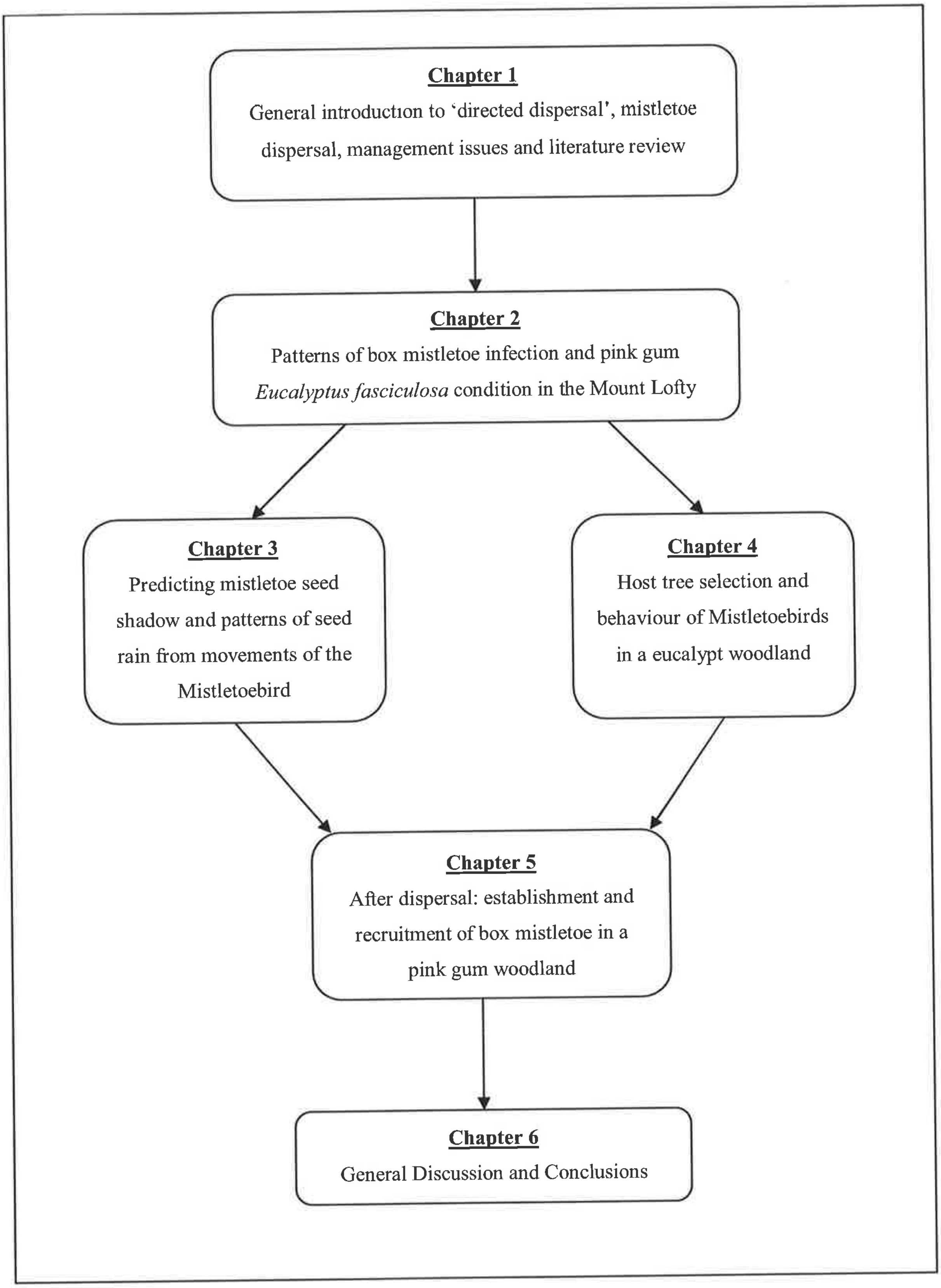

Fig. 1.1. Flow chart of the following dissertation.

Below I give a brief description of Aldinga Scrub, with much of the detail gleaned from Wollaston (1989) and the Australian Heritage database (http://www.deh.gov.au/heritage/ahdb/index.html and http://www.environment.gov.au/cgi-bin/ahdb/search.pl?mode=place_detail;search=place_name%3DAldinga%2520Scrub%3Bkeyword_PD%3Don%3Bkeyword_SS%3Don%3Bkeyword_PH%3Don%3Blatitude_1dir%3DS%3Blongitude_1dir%3DE%3Blongitude_2dir%3DE%3Blatitude_2dir%3DS%3Bin_region%3Dpart;place_id=18372).

Aldinga Scrub

Aldinga Scrub is located on the Willunga Plains, approximately 45 km south of Adelaide, South Australia (138° 27′ E, 35° 18′ S, Fig. 2), within the Mount Lofty Ranges (for a description of the MLR see chapter 2). The climate at Aldinga is temperate, with maximum temperatures in winter and summer averaging 15° C and 27° C respectively. Mean annual rainfall is approximately 450 mm, with most precipitation occurring in the winter months (Commonwealth Bureau of Meteorology 2005).

Prior to European settlement, the area of Aldinga Scrub was the territory of the Kaurna tribe, which occupied the Adelaide plains south to Cape Jervis (Fig. 1.2). Being the catchment area for the adjacent Willunga Hills, the area was wet, yet also provided ideal open country for kangaroo and emu. The area of Aldinga Scrub provided shelter for locals, as indicated by the seventeen campsites distributed within the reserve (Campbell 1989). It also provided numerous abundant plant foods (e.g. native peach *Santalum acuminatuum*, weeping pittosporum *Pittosporum phylliraeoides* and white currants *Leucopogon parviflorus*), as well as shell-fish, fish, a variety of mammals and numerous waterbirds (Campbell 1989; Gardiner 1989). Stone tools in the area indicate Aboriginal presence for at least 20 000 years, but shortly after European arrival the local Kaurna people declined rapidly.

European settlement also had a massive impact on the natural environment of the Willunga Plains and of Aldinga Scrub. Apart from the wide-scale clearance of native vegetation, the most dramatic change to the Aldinga Scrub area was the loss of surrounding water bodies, through drainage of the land for agriculture. A large lagoon in the north-east corner is now only reflected by the presence of river red gums, while a boggy swamp which occurred on the eastern boundary is no longer present (Gardiner 1989). Two wetlands occurred south of the park, including the large washpool, which is now the only remaining major wetland of the area and is a focus of contemporary Aboriginal identity. The loss of all these water bodies has probably played a major role in the current deteriorated state of many of the vegetation communities in the park.

The park was proclaimed in 1985, and in its current state is approximately 300 ha and surrounded by agriculture and housing to the south and east, and housing to the north and the west (Fig. 1.3). The continued encroachment of housing, including a housing development on the northern boundary of the park in 2004, continues to cause anger and protests amongst locals concerned about the cultural and environmental values of the park, because Aldinga Scrub represents the last remnant of native coastal woodland on the Adelaide plains.

Aldinga Scrub is noted for its unusual plant associations, including species characteristic of sclerophyll forest, mallee scrub and coastal sands (Wollaston 1989). Eleven plant communities occur in the scrub containing five rare plant species, one rare lichen, and five uncommon plant species (Kraehenbuehl 1989). Aldinga Scrub, being the only substantial remnant in the Adelaide coastal region, is also home to several declining woodland bird species, including dusky woodswallows *Artamus cyanopterus*, hooded robins *Melanodyras cucullata* and crested shriketits *Falcunculus frontatus*. Although 166 bird species have been recorded in Aldinga Scrub over the period 1976-86, including many water birds in the washpool (Ashton 1989), many species in that list no longer occur (pers. obs.).

The major vegetation communities in Aldinga Scrub, based on extent, are low and open pink gum *Eucalyptus fasciculosa* woodlands (Fig. 1.3). The largest pink gums in the eastern portion of the park are in excess of 10 m tall, and closer to the coast the pink gums are smaller and rarely reach a height over 5 m. The average height of all pink gums used in the following studies in Aldinga Scrub was around 7 m. These pink gum woodlands an understorey layer of small trees such as *Acacia pycnantha*, shrubs such as *Leucopogon parviflorus* and heathland plants such as *Banksia marginata* and *Leptospermum myrsinoides.*

The condition of many of the pink gums in Aldinga Scrub is poor. Although a specific cause has not been investigated, it is possible it has resulted from significant changes in hydrology, with the draining of much of the surrounding water bodies and potential lowering of the ground water. In addition, there are high box mistletoe abundances, which would cause added water stress on trees. These high box mistletoe abundances primarily occur in the eastern portion of the park, where pink gums are significantly taller and have larger canopy volumes. It is here that Mistletoebirds are more common and trapping of Mistletoebirds possible, and therefore where the majority of field work for the following dissertation took place.

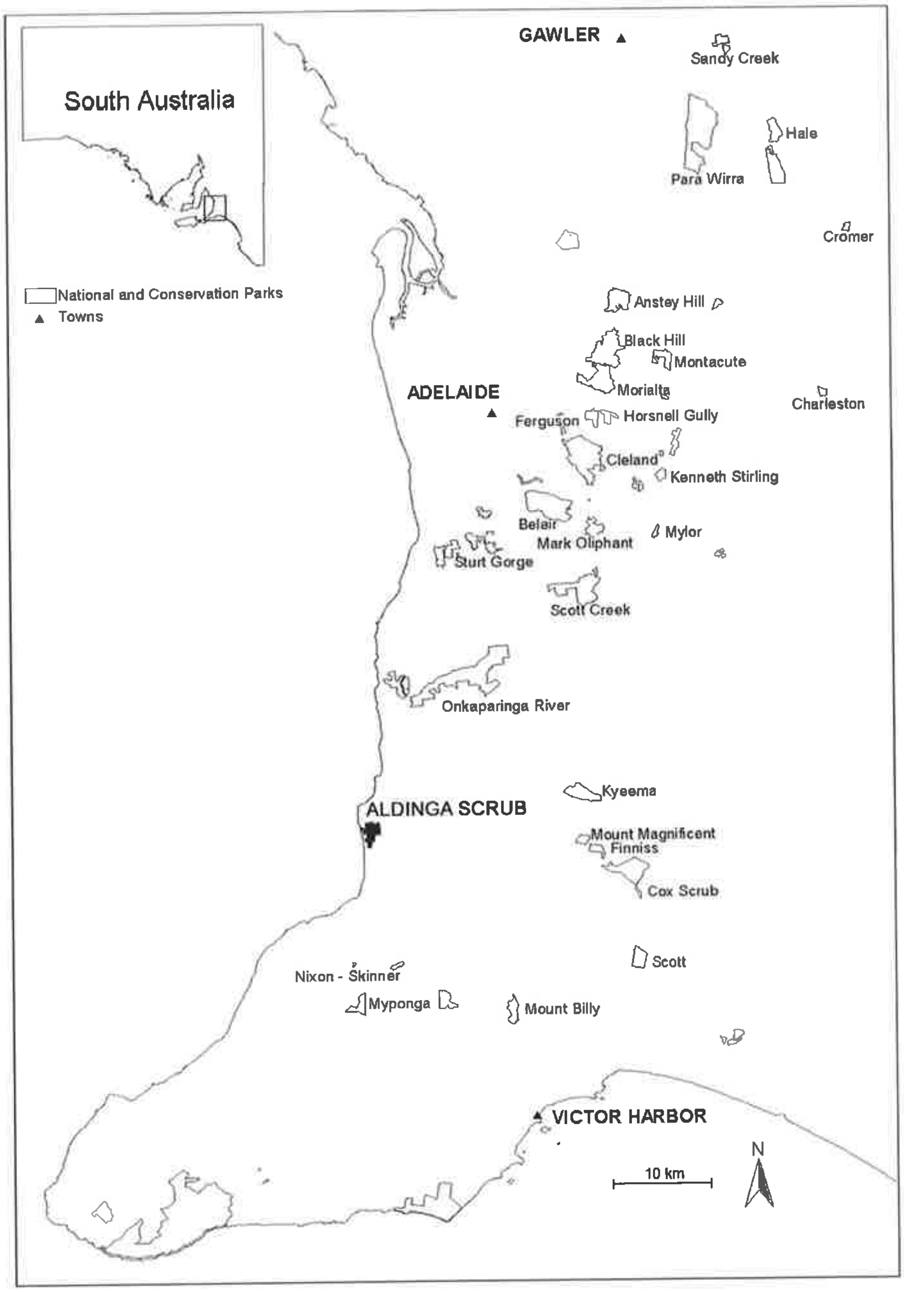

Fig 1.2. Reserves within study region, the southern Mount Lofty Ranges, in South Australia. Note the location of Aldinga Scrub, the primary study site for Chapters 3, 4 and 5.

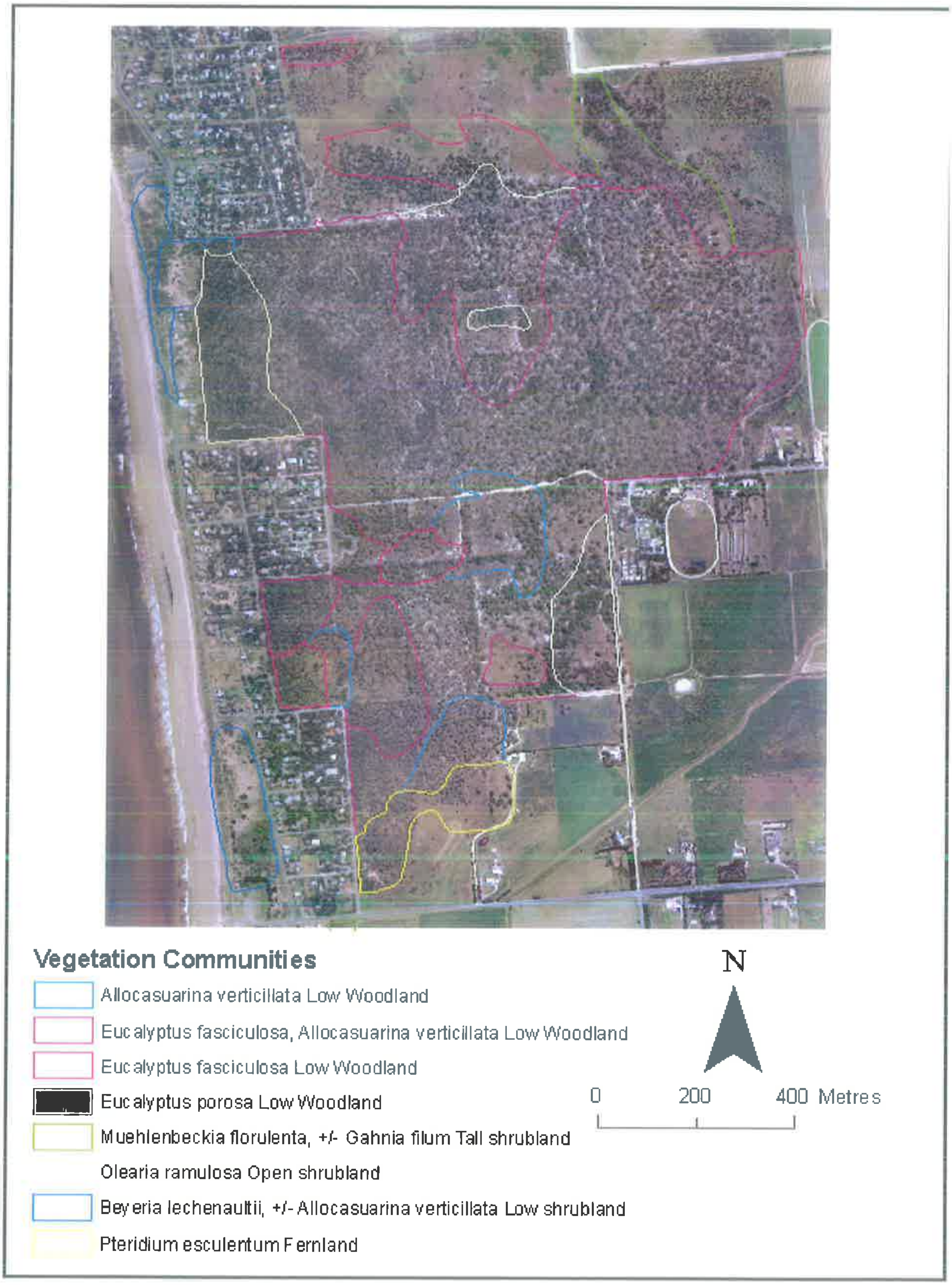

Fig. 1.3. Aerial photograph of Aldinga Scrub showing the location of different vegetation communities. The scrub is bordered to the south and east by agriculture, and to the west and north by housing.

Typical dieback seen in pink gum *Eucalyptus fasciculosa* woodlands of the Mount Lofty Ranges, South Australia. Many trees without box mistletoe *Amyema miquelii* were in similar condition. This photo was taken in Sandy Creek Conservation Park, a reserve in which pink gum condition is dire.

CHAPTER 2

PATTERNS OF BOX MISTLETOE INFECTION AND PINK GUM CONDITION

Chapter 2 Preamble

Chapter 2 presents a survey of box mistletoe infection across the Mount Lofty Ranges, South Australia. In the context of the thesis, it paints a scene of frequent mistletoe infection in pink gum woodlands, and provides direction for further research into mistletoe ecology within these woodlands. I was responsible for the design of the survey, and the use of an information-theoretic approach for data analysis.

This chapter was submitted for publication to *Forest Ecology and Management* on 16th June 2004, and accepted on the 22nd March 2005. Permission to reproduce this manuscript has been granted (see Appendix 1). The reference for the manuscript is: Ward, M. J. (2005). Patterns of box mistletoe *Amyema miquelii* infection and pink gum *Eucalyptus fasciculosa* condition in the Mount Lofty Ranges, South Australia. *Forest Ecology and Management* 213, 1-14.

CHAPTER 2

PATTERNS OF BOX MISTLETOE *AMYEMA MIQUELII* INFECTION AND PINK GUM *EUCALYPTUS FASCICULOSA* CONDITION IN THE MOUNT LOFTY RANGES, SOUTH AUSTRALIA

2.1 ABSTRACT

Mistletoe occurrence, host condition and habitat variables were assessed in reserves throughout the Mount Lofty Ranges, South Australia, to: 1) document the presence and abundance of box mistletoe *Amyema miquelii* in *Eucalyptus* woodlands; 2) compare the condition of pink gums *E. fasciculosa* with and without box mistletoe; and 3) investigate correlations between box mistletoe presence, landscape features and individual pink gum tree features. Box mistletoe frequency was highest on pink gums, with 28% of trees across the study area hosting at least one box mistletoe, and 5% hosting at least five. Logistic regression models indicated that woodland type was more influential than other landscape features, such as fragmentation and edge effects, in determining mistletoe presence. Individual pink gums with less foliage cover surrounding their canopy were more likely to host box mistletoe. The condition of pink gums was poor for infected (58% canopy dieback) and uninfected trees (43%) across all size classes, and there was no relationship between mistletoe abundance or presence and canopy dieback. Further investigations are required to determine why pink gums are more susceptible to box mistletoe proliferations than other woodland types.

KEYWORDS:

Box Mistletoe *Amyema miquelii*; Pink Gum *Eucalyptus fasciculosa*; tree decline, tree condition; logistic regression.

2.2 INTRODUCTION

Mistletoes from the family Loranthaceae are arboreal, hemiparasitic flowering plants which produce their own photosynthetic products, but which rely on the xylem sap of their host to provide water, mineral nutrients and heterotrophic carbon (Calder and Bernhardt 1983; Raven 1983; Ehleringer and Marshall 1995; Watling and Press 2001). They are dependent on birds for the direct dispersal of seeds to suitable locations on the small branches of host plant species, and the distribution of mistletoes across a landscape is therefore strongly dependent on disperser foraging behaviour and movements (Reid 1989; 1990; 1991; Martinez del Rio *et al.* 1996; Lopez de Buen and Ornelas 2001). The presence and abundance of mistletoes is also regulated by a range of abiotic and other biotic factors which act at differing spatial scales (Norton and Reid 1997; Aukema 2004).

At a landscape scale, mistletoe presence and abundance can be influenced by the distribution of suitable host species, dispersers and pollinators (Norton and Reid 1997), habitat fragmentation (Lavorel *et al.* 1999), fire (Kelly *et al.* 1997), herbivory (Reid and Yan 2000) and topographical features such as elevation, steepness of slope and aspect (Hawksworth 1961; 1968; Smith 1972; Ganguly and Kumar 1976; Merrill *et al.* 1987; Aukema 2004). On an individual tree scale, mistletoe abundance generally increases with tree height, diameter and basal area (Downey *et al.* 1997; Bannister and Strong 2001), and trees closer to an 'edge' or an infested conspecific are more likely to host mistletoe (Lopez de Buen *et al.* 2002). The establishment of mistletoes is also influenced by the water status and canopy light regimes of individual hosts (Lamont 1983b; Reid and Lange 1988), and very high mistletoe abundances can result from the preferential feeding of mistletoe dispersers in previously infected hosts (Martinez del Rio *et al.* 1995; Aukema and Martinez del Rio 2002).

High mistletoe abundances may cause reductions in the height, diameter, foliage growth, reproductive output and survival of infected trees (Reid *et al.* 1994). Mistletoes are therefore linked to tree damage and tree decline in plantations, orchards, ornamental trees and natural forests and woodlands around the world (Hawksworth 1983), leading to study on the control of mistletoe (Minko and Fagg 1989; Kelly *et al.* 1997). Before control of mistletoe is carried out, however, the links between mistletoe proliferations and tree decline are worth investigating because: a) high mistletoe abundances are often symptomatic of larger landscape changes (Reid and Yan 2000); and b) mistletoes are keystone resources for biodiversity (Watson 2001).

Tree decline in fragmented eucalypt (*Eucalyptus*) woodlands of south-eastern Australia, for example, is often attributed to high abundances of box mistletoe *Amyema miquelii*. Although there is no published evidence for an increase in distribution or abundance in box mistletoe, it is generally accepted to have increased as a result of broader landscape changes, including a lack of canopy fires, reduced herbivory by arboreal marsupials, and improved habitat quality for mistletoe establishment and dispersal (Reid and Yan 2000). Yet many cases of tree decline do not involve mistletoe but rather changes in hydrology (Yates *et al.* 2000), insect attack (Landsberg and Wylie 1983) or pathogens (Paton *et al.* 2000; Reid and Landsberg 2000). Given this uncertainty, investigations which highlight patterns of mistletoe abundance, host condition and influences on mistletoe occurrence are required in landscapes where links are drawn between mistletoes and tree decline.

In the Mount Lofty Ranges, South Australia, mistletoes are more abundant on some *Eucalyptus* species than on others (pers. obs.). Also, the condition of these trees is often poor, leading to calls for investigations into mistletoe abundance and tree health. Epidemiology of mistletoe proliferations, however, is difficult because of the wide and interrelated range of regulating factors, and the fact that the primary drivers of mistletoe proliferations are likely to vary at differing spatial scales (Aukema 2004).

This study investigates mistletoe abundances and tree health in temperate eucalypt woodlands of the Mount Lofty Ranges, South Australia, at a range of scales. Specifically, the study objectives were to: 1) quantify mistletoe occurrence on different eucalypt species in reserves in the Mount Lofty Ranges (MLR); 2) investigate the relationship between Box Mistletoe presence and tree condition for the primary host of box mistletoe in the MLR, pink gum *Eucalyptus fasciculosa*; and 3) investigate correlations between box mistletoe presence, landscape features and individual pink gum tree features.

2.3 METHODS

Study site

The study was carried out in the southern Mount Lofty Ranges (MLR) of South Australia (138° 42′ E, 34° 59′ S), between July and November 2003. The climate is temperate, with maximum temperatures in winter and summer averaging 16° C and 28° C (Laut *et al.* 1975). Mean annual rainfall varies from 400 - 1100 mm, with most precipitation occurring in the winter months (Laut *et al.* 1975). In the 2 years prior to the study, the MLR received average rainfall and was not in drought (Commonwealth Bureau of Meteorology 2004). Vegetation of the MLR is primarily eucalypt woodland, particularly *Eucalyptus baxteri*, *E. obliqua*, *E. fasciculosa*, *E. leucoxylon* and *E. viminalis*. More than 90% of native vegetation cover has been cleared (Bryan 2000; Paton *et al.* 2000), with eucalypt woodlands in lower elevation areas of the MLR having been disproportionately cleared due to greater agricultural suitability (Paton *et al.* 2000). As a result, many of the remnant vegetation patches and reserves of the MLR are highly fragmented and occur on poor quality land. There are a total of about 4000 native woodland patches in the MLR, with an average size of 13.1 ha (Westphal *et al.* 2003).

Site selection

The study was confined to National Parks and Conservation Parks ('reserves' herein) of the MLR. Thirty three distinct reserve patches, containing fragments ranging in size from approximately 8 ha to 2127 ha (mean = 496.8 ha, median = 296.1 ha) were sampled (Fig 1.2, Table 2.1). Using ArcView 3.2 (ESRI 1999), the reserves were partitioned with a 500 m x 500 m theoretical grid. Study sites in each reserve were then selected by randomly choosing up to six points where the 500 m x 500 m grid lines intersected. Hence the minimum distance between any study plot centre was 500 m, limiting spatial autocorrelation. There was at least one study site in each of the 33 reserve patches. Some potential sites were not used because of inaccessibility, and several supplementary sites were chosen so that a representative proportion of all major woodland types was covered. Eighty seven sites were selected in total.

Mistletoe frequency on eucalypt species

To investigate mistletoe frequency on different eucalypt species, a 20 m wide x 200 m long belt transect running east to west was established at each of the 87 study sites. Within this transect, box mistletoe abundance was assessed by counting the number of live and dead box mistletoes on each eucalypt, and the species of eucalypt was recorded. This was carried out until either 50 trees had been surveyed, or all trees in the plot had been assessed.

Pink gum condition - box mistletoe presence

In order to investigate the relationship between tree condition and the presence and abundance of box mistletoe, 28 of the 87 belt transects which were located in pink gum woodlands were assessed for: 1) size distribution of pink gums; 2) the condition of the box mistletoe on individual pink gums; 3) the extent of canopy dieback on each pink gum; and 4) the proportion of epicormic growth of each pink gum. Size distribution of pink gums was assessed by measuring the diameter at breast height (DBH) of every fifth pink gum encountered along the transect with a ruler. DBH was averaged for multi-stemmed pink gums. The condition of box mistletoes on each tree was scored as either the majority of mistletoes on a pink gum being non-vigorous (demonstrating signs of dieback, particularly loss of foliage), or the majority of mistletoes vigorous. Canopy dieback of individual trees was determined by visually estimating the proportion of canopy foliage that had senesced. Eucalypt trees that have suffered stress often produce epicormic shoots along their branches or trunk. The degree of epicormic growth was therefore recorded as the proportion of canopy foliage that was made up of epicormic growth.

Table 2.1. Characteristics of reserves and belt transect locations in which box mistletoe *Amyema miquelii* presence was assessed in the Mount Lofty Ranges, South Australia.

Reserve	Reserve Area (ha)	Approx. fragment area	Approx. area of reserved *E. fasciculosa* woodland	No. of transect sites in reserve	No. of 'pink gum' transects	Average distance (m) from transect start to nearest edge of vegetation (range)
Aldinga*	266.2	266.2	138.6	4	3	171.1 (7.3 – 374.9)
Anstey*	364.0	197.4	197.4	6	3	171.3 (7.4 – 479.1)
Belair	859.1	1210.5	28.9	7	-	119.0 (10.7 – 439.9)
Black Hill	700.8	669.8	3.6	2	-	98.8 (20.6 – 241.2)
Charleston	54.2	54.2	0	3	-	147.3 (48.4 – 246.2)
Cleland	996.7	1143.2	0	1	-	129.1 (25 – 262.7)
Cox Scrub	544.9	544.9	0	2	-	212.12
Cromer*	44.1	106.5	27.0	2	1	29.6 (20.3 – 39.0)
Ferguson	8.0	8.0	0	1	-	69.0
Finniss*	103.0	219.9	27.9	1	1	213.2
Hale	7.9	1339.1	0	4	-	172.2 (74.1 – 234.4)
Horsnell Gully-1	110.4	914.0	14.6	2	-	83.1 (20.5 – 145.8)
Horsnell Gully-2	137.6			3	-	206.0 (23.2 – 371.9)
Kenneth Stirling-1	84.3	841.9	0	1	-	342.7
Kenneth Stirling-2	17.3	144.8	0	1	-	111.8
Kyeema	346.9	442.1	0	1	-	344.7
Lenswood	20.7	20.7	0	1	-	59.0
Manning*	43.4	43.4	43.4	1	1	92.0
Mark Oliphant	192.1	446.0	0	1	-	75.1
Montacute	200.3	1319.4	0	1	-	192.8 (52.9 – 312.7)
Morialta	540.2	783.1	0	3	-	73.6
Mt Billy*	198.8	310.4	169.1	4	1	227.6 (143.2 – 300.1)
Mt Crawford$^+$	190.5	190.5	10.3	3	-	166.5 (81.4 – 251.6)
Mt Magnificent	89.9	290.1	40.2	3	-	122.9 (10.0 – 299.1)
Mylor*	45.8	76.2	4.7	2	1	106.4 (34.9 – 178.0)
Myponga*	168.2	302.0	68.7	2	1	140.9 (10.0 – 271.8)
Nixon Skinner	7.8	10.5	1.3	1	-	45.5
Onkaparinga*	1548.0	184.5	83.2	6	5	151.2 (6.5 – 338.5)
Para Wirra*	1426.2	2127.0	671.8	7	5	301.8 (75.0 – 721.5)
Sandy Creek*	143.2	348.3	175.5	6	5	143.40 (72.9 – 233.4)
Scott*	211.5	325.0	168.8	4	1	191.5 (5.3 – 444.5)
Scott Creek	703.0	26.2	26.2	1	-	4.9
Sturt Gorge	223.3	120.7	120.7	1	-	178.5
Mean (Total)	264.4	496.8	63.8 (2021.9)	(87)	(28)	134.2

* Reserves in which pink gum *Eucalyptus fasciculosa* transects were located (see Table 2.3).

$^+$ 'Mt Crawford' reserve represents a small fragment of the larger Mt Crawford Forest Reserve

Landscape features – box mistletoe presence / absence

To investigate the relationship between broad landscape features and box mistletoe presence, certain landscape features were recorded for each of the 87 transects assessed for box mistletoe occurrence on different eucalypt types. Landscape features determined were woodland type, topography, solar radiation, dominant soil type, distance to the nearest edge and fragmentation.

Woodland type (WT) was determined from the dominant eucalypt within each transect's vegetation association and classified as either: blue gum (*E. leucoxylon*); red gum (*E. camaldulensis*); pink gum (*E. fasciculosa*); box eucalypt (*E. microcarpa, E. odorata, E. goniocalyx* and *E. porosa*); manna gum (*E. viminalis* subsp. *cygnetensis* and *E. viminalis* subsp. *viminalis*); or stringybark (*E. obliqua* and *E. baxteri*) woodland. Topography (TOPO) was classified in the field as either gentle, slope, valley / creek or hill top / ridge. A solar radiation index (RAD) was obtained from a physical environmental model linked to a digital elevation model within a GIS (Bryan 2003). The amount of solar radiation received at a site is a function of location, slope, aspect and topographic shading at a particular site. Soil type (SOIL) was categorised from a GIS soil map of the region (PIRSA 2001). Distance to edge (EDGE) was defined as the distance from the middle of the transect to the nearest edge of the remnant vegetation patch, and was calculated from a vegetation map (Smith and Goodwins 2001). Fragmentation (FRAG) was calculated by creating theoretical buffers of 300 m radius around the midpoint of each transect, and calculating the Mean Shape Index for the vegetation within these buffer zones using Patch Analyst (Elkie *et al.* 1999), an extension in ArcView. Larger buffers (e.g. 1 km) were not chosen because these would have a large degree of overlap between transect sites. Mean Shape Index equals one when the buffer patch consists of an unbroken circular patch of vegetation, and increases infinitely as the vegetation patch shape becomes more fragmented and irregular (McGarigal and McComb 1995). Other buffer sizes were also tested (150, 200, 250 and 350 m), however, analyses revealed variation in buffer size within this range did not affect the results presented here. Therefore, only FRAG values based on buffers of 300 m radius are presented.

Individual tree features - box mistletoe presence

To determine which individual tree characteristics influenced the presence of box mistletoe, a more detailed study was made of 175 individual pink gums (95 infected and 80 uninfected) at 20 study sites where box mistletoe was abundant (four sites at Aldinga Scrub, one at Anstey Hill, one at Cromer, six at Onkaparinga River, three at Parra Wirra and five at Sandy Creek). Belt transects that had previously been used for landscape and pink gum woodland health surveys were divided into five 20 m x 40 m cells. At the beginning and in the middle of each cell (10 m either side), the closest pink gum > 3 m in height (infected or uninfected) was chosen as the first survey tree. Following this, the closest pink gum within the same cell and at least 5 m away from the previously surveyed tree was chosen as the second survey tree. If the first tree surveyed within a cell was an infected tree, the second tree chosen (also > 3 m in height) was an uninfected pink gum, and vice versa. If there was no infected or no uninfected pink gums within one of the 20 m x 40 m cells, then only one pink gum was recorded for that cell.

On each sampled pink gum the presence of live and dead box mistletoe was recorded. Tree characteristics recorded included: diameter at breast height (DBH), height (HEIGHT), height of lowest canopy, north-south and east-west canopy diameters, relative height difference (RHD) between the pink gum and surrounding vegetation, surrounding canopy cover (SUR.COVER), dieback (DIEBACK), distance to the nearest infected eucalypt (regardless of whether it was contained in the sampling cell, NRST.MTOE) and the density of live box mistletoe (number of box mistletoe / m^2) within 5 m of the canopy edge of selected trees. The horizontal distribution of mistletoes within pink gum canopies was also recorded, occurring either in the inner or outer half of the canopy and expressed as the proportion (percent of total number of mistletoes) occurring in either category (assuming a cylindrical canopy, based on halving the radius of the canopy from the trunk and adjusted for the greater area of the outer canopy half). The vertical distribution of mistletoe was recorded as either the lower, mid or upper third of the canopy, and expressed as the proportion (percent of total number of mistletoes) occurring in these categories, assuming a cylindrical canopy.

The height of each pink gum was measured using a clinometer. In order to make tree measurements more efficient (many pink gums were multi-stemmed), DBH was measured using a ruler. For multi-stemmed trees DBH was averaged. Canopy area was determined by measuring north-south and east-west diameters for each pink gum, and calculated using the formula for the area of an ellipse (Πab where a and b = the North-South and East-West diameters divided by 2 respectively). Canopy volume (CA.VOL) was determined by measuring the height of the lowest canopy with a clinometer, subtracting this from the height of the tree to obtain r, and using the formula for the volume of a sphere ($4/3\Pi abr$). Crown shape ratio (CSR, Tanabe *et al.* 2001) is the ratio of canopy height : crown radius (average of canopy radius in 4 directions). The smaller the CSR, the more planar the canopy.

Both Relative Height Difference (RHD) and canopy cover surrounding each tree sampled (SUR.COVER) were assessed at 1 m, 3 m and 5 m beyond the edge of the canopy of each tree in four cardinal directions, so that a total of 12 recordings were made per tree for each attribute. Each RHD component was assessed by estimating (to closest 0.5 m) the height difference between the top of the pink gum and the tallest vegetation within a 1 m radius around each measuring point. A mean RHD was calculated for each tree from the 12 recordings taken (e.g. an RHD of + 2 m indicated the pink gum was on average 2 m taller than the surrounding vegetation). SUR.COVER was measured by looking vertically through a 55 mm long x 50 mm diameter cylinder divided into 4 quarters, counting the number of quarters (0 - 4) in which foliage (above 3 m in height) was present, and expressing the total count (between 0 and 48 for all 12 measurements around each pink gum) as percent cover.

Data analyses

Various statistics were calculated for analysis of box mistletoe frequency on different eucalypt types, and of correlations between pink gum condition and box mistletoe presence. A Pearson's goodness of fit test was used to determine whether observed proportions of different eucalypt species infested with box mistletoe were significantly different from their relative abundances. For pink gum woodlands, simple linear regression was used to investigate the relationship between the condition of pink gums relative to box mistletoe abundance, between the size of fragments and box mistletoe abundance, and a Pearson's goodness-of-fit test was used to determine whether the proportion of trees infested with box mistletoe was significantly different between size classes. For individual pink gums, basic *t*-tests were used to determine statistical significance between the individual tree architectures of pink gums with and without mistletoe.

Logistic regression models were used to investigate the relationship between landscape and individual tree features and mistletoe presence / absence. Because of the large numbers of zeros in the data sets, regression models of mistletoe abundance (as opposed to presence / absence) were not considered in this study. Initial analysis of mistletoe abundance with Poisson and Negative Binomial Regression indicated poor model fit, and suitable Zero-Inflated Poisson (ZIP) models were not available for the data sets. However, this may be conducted in the future.

Landscape attributes (WT, TOPO, RAD, EDGE, SOIL and FRAG) and individual tree features (HEIGHT, SUR.COVER, CSR, NRST.MTOE, CA.VOL and DIEBACK) were used as explanatory variables in the *a priori* development of a set of 20 and 17 models of mistletoe presence / absence at a landscape and individual tree scale respectively. These model sets included global models with all explanatory variables. Prior to parameter selection, simple linear regressions were performed between continuous variables, contingency tables for comparisons between categorical variables and one-way ANOVA for comparisons between continuous and categorical variables, so that the final chosen parameters were not correlated. Interactions among the variables were not considered, and post-hoc analysis revealed interaction terms did not improve model fits.

Models were fitted using generalised linear models (GLM) assuming a binomial error structure (1= mistletoe presence, 0 = mistletoe absence) with a logit link function (logistic regression) using S-PLUS 6.1 (Insightful 2002). Candidate models were ranked using Akaike's Information Criterion (AIC, Burnham and Anderson 2001; 2002). For all candidate models in the present study, model selection was based on a second-order bias corrected form of AIC (AICc) because n/K (sample size / number of parameters) was less than 40 (14.5 and 29.2) for the models of mistletoe presence at a landscape and individual tree scale respectively).

The proportion of variance explained by the chosen parameters was assessed by calculating, for the global models, the deviance ratio: [(Null Deviance - Residual Deviance) : Null Deviance]. Candidate models were then ranked by evaluating the difference (Δ_i) between the AICc for model *i* and the minimum AICc. The plausibility of each model was also ranked using the log Likelihood of each model ($\log(\Lambda)$), as well as Akaike weights (w_i). The larger the Δ_i, the less likely that model is the best model in the set of candidate models being considered, given the data, and models having $\Delta_i \leq 2$ have substantial empirical support as candidate models (Burnham and Anderson 2001; 2002). Akaike weights (w_i) can be considered as the probability of model *i* being the actual K-L best model given the set of candidate models being considered (Burnham and Anderson 2001; 2002). Only those models that make up the top 90% of Akaike weights should be used in making inferences (Burnham and Anderson 2002), and similar parameterisation across the best models can suggest an important influence of those parameters (e.g. Pardon *et al.* 2003).

2.3 RESULTS

Mistletoe frequency on different eucalypt types

A total of 4221 individual eucalypt trees, representing 11 different species, were assessed for box mistletoe presence across the MLR (Table 2.2). For all species considered, 12.6% of trees were infected with live box mistletoe, and the 530 infected trees had on average 2.7 ± 0.1 (mean ± s.e.) live box mistletoes per tree.

The proportion of trees infected with *A. miquelii* was significantly different among eucalypt species ($\chi^2 = 564.9$, d.f. = 6, 4130, $P < 0.0001$). Pink gums had a greater proportion of individual trees infected with box mistletoe than other eucalypt species, with 28.5% of all pink gums surveyed hosting at least one live box mistletoe, and almost 10% and 5% hosting greater than three and five live box mistletoes respectively. In comparison, 10.9%, 3.4% and 1.7% of all blue gum *E. leucoxylon* were infected with at least one, three and five live box mistletoe respectively, followed by box eucalypt species *E. microcarpa*, *E. odorata* and *E. porosa* (5.3%, 1.3% and 0.9%). For the six other eucalypt species encountered the frequency of box mistletoe infection was less than 5% (Table 2). Box mistletoe occurrence on infected trees was similar between pink gum and blue gum (both 2.7 live mistletoe per tree). Comparisons between other eucalypt species were not made because of the small number of host trees (Table 2.2). Note that for all stringybark and manna gum trees measured, only three hosted box mistletoe, which is consistent with the fact that drooping mistletoe is the more common mistletoe which infests these species.

For woodlands (as opposed to individual trees), there was roughly an equal probability of box mistletoe presence in pink gum (78%), blue gum (81%) and box eucalypt (77%) woodlands, followed by red gum (50%), manna gum (16%) and stringybark (12%) woodlands (Table 2.2).

Pink gum condition - box mistletoe presence

Of the 1200 pink gums surveyed within pink gum dominated woodlands, 31.9% were infected with live box mistletoe, while 37.8% were infected with live and / or dead box mistletoe. On average (± s.e.) there were 0.9 ± 0.1 live and 0.2 ± 0.0 dead mistletoes per pink gum, and an average (± s.e.) of 2.8 ± 0.2 live mistletoes and 0.6 ± 0.1 dead mistletoes on host pink gums. Simple linear regressions revealed no strong relationship between the number of live mistletoe and canopy dieback (r^2 = 0.01), or between the number of live mistletoe and the area of the fragment within which the tree were measured ($r^2 < 0.01$). Of all pink gums measured, 83.4% and 16.6% had primarily vigorous and primarily non-vigorous box mistletoe respectively. The mean level of canopy dieback for all pink gums was 48%, and 52% of all pink gums had at least 40% ('substantial') canopy dieback (Table 2.3). Infected pink gums had 58% canopy dieback (65% with substantial dieback) compared to 43% for uninfected pink gums (45.7% with substantial dieback). Mean epicormic growth for both infected and uninfected pink gums was 39% (Table 2.3).

The size class of 104 infected pink gums and 144 uninfected pink gums was assessed (Fig. 2.1). The observed proportion of trees infected with box mistletoe was significantly different amongst size classes from their proportional abundance in each size class ($\chi^2 = 53.0$, d.f. = 5, $P < 0.0001$), and pink gums with a DBH 11 – 15 cm were more commonly infected with box mistletoe. Mean canopy dieback (F=

0.12, d.f = 1, 245, $P = 0.73$) and epicormic growth (F=0.07, d.f. = 1, 245, $P = 0.40$) did not differ between pink gum size classes.

Table 2.2. Incidence and severity of box mistletoe *Amyema miquelii* infection on various *Eucalyptus* species. Three 'box eucalypt' species were combined (*E. microcarpa*, *E. odorata* and *E. porosa*). 'Long-leaved box' (*E. goniocalyx*) was not combined as there were sufficient samples for individual analysis. Two 'stringybark' species (*E. obliqua* and *E. baxteri*) were also combined. The proportion (%) of each tree species which was infected with at least one, three or five box mistletoe, as well as the mean number of box mistletoe per tree for infected trees, is given. Mistletoe abundances of 0 are given for eucalypt species with low sample sizes. Probability of mistletoe presence is given for rectangular 0.4 ha transect plots (200m x 20m) in different woodland types (WT). No probability is given for *E. cosmophylla* (cup gum) because no transect plots occurred in a predominantly cup gum woodland

Eucalyptus species (WT)	No. of trees assessed	Trees infected with x live *A. miquelii* (%)		*A. miquelii* per infected tree mean ± s.e. (n)	Probability of mistletoe presence in woodland type
		$x \geq 1$	$x \geq 5$		
E. *fasciculosa* (pink gum)	1494	28.5	4.7	2.7 ± 0.1 (425)	0.78
E. *leucoxylon* (blue gum)	643	10.9	1.7	2.7 ± 0.4 (70)	0.81
E. microcarpa / E. odorata / E. porosa (box eucalypt)	228	5.7	0.9	2.3 ± 09 (13)	0.77
E. *cosmophylla* (cup gum)	163	4.3	0	0 (7)	-
E. *camaldulensis* (red gum)	465	2.2	0.2	2.9 ± 1.3 (10)	0.50
E. *goniocalyx* (box eucalypt)	232	0.9	0	0 (2)	0.77
E. *viminalis* (manna gum)	232	0.4	0	0 (1)	0.16
E. baxteri / E. *obliqua* (stringybark)	764	0.3	0	0 (2)	0.12
All	4221	12.6	2.0	2.7 ± 0.1 (530)	12.6

Table 2.3. Comparison of canopy dieback and epicormic growth of pink gums *Eucalyptus fasciculosa* with (infected) and without (uninfected) box mistletoe *Amyema miquelii.*

Measurement	Uninfected *E. fasciculosa* (n = 817)	Infected *E. fasciculosa* (n = 383)	All *E. fasciculosa* (n = 1200)
Canopy dieback (mean ± s.e.) (%)	43.3 ± 1.3	57.7 ± 1.7	47.9 ± 1.1
Epicormic growth (mean ± s.e.) (%)	38.5 ± 1.5	39.4 ± 2.0	38.8 ± 1.2
E. fasciculosa with at least 40% canopy dieback (%)	45.7	64.5	51.7

'Canopy dieback' represents an estimation of the percentage of the potential canopy that is no longer present as a result of dieback. 'Epicormic growth' was estimated as that percentage of the present canopy that is made up of recent epicormic growth.

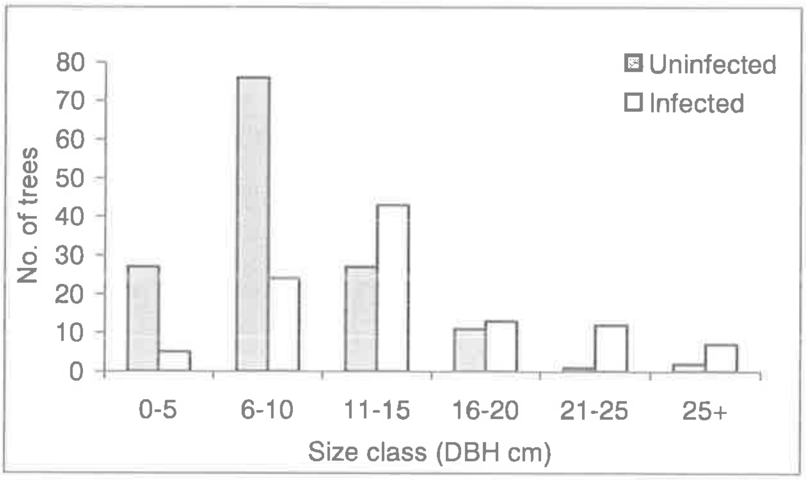

Figure 2.1. Size class frequency distribution of pink gums *Eucalyptus fasciculosa* in the southern Mount Lofty Ranges, South Australia. Size classes were determined from 248 pink gums (104 infected and 144 uninfected pink gums).

Landscape features - box mistletoe presence

For logistic regression models of mistletoe presence and landscape features, the deviance ratio calculated from the global model with all parameters showed good model fit, with 48.4% of the variance in the data explained by the included parameters.

AICc model selection criteria indicated that woodland type (WT) was found to be the best fit model, having a 54% probability of being the best model of box mistletoe presence from the candidate set (as indicated by the Akaike weight, w_i, Table 2.4, Burnham and Anderson 2002). The next best model of box mistletoe presence / absence was a combination of woodland type and fragmentation ($\underline{w_i}$ = 0.35). All other models were comparatively unlikely ($w_i \leq 0.06$,). The top two models made up the top 90% of Akaike weights, and the top five models included woodland type (WT) as a parameter (Table 2.2). This indicates that woodland type was the strongest correlate with variation in box mistletoe presence / absence. Given the large difference in Akaike weights and the similar parameterisation of these models, model-averaging procedures were not required, and post-hoc modelling indicated that model fit decreased considerably with the removal of the parameter WT.

Individual tree features - box mistletoe presence

For infected pink gums assessed in the individual tree features survey (as opposed to pink gums encountered in the broader pink gum condition / mistletoe presence survey), there were on average (± s.e.) 3.5 ± 0.4 live mistletoes per tree, and 0.9 ± 0.2 dead mistletoes per tree (Table 2.5). On a horizontal plane, mistletoes in infected pink gums occurred in roughly the same proportion between the inner (50.3%) and outer (49.7%) canopy. On a vertical plane, there was a roughly equal spread of mistletoes in the upper (46.5%) and mid (36.7%) parts of the canopy, with fewer in the lower portion of the canopy (16.8%).

Comparison of tree features of infected and uninfected pink gums showed that infected pink gums were taller (6.8 m for infected c.f. 5.6 m for uninfected, *t*-test = -3.8, d.f = 173, $P = 0.0003$); had larger diameter (DBH = 13.6 c.f. 10.3 cm, *t*-test =

-4.2, d.f. = 173, $P < 0.0001$), canopy area (29.9 c.f. 9.6 m^2, *t*-test = -4.8, d.f. = 173, $P < 0.0001$) and canopy volume (93.1 c.f. 23.6 m^3, *t*-test = -4.3, d.f. = 173, $P < 0.0001$); were more planar in shape (CSR = 1.5 and 2.9 for infected and uninfected pink gums, *t*-test = 3.8, d.f. = 173, $P = 0.0002$); but had similar levels of canopy dieback (48.3 c.f. 43.3 %, *t*-test = 0.9, d.f. = 173, $P = 0.38$, Table 2.5). On average, canopy cover surrounding infected trees (21.7%) was less than for uninfected trees (29.4%, *t*-test = 4.5, d.f. = 173, $P < 0.0001$), and infected trees generally were taller relative to the surrounding vegetation (+3.0 m) than uninfected trees (+1.0 m, *t*-test = - 7.8, d.f. = 173, $P < 0.0001$). Uninfected pink gums were slightly further away from another mistletoe infected tree (9.8 m) than were infected pink gums (7.0 m), but this was not statistically significant (*t*-test = 0.8, d.f. = 173, $P = 0.39$). The density of mistletoes within 5 m of infected pink gum canopies (0.6 mistletoes / m^2) was higher than for uninfected pink gums (0.3 mistletoes / m^2), but not significantly so (*t*-test = - 0.2, d.f. = 173, $P = 0.87$).

Logistic regression model fit of mistletoe presence and individual tree features was strong, with 36.4% of the variance in the global model explained by the given parameters. Post-hoc modelling demonstrated this did not increase with the inclusion of more parameters or differing models. Model ranking indicated that surrounding canopy cover (SUR.COVER) was the best fit logistic regression model, having a 34% probability (as indicated by Akaike weights) of being the best model for box mistletoe presence in individual pink gums from the candidate set (Table 2.6). The other candidate models with reasonable support were HEIGHT (w_i = 0.21), followed by a combination of SUR.COVER and NRST.MISTLETOE (w_i = 0.13). Although the best three models indicated a degree of model uncertainty with Akaike weights < 0.4, model averaging was thought unnecessary because of the similar and parsimonious nature of those models which made up the top 90% of Akaike weights. Those models which made up the top 90% of Akaike weights all only contained one or two parameters, including either SUR.COVER and / or HEIGHT. Box mistletoe presence on individual pink gums in pink gum woodlands, therefore, was primarily correlated with variations in the degree of foliage cover within 5 m of the canopy of individual trees, and variation in the height of the tree.

Table 2.4. Ranking of logistic regression models, using AIC model ranking procedures (Burnham and Anderson 2002), of box mistletoe *Amyema miquelii* presence / absence in 87 sites in the southern Mount Lofty Ranges, South Australia

	Candidate model	log(Λ)	K	AIC	Δ_i	w_i
1	**WT**	**-126.98**	**5**	**267.02**	**0.00**	**0.54**
2	**WT + FRAG**	**-126.01**	**6**	**267.89**	**0.87**	**0.35**
3	WT + RAD	-128.08	6	271.57	4.56	0.06
4	WT + FRAG + EDGE	-128.01	7	273.86	6.85	0.02
5	WT + EDGE	-129.65	6	274.71	7.70	0.01
6	EDGE	-135.59	1	275.32	8.30	0.01
7	FRAG	-136.25	1	276.64	9.62	< 0.01
8	FRAG + EDGE	-135.18	2	276.65	9.63	< 0.01
9	RAD	-136.59	1	277.32	10.31	< 0.01
10	TOPO	-136.50	6	288.42	21.41	< 0.001
11	TOPO + RAD	-136.47	7	290.79	23.78	< 0.001
12	TOPO + EDGE	-136.53	7	290.90	23.89	< 0.001
13	TOPO + FRAG + EDGE	-135.61	8	291.55	24.53	< 0.001
14	FRAG + TOPO + RAD	-135.80	8	291.94	24.92	< 0.001
15	WT + TOPO	-132.32	11	292.86	25.84	< 0.001
16	WT + TOPO + RAD	-134.22	12	299.42	32.40	< 0.001
17	WT + SOIL	-140.08	12	311.15	44.13	< 0.001
18	SOIL	-146.79	7	311.43	44.41	< 0.001
19	SOIL + TOPO + RAD	-146.74	14	330.24	63.22	< 0.001
20	GLOBAL	-157.31	20	370.84	103.82	< 0.001

Explanatory variables in candidate models were: WT = woodland type; FRAG = fragmentation index; EDGE = distance to the nearest edge; RAD = solar radiation index; TOPO = topography; and SOIL = dominant soil type. GLOBAL = global model including all parameters listed above. Log(Λ) is the log Likelihood of the model, K is the number of estimated parameters, AIC is the selection criterion, Δ_i = the difference between that model's second order bias corrected form of Akaike's Information Criteria (AICc) and the minimum AICc value, and w_i = Akaike weights. Candidate models with significant levels of empirical support ($\Delta_i < 2$) are shown in **bold.** Percentage of deviance explained by included parameters = 48.4%.

Table 2.5. Summary statistics of individual *Eucalyptus fasciculosa* / *Amyema miquelii* survey

Measurement	Uninfected (n = 80) *E. fasciculosa* (mean ± s.e.)	Infected (n = 95) *E. fasciculosa* (mean ± s.e)	*t*-test
Number of live mistletoe / tree	0	3.5 ± 0.4	
Number of dead mistletoe / tree	0	0.9 ± 0.2	
Height (HEIGHT) (m)	5.6 ± 0.2	6.8 ± 0.2	$^{+}$
Diameter at breast height (DBH) (cm)	10.3 ± 0.5	13.6 ± 0.6	$^{++}$
Canopy area (m^2)	9.6 ± 1.6	29.9 ± 3.7	$^{++}$
Canopy volume (CA.VOL) (m^3)	23.6 ± 5.3	93.1 ± 14.3	$^{++}$
Crown shape ratio (CSR)	2.9 ± 0.4	1.5 ± 0.1	$^{+}$
Canopy dieback (DIEBACK) (%)	43.3 ± 4.1	48.3 ± 3.3	
Surrounding Canopy Cover (SUR.COVER) (%)	29.4 ± 1.1	21.7 ± 1.2	$^{++}$
Tree height relative to surrounding vegetation (RHD) (m)	+ 1.0 ± 0.2	+ 3.0 ± 0.2	$^{++}$
Distance to nearest mistletoe infested tree (NRST.MTOE) (m)	9.8 ± 1.3	7.0 ± 0.7	
Density of mistletoe (live or dead) within 5m of pink gum canopy (no. mistletoe/m^2)	0.3 ± 0.0	0.6 ± 0.1	

'Tree' refers to *E. fasciculosa*, and 'mistletoe' refers to box mistletoe. 'Infected *E. fasciculosa*' is a pink gum infected with one or more live box mistletoe, 'uninfected *E. fasciculosa*' is a pink gum with no live or dead box mistletoe. $^{+}$ Statistically significant differences between the means of infected and uninfected *E. fasciculosa* at $P < 0.001$.$^{++}$ Statistically significant differences between the means of infected and uninfected *E. fasciculosa* at $P < 0.0001$.

Table 2.6. Ranking of logistic regression models, using AIC model ranking procedures (Burnham and Anderson 2002), of *Amyema miquelii* presence / absence on 175 individual *Eucalyptus fasciculosa* at 17 sites in the southern Mount Lofty Ranges, South Australia

	Candidate model	log (Λ)	K	AIC	Δ_i	w_i
1	**SUR.COVER**	**-271.47**	**1**	**547.02**	**0**	**0.34**
2	**HEIGHT**	**-271.96**	**1**	**547.98**	**0.96**	**0.21**
3	**SUR.COVER+NRST.MTOE**	-271.37	**2**	**548.88**	**1.86**	**0.13**
4	HEIGHT+NRST.MTOE	-271.48	2	549.10	2.08	0.12
5	SUR.COVER+DIEBACK	-271.54	2	549.22	2.20	0.11
6	HEIGHT+DIEBACK	-272.01	2	550.16	3.14	0.07
7	HEIGHT+SUR.COVER	-273.65	2	553.45	6.43	0.01
8	DIEBACK	-276.15	1	556.38	9.36	< 0.001
9	NRST.MTOE	-276.16	1	556.39	9.37	< 0.001
10	CSR	-283.13	1	570.33	23.31	< 0.001
11	SUR.COVER+CSR	-282.20	2	570.54	23.52	< 0.001
12	HEIGHT+CA.VOL	-283.66	2	573.46	26.44	< 0.001
13	CSR+NRST.MTOE	-283.67	2	573.48	26.46	< 0.001
14	CSR+DIEBACK	-284.36	2	574.87	27.85	< 0.001
15	SUR.COVER+CA.VOL	-287.36	2	580.87	33.85	< 0.001
16	CA.VOL	-288.43	1	580.93	33.91	< 0.001
17	GLOBAL	-304.35	6	623.37	76.35	< 0.001

Explanatory variables in candidate models were: WT = woodland type; FRAG = fragmentation index; EDGE = distance to the nearest edge; RAD = solar radiation index; TOPO = topography; and SOIL = dominant soil type. GLOBAL = global model including all parameters listed above. Log(Λ) is the log Likelihood of the model, K is the number of estimated parameters, AIC is the selection criterion, Δ_i = the difference between that model's second order bias corrected form of Akaike's Information Criteria (AICc) and the minimum AICc value, and w_i = Akaike weights. Candidate models with significant levels of empirical support ($\Delta_i < 2$) are shown in **bold.** Percentage of deviance explained by included parameters = 48.4%.

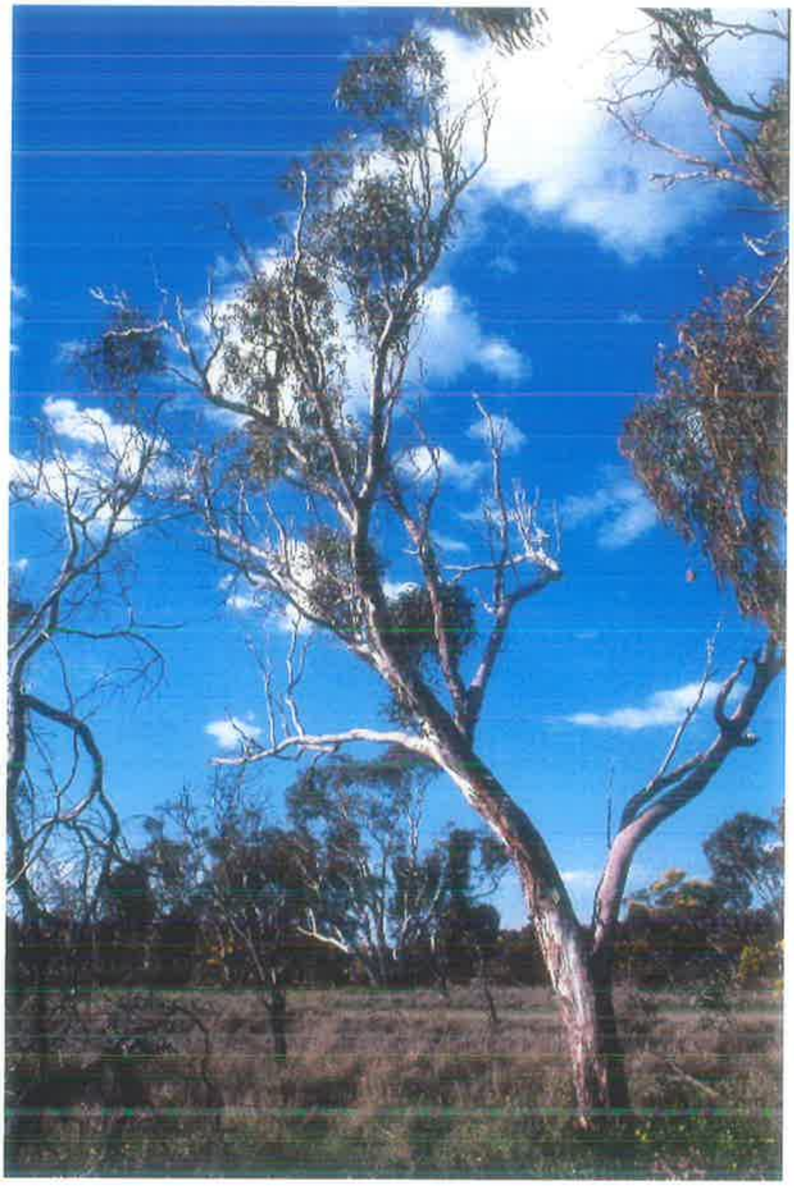

Plate 2.1. *Eucalyptus fasciculosa* with significant dieback in Aldinga Scrub Conservation Park.

2.4 DISCUSSION

At a landscape scale, box mistletoe presence in reserves of the Mount Lofty Ranges (MLR) was primarily correlated with woodland type, with the highest incidence of mistletoe presence in pink gum, blue gum and box eucalypt woodlands (all members of the Adnataria section of the Symphomyrtus subgenus, Nicolle 1997). However, the incidence and severity was highest on pink gums, with 28% of pink gums infected with at least one box mistletoe, and almost 5% infected with at least five box mistletoes.

Despite low host specificity across its range (Barlow 1984; Downey *et al.* 1997), the higher frequency of box mistletoe on a particular eucalypt type, as demonstrated for pink gums in the present study, is not atypical (Lamont 1985b; Reid *et al.* 1994; Yan and Reid 1995; Downey *et al.* 1997; Fagg 1997). Also, high incidences of box mistletoe infection have been demonstrated for other eucalypt types in previous studies. For example, Lamont (1985b) found 54% of *E. calophylla* carried box mistletoe in Western Australia, and Reid and Yan (2000) recorded mistletoe occurrence frequencies ranging from 32.7% to 49.0% on five common eucalypt hosts in northern New South Wales. However, both studies focused on narrow vegetation corridors where mistletoe abundances are generally high. In comparison, the present study was conducted across an entire region at randomly selected points within remnant patches of vegetation, where edge effects should be less important (mean distance to edge = 134.2 m, range = 4.9 – 721 m). This indicates that the incidence of mistletoe infection on pink gums demonstrated in the present study can be considered high.

Fragmentation and edge effects are generally accepted as key drivers of mistletoe proliferation in Australian woodlands (Norton *et al.* 1995; Norton and Reid 1997; Reid and Yan 2000) and overseas forests (Lopez de Buen *et al.* 2002). It is likely these effects have also contributed to the extensive occurrence of box mistletoe across the MLR, and for initial occurrence on trees close to habitat edges. Despite this, the present study found no strong relationship between fragment size or edge effects and mistletoe incidence and severity. However, the highly fragmented state of reserved remnant vegetation in the MLR (median fragment area sampled = 296.1

ha, range = 8 – 2127 ha) and the high incidence of mistletoe infection of pink gums, have probably made identification of such effects difficult.

The comparisons between the architectures of individual infected and uninfected pink gums, and their surrounding environments, are consistent with patterns of mistletoe occurrence on individual trees in Australia (Reid and Lange 1988; Norton *et al.* 1995; Downey *et al.* 1997) and overseas (Lekunze and Hassan 2001; Lopez de Buen *et al.* 2002). In general, infected pink gums were taller, had a greater girth and were more voluminous. This probably reflects that larger, older trees are exposed to mistletoe colonisation for a longer period, and have a greater abundance of smaller twigs and potential perch sites for bird vectors, therefore increasing the probability of mistletoe establishment.

In addition, logistic regression modelling demonstrated that box mistletoe presence on pink gums was correlated with reduced canopy cover immediately surrounding individual trees, albeit in woodlands with abundant mistletoe. Without experimental manipulation, we can presently only speculate as to the cause of this pattern. For example, the higher irradiance that would result from lower surrounding canopy cover may benefit germination and establishment of mistletoes (Lamont 1983a; Yan and Reid 1995). Also, variations in surrounding canopy cover may influence mistletoe presence by affecting canopy access for dispersers. The primary disperser of mistletoe in the MLR, the Mistletoebird *Dicaeum hirundinaceum*, moves rapidly and directly between trees, and when alighting on pink gums of the study area more commonly alights on exposed branches on the outer portion of trees (author's unpublished data). It is likely, therefore, that trees with canopies that are not physically or visually obscured by surrounding canopies are likely to receive a greater number of visits from Mistletoebirds, and consequently have a greater chance of hosting mistletoe. However, only further investigations will shed further light on this.

The condition of pink gums demonstrated in the present study is cause for concern: 52% of all pink gums demonstrated evidence of considerable dieback (> 40% canopy loss), and on average 48% of the canopy of infected and uninfected pink gums had senesced. Furthermore, levels of canopy dieback and epicormic growth were similar across all pink gum size classes. Dieback of this severity is more often seen on scattered eucalypts in agricultural lands of south-eastern Australia rather than in reserve settings (Paton and Eldridge 1994; Paton *et al.* 2000), and other eucalypt species in the MLR do not demonstrate similar levels of dieback (pers. obs).

Two interesting ecological and management questions arise from the study's results in regards to mistletoe. First, is the poor condition of pink gums a result of the high incidence and severity of mistletoe infection? Second, why is mistletoe abundance so high on pink gums?

Although uninfected pink gums had less canopy dieback than infected trees, the present study does not suggest a direct relationship between host condition and incidence or severity of box mistletoe. For example, there was no relationship between the number of mistletoes on pink gums and levels of canopy dieback in all pink gum woodlands sampled. Also for the 175 individual pink gums sampled, canopy dieback was a poor model for mistletoe presence and there was no statistical difference between dieback levels of infected and uninfected pink gums.

In the south-east of South Australia, *E.fasciculosa* is thought to suffer from water-induced stress through the drowning of roots during winter followed by acute water shortages during summer (White 1969). This leads to insect attack through outbreaks of the psyllid *Cardiaspina densitexta*. In the MLR, however, pink gums are not known to be widely affected by insect attack. A credible alternative hypothesis for poor pink gum condition is that the remaining pink gums occur on very poor quality soils, and their stress has been exacerbated by significant changes in hydrology. Pink gum woodlands may be, to some extent, phreatophytic (groundwater dependent) ecosystems which are not robust to changes in underlying hydrology. This is often cited as a cause of deterioration in terrestrial vegetation condition in rural areas of Australia (e.g. Groom *et al.* 2000; Sinclair Knight Merz 2001; Murray *et al.* 2003), and deserves urgent attention for pink gums in the MLR.

Why do pink gum woodlands support a higher incidence of mistletoe infection? Similar percentages of 200 m x 20 m plots in pink gum, blue gum and box eucalypt woodlands contained mistletoe (Table 2.2), indicating that pink gum woodlands *per se* are not more susceptible to initial mistletoe infection. However, the higher incidence of box mistletoe infection on individual trees indicates that pink gums and pink gum woodlands do support the appropriate conditions which can promote and/or sustain a box mistletoe proliferation.

For example, establishment percentages may be higher on pink gums than on other eucalypt types, or herbivory of box mistletoe leaves and seeds may be lower because the remaining pink gum woodlands may not provide suitable habitat for herbivores such as brush-tailed possums *Trichosurus vulpecula* (Reid 1997b), rosella parrots (*Platycercus* spp., Yan and Reid 1995) or herbivorous insects (Ward and Paton, unpublished data). Without further studies on these effects, however, we can only use the results of the present study to hypothesise about possible causes.

The present study demonstrated that box mistletoe was more likely to be present on trees with less foliage immediately surrounding their own canopies. This is in keeping with the aforementioned behaviour of Mistletoebirds, which may prefer to access perch sites on the outer edge of a tree's canopy. It is plausible, therefore, that mistletoe dispersal is more efficient because Pink Gum woodlands are relatively open woodlands (Specht 1972) and many individual pink gums, particularly those on poorer quality soils, have 'sparse' canopies. Such conditions would provide easy manoeuvrability for Mistletoebirds, and the considerable dieback and further 'opening' of these woodlands may have further enhanced mistletoe dispersal effectiveness by providing more accessible canopies and perch sites.

A comprehensive understanding of why box mistletoe is so common in pink gum woodlands, therefore, will require further investigations into box mistletoe establishment (e.g. Yan and Reid 1995), as well as disperser movements and behaviour (e.g. Reid 1984; 1989; Monteiro *et al.* 1992; Martinez del Rio *et al.* 1995; Aukema and Martinez del Rio 2002). The present study has, however, highlighted important correlations between mistletoe presence and landscape and individual tree features in eucalypt and pink gum woodlands at differing scales. It has also demonstrated that the poor condition of the primary host of box mistletoe, pink gum, is not directly related to box mistletoe presence or abundance.

Adult male Mistletoebird *Dicaeum hirundinaceum* with lightweight radio transmitter attached. Chapter 3 describes the movements of 14 individual Mistletoebirds which were caught and radio-tracked in Aldinga Scrub in Spring 2004.

CHAPTER 3

PREDICTING MISTLETOE SEED SHADOW AND SEED RAIN FROM MISTLETOEBIRD MOVEMENTS

Chapter 3 Preamble

Chapter 3 describes the movements of 14 individual Mistletoebirds which were radio-tracked in Spring 2004 in Aldinga Scrub. It provides the first rigorous description of the local movements of Mistletoebirds, certainly the first using radio-telemetry. It then uses these data to make predictions of the seed shadow of box mistletoe, and the patterns of seed rain in Aldinga Scrub. I conducted all trapping, radio-telemetry and data analysis.

This chapter was submitted to *Austral Ecology* on 25th July 2005, and accepted for publication on March 7th 2006, and is currently in press with myself and my supervisor David Paton as co-authors. It is, therefore, written in plural. I was responsible for the field work, data analysis and writing. David Paton provided invaluable supervision and guidance. Permission to reproduce this manuscript has been granted (see Appendix A). The chapter here represents the accepted manuscript, plus an additional section in the discussion (*Implications for management*). Also, Table 3.1 occurs as an electronic appendix in the published manuscript. The reference for the manuscript currently is: Ward, M. J., and Paton, D. C. (in press). Predicting mistletoe seed shadow and patterns of seed rain from movements of the Mistletoebird, *Dicaeum hirundinaceum*. *Austral Ecology*.

CHAPTER 3

PREDICTING MISTLETOE SEED SHADOW AND PATTERNS OF SEED RAIN FROM MOVEMENTS OF THE MISTLETOEBIRD, *DICAEUM HIRUNDINACEUM*

3.1 ABSTRACT

At the scale of an individual host, mistletoes are aggregated in space, resulting from the preferential perching of mistletoe dispersers on previously infected plants. We hypothesised that the landscape scale movement patterns of mistletoe dispersers will also promote the aggregation of mistletoes. This hypothesis was tested by predicting the seed shadow for box mistletoe *Amyema miquelii* (Loranthaceae) and patterns of seed rain, by combining radio-telemetry data of Mistletoebird *Dicaeum hirundinaceum* (Dicaeidae) movements with existing gut passage time data. 13 adult Mistletoebirds had a mean home range of 20 ha, with core activity areas of approximately 1 ha, and birds more often used areas with high levels of mistletoe infestation. The predicted seed shadow of box mistletoe was leptokurtic, with a 12%, 35% and 23% probability of mistletoe seed being deposited 0 m (same host tree), 1-50 m and 51-100 m from the host tree, respectively. Although rare (3% probability), long distance dispersal of mistletoe seed (> 500 m) can occur. The predicted patterns of seed rain were strongly aggregated, with birds dispersing large amounts of seed (> 66 000 per ha) in areas with higher mistletoe infestation levels. The movements of mistletoe dispersers will therefore promote mistletoe aggregation at a landscape scale.

KEYWORDS: mistletoe dispersal, Mistletoebird *Dicaeum hirundinaceum*, box mistletoe *Amyema miquelii*, seed rain, radio telemetry.

3.2 INTRODUCTION

Seed dispersal mechanisms strongly influence the spatial arrangement of plants and the physical environment in which the plants grow (Howe and Smallwood 1982; Wenny and Levey 1998). Many plants develop fleshy fruits adapted for consumption and seed dispersal by animal frugivores (van der Pijl 1969). Three non-exclusive advantages for the plant of animal mediated seed dispersal are: 1) escape from high seedling mortality under and near the parent tree; 2) colonisation of unpredictable, ephemeral or newly created sites; and 3) 'directed dispersal' to favourable microhabitats (Janzen 1970; Howe and Smallwood 1982; Howe 1986).

With the exception of the wind dispersed *Nuytsia floribunda* (Lamont 1985a), the explosively dispersed American dwarf mistletoes *Arceuthobium* (Kuijt 1969), and the mammalian dispersed *Tristerix corymbosus* (Amico and Aizen 2000), mistletoes of the Loranthaceae and Viscaceae produce fleshy fruits that attract avian vectors (Docters van Leeuwen 1954; Davidar 1983; Godschalk 1983b; Reid 1989; Lopez de Buen and Ornelas 1999). Successful mistletoe dispersal occurs under the directed dispersal strategy, where birds directly deposit seeds on the small branches of potential host species. Avian mistletoe dispersers include flowerpeckers (Dicaeidae) and honeyeaters (Meliphagidae) in the Old World (Kuijt 1969; Reid 1990; Yan 1993c), and tanagers (Thraupidae) and tyrant flycatchers (Tyrannidae) in the New World (McKey 1975; Monteiro *et al.* 1992; Lopez de Buen and Ornelas 2001).

In these systems, mistletoes are generally aggregated in space, particularly at the scale of the individual tree (Godschalk 1983b; Donohue 1995; Martinez del Rio *et al.* 1995; Bannister and Strong 2001; Aukema 2004). This contagious distribution is influenced by both the compatibility of host plants (Lopez de Buen *et al.* 2002; Ward 2005) and the behaviour and movements of their respective dispersers. In an example of the latter, the preferential feeding and defaecation of mistletoe dispersers on previously infected host plants has been demonstrated to result in the aggregated distribution of mistletoes on individual hosts (Aukema and Martinez del Rio 2002; Medel *et al.* 2004).

The influence of mistletoe dispersers on mistletoe distribution at scales larger than individual hosts, however, is not well understood. Critical to this distribution is the ‘seed shadow’ of mistletoes (the spatial distribution of seeds dispersed around a parent plant, Janzen 1971), and ‘seed rain’ (the distribution of seeds within the habitat occupied by the population, Alcantara *et al.* 2000). Describing the seed shadow and seed rain of mistletoes, however, requires detailed information on the movements of dispersers and the gut passage times of mistletoe seeds. While there have been calculations of gut passage times in mistletoe dispersers (Murphy *et al.* 1993), and of flight distances in mistletoe dispersers such as phainopeplas *Phainopepla nitens* (Aukema and Martinez del Rio 2002) and barbet *Pogoniulus* species (Godschalk 1985), there have been no predictions of mistletoe seed shadow or seed rain at a landscape scale.

We hypothesise that the landscape movements of mistletoe dispersers will produce small seed shadows for mistletoes, and an aggregated pattern of mistletoe seed rain in a landscape, possibly for two reasons. First, given that 8 mistletoe fruits may increase a disperser’s body weight by up to 10% (Liddy 1982), there are physical constraints on the movements of mistletoe dispersers whilst they are processing fruit. Second, if mistletoe dispersers preferentially forage in previously infected hosts, then it is likely that on a landscape scale mistletoe dispersers also restrict their movements to areas of mistletoe infection. In this study, we predict the seed shadow and broad patterns of seed rain for box mistletoe, *Amyema miquelii* (Loranthaceae), by documenting the local movement patterns of its primary disperser, the Mistletoebird *Dicaeum hirundinaceum* (Dicaeidae), in a temperate *Eucalyptus* woodland in southern Australia. This study forms a preliminary step in more detailed modelling of box mistletoe spread which will include information on mistletoe germination rates, mistletoe demographic data and detailed information on Mistletoebird foraging behaviour.

Specifically, this study addresses three questions:

1) What is the home range of a Mistletoebird and do they more commonly use areas with higher levels of mistletoe infection?
2) What is the predicted seed shadow of box mistletoe?
3) What is the predicted landscape pattern of seed rain?

3.3 METHODS

Study site

The study was carried out from early September to mid November 2004 in Aldinga Scrub Conservation Park (Aldinga Scrub hereafter, 138° 27′ E, 35° 18′ S), approximately 40 km south of Adelaide, South Australia. The climate is temperate, with maximum temperatures in winter and summer averaging 15° C and 27° C respectively. Mean annual rainfall is approximately 450 mm, with most precipitation occurring in the winter months (Commonwealth Bureau of Meteorology 2005). Aldinga Scrub, at 266 ha, represents the last remnant of native coastal woodland on the Adelaide plains. The park is surrounded by coastline and housing on the west side, and agriculture on all other sides. Almost all of the park contains *Eucalyptus* woodland, primarily pink gum *E. fasciculosa* and mallee box *E. porosa*. Surveys in 2003 (Ward 2005) demonstrated that the frequency and density of box mistletoe *Amyema miquelii* infection was high on some pink gums in Aldinga Scrub.

Radiotelemetry

Radio telemetry was used to investigate local movement patterns and home ranges of Mistletoebirds. Birds were caught using mist nets placed in various positions close to box mistletoe in Aldinga Scrub. Five Mistletoebirds were caught and attached with transmitters during the first week of each of September (two females, three males), October (three females, two males), and November 2004 (two females, two males, one juvenile). One female Mistletoebird radio-tracked in October (ID9) attended a nest, and was radio-tracked again in November whilst it fed two fledglings. The independent juvenile Mistletoebird (ID13, apparently unrelated to the breeding female ID9), was tracked in November to give an indication of the area used and movement patterns of young birds. Therefore, 14 individual Mistletoebirds were radio-tracked in total. Each bird caught was banded with a uniquely marked metal band provided by the Australia Bird and Bat Banding Scheme.

Single stage radio transmitters (< 400 mg, Titley Electronics Pty Ltd, Australia) were attached to seven adult male Mistletoebirds, six adult female Mistletoebirds and one juvenile Mistletoebird (Table 3.1). So that attached transmitters did not affect bird movements (Kenward 2000), each radio transmitter weighed less than 5% of the bird's mean (± s.e.) body mass (9.25 ± 0.06 grams). All radio transmitters were attached on the back of the bird below the interscapular region but above the lower rump. Prior to attachment, an area of feathers approximately the same size as the transmitter was trimmed down to approximately 2 mm of feather shaft. Radio transmitters were attached using a fast drying glue to a small piece of chiffon, and then attached to the trimmed feathers. Weighing, banding and attachment of the radio transmitter took approximately 25 min for each bird. Immediately following release, all radio-tagged Mistletoebirds were followed to ensure the radio transmitter was not hindering the birds. Some birds showed slight discomfort initially, however all birds resumed normal flight patterns within an hour of release.

Mistletoebird locations (fixes) were determined using a hand held receiver, a 3-element Yagi antenna (Sirtrack Ltd, New Zealand) and a Global Position System (Garmin GPS 72). Because of the small size of the radio transmitters, batteries lasted generally less than 10 days, and therefore radio telemetry data were collected intensively over a short period of time for each bird. In each of the three radio-telemetry months, fixes were obtained on Mistletoebirds over the life of the radio transmitters or until the Mistletoebird was no longer present or detectable in the study site. Fixes were obtained for each Mistletoebird during daylight hours (between 30 min after sunrise and sunset). Initially after sunrise, individual fixes were obtained for each of the Mistletoebirds. For the remainder of each tracking day, attempts were made to follow each Mistletoebird sequentially for at least 25 min (the sequence in which Mistletoebirds were radio-tracked differed on each radio-tracking day). This period of time was chosen to encompass the average Gut Passage Time (GPT) of *Amyema* fruits in Mistletoebirds, which is approximately 15 min (Murphy 1991; Murphy *et al.* 1993). Each of these 25 min tracking periods was deemed a 'movement path'. The initial fix in each movement path was obtained when a Mistletoebird was located in a tree and observed to be feeding on box mistletoe fruit. Fixes in each movement path were obtained when the observer (MJW) could determine the individual tree or mistletoe in which the Mistletoebird was located. Because of their small size and the sometimes dense mistletoe foliage, however, a bird's location sometimes had to be identified by circling the tree and assessing that the radio signal continually came from the same tree. When Mistletoebirds remained in a single location for extended periods, fixes were obtained every 3-5 min.

Home range

Fixes which were obtained at least 3 min apart were used in the estimations of home range. An interval of 3 min was allowed for independence of fixes (Swihart and Slade 1985), as Mistletoebirds could easily fly the length and breadth of Aldinga Scrub within this time. Only fixes made at least three hours after the fitting of transmitters and release were used in analyses. Kernel analysis and Minimum Convex Polygons (MCP) were performed in Ranges6 (Kenward *et al.* 2003) to estimate home range size of Mistletoebirds. Utilisation plots of 5% kernels showed that 30% kernels were an appropriate core area (Kenward *et al.* 2003) to use. Differences in the size of home ranges and core areas were compared between the sexes using *t*-tests. The proportion of home range overlap between birds was also measured using Ranges6.

Habitat

In order to assess habitat use by Mistletoebirds, mistletoe infection level was estimated at 100 m intervals in a regular grid across Aldinga Scrub. At each 100 m point (252 in total), the distance to the nearest tree (greater than 3 m in height) in a north, east, west and south direction was measured. The number of adult mistletoes on each of these trees was also counted. Mistletoe density (no. mistletoes per hectare) was estimated by calculating tree density (trees per hectare) using the point quarter method (Cottam and Curtis 1956), and multiplying this with the average number of mistletoes from the four measured trees from each sampling point. Given the relatively low density of trees in Aldinga Scrub (mean absolute density = 42.1 ± 4.0 trees per ha), this method calculated mistletoe density to a sufficient level of accuracy. From these data, five levels of mistletoe infection were assigned: minimal (0-10 mistletoes ha^{-1}), low (10-50 mistletoes ha^{-1}), moderate (50-100 mistletoes ha^{-1}), high (100-250 mistletoes ha^{-1}) and very high (> 250 mistletoes ha^{-1}).

The following calculations were then made using Ranges6 (Kenward *et al.* 2003): 1) the relative abundance (availability) of hectare cells with different mistletoe infection levels for the entire study area; 2) the proportion of different mistletoe infection levels in each animal's 95% kernel home range; and 3) the proportion of all bird fixes which occurred on the different mistletoe infection levels. Compositional Analysis (Aebischer *et al.* 1993) in the Resource Selection program (Leban 1999) was used to compare the proportion of the 95% kernel home ranges and fixes in each mistletoe infection level with the proportions available (at a 1 ha scale). These comparisons use log-ratios of used and available habitats, and resulted in a ranking of the habitats in order of use.

Movement paths and seed shadow

Movement paths were used to: 1) calculate the location of Mistletoebirds, at different time intervals, relative to the original tree in which they were found; 2) predict the seed shadow for box mistletoe (combining bird movements and a range of gut passage times, GPTs); and 3) predict broad patterns of seed rain of box mistletoe in Aldinga Scrub (combining seed shadow, mistletoe infection levels and mistletoe fruit abundance). Movement paths were only calculated for the 13 adult birds.

Seed shadows were estimated in a manner similar to Murray (1988) and Holbrook and Smith (2000), by combining bird movement data and seed gut passage times. From movement paths, the mean linear distance of birds from the original tree in which they were originally located feeding (first fix), and their position at 5 min intervals (0-5, 6-10, 11-15, 16-20, 21-25 and 26-30 min) were calculated and expressed as the probability of an individual Mistletoebird being a certain distance from the origin at t min, where t varies in 5 min intervals between 0 and 30 min. Also, the probability of seed emergence, that is the probability of a Mistletoebird passing a seed in these 5 min time intervals between 0 and 30 min, was calculated from the frequency distribution of GPTs for Mistletoebirds taken from Murphy

(1991) and Murphy *et al.* (1993). For each 5 min time interval, the probability of seed emergence was multiplied by the probability distributions of bird movement. For each distance interval, these products were then summed over all time intervals to generate the seed shadow (Murray 1988). Because of the very similar size between *A. miquelii* and *A. quandang* fruits (6 - 12 mm cf. 8 - 12 mm respectively, Reid 1986), GPTs are unlikely to vary considerably between these two mistletoe species. In order to examine how variations in GPTs would affect seed shadow, the distances of Mistletoebirds from original feeding tree were averaged for each time interval, square-root transformed (for assumptions of normality) and compared across time intervals using one-way ANOVA.

Seed rain

In order to predict broad patterns of mistletoe seed rain in Aldinga Scrub, we estimated the amount of mistletoe fruit on each mistletoe plant that may be available for dispersal by Mistletoebirds. This was achieved by counting the total number of fruit on 50 mistletoes of varying size and health in June 2004, before fruit had ripened, therefore representing the maximum possible yield for a mistletoe. For each mistletoe, the maximum vertical diameter of the mistletoe and the diameter of the host pink gum branch were both measured. Mistletoe health was classified as being one of the following health categories: '1' (mistletoe non-vigorous and demonstrating considerable dieback); '2' (mistletoe demonstrating some dieback but relatively vigorous); or '3' (mistletoe vigorous and showing no signs of dieback). Using the grid of mistletoe hectare cells ('cells' hereafter) as a base map of Aldinga Scrub (Fig. 3.3), the numbers of fruit dispersed to each hectare 'recipient' cell from surrounding 'supply' cells was calculated using the following equation,

$$seed\_rain = 391X_0\left(P\left(Z_0\right)+P\left(Z_1\right)\right)+\sum_{j=1}^{5}\frac{391X_j\left(P\left(Z_{(2j)}\right)+P\left(Z_{(2j+1)}\right)\right)}{8j}$$

where;

1) 391 represents the average number of fruit per mistletoe (see results);

2) X_j = the total number of mistletoes in surrounding supply cells, and j = the number (0 – 5) of cells the source cells are away from the recipient cell (ie. X_0

= the recipient cell, X_1 = the total number of mistletoes in the eight cells contiguous with the recipient cell, X_2 = the total number of mistletoes in the 16 cells contiguous with the eight X_1 cells, etc.);

3) $P(Z_j)$ = the probability of seeds being dispersed different distances, as calculated from mistletoe seed shadow (Fig. 3.2), where $Z_0 = 0$ m (same tree), Z_1 = 1-50 m, Z_2 = 51-100 m,……, Z_{11} = > 500 m;
4) for each cell, the direction of seed dispersal to surrounding cells is equal (e.g. an eighth of all fruit dispersed from a source cell will be dispersed to each of the contiguous eight cells);
5) all mistletoe seeds are dispersed from the centre of each cell; and
6) all fruit from mistletoe plants are removed over the fruiting season (unpublished data).

Using seed rain calculations for each cell, a raster map of seed rain for Aldinga Scrub was then produced using ArcMap 9.0 (ESRI 2004). One hectare cells were used as the size of grid cells in the present study because we aimed only to give broad landscape patterns of seed rain. More detailed patterns of seed rain, for example on an individual tree scale, requires far more detailed and complex modelling involving information on bird behaviour within trees (Chapter 4), as well as mistletoe demographic data (Chapter 5). More detailed patterns of seed rain will need to be the focus of future research.

3.4 RESULTS

The 14 individual Mistletoebirds were radio-tracked for a total of 83 radio-tracking days. A total of 1140 fixes was obtained, with an average of 81.4 ± 8.7 fixes per Mistletoebird (Table 3.1).

Home range and habitat use

Adult Mistletoebirds occupied a mean (± s.e.) home range of 21.8 ± 5.8 ha estimated with 100% MCP and 19.6 ± 5.9 ha with 95% kernel analysis (Table 3.1). Mean core areas for adult birds (30% kernel) were 0.8 ± 0.2 ha (Table 3.1). Home range size for adult birds was not correlated with the number of fixes obtained (MCP: r = 0.26, P = 0.07; 95% kernel: r = 0.22, P = 0.11). There were no significant differences in the sizes of home ranges between the sexes of adult birds (MCP: t_{11} =

1.28, $P = 0.23$; 95% kernel: $t_{11} = 1.684$, $P = 0.12$; 30% kernel: $t_{11} = -0.188$, $P = 0.85$). The breeding female Mistletoebird (ID9), her male partner (ID10) and the juvenile bird (ID13) all had far smaller home ranges and core activity areas than the mean for all adult birds (Table 3.1). For 182 possible overlap interactions between the 95% kernel home ranges of 14 Mistletoebirds, the mean overlap was 28.7 % (range 0 to 100 %). 25.8% and 31.8% of all possible home range overlap interactions had 0% and 1-10% overlap respectively, and 5.5% of all overlap interactions between Mistletoebirds had overlap of 90-100%.

Across Aldinga Scrub, estimations of mistletoe infection levels ranged from 0 mistletoes ha^{-1} to 877 mistletoes ha^{-1} (Fig. 3.1). Mistletoebird 95% kernel home ranges did not contain areas of differing levels of mistletoe infection in proportion to their relative abundance across Aldinga Scrub ($\chi^2_4 = 14.9$, $P < 0.05$). A simplified matrix ranked mistletoe infection levels in order of preference by Mistletoebirds (based on 95% kernels) as: high > very high > low > moderate > minimal (Table 3.2). The proportion of fixes in each mistletoe infection level differed from the relative availability of each infection level ($\chi^2_4 = 18.8$, $P = 0<0.001$). 95% kernels were smaller when they contained greater amounts of high and very high mistletoe infections (all birds, $r^2 = 0.32$, $P = 0.036$; excluding largest, ID6, and smallest, ID13, home range, $r^2 = 0.37$, $P = 0.03$).

Movement paths and seed shadow

For the 13 adult Mistletoebirds, a total of 141 movement paths was recorded (8.5 ± 0.2 fixes movement path^{-1}) over a total of 3571 min (mean movement path time ± s.e. = 25.3 ± 0.6 min bird^{-1}). Mistletoebirds travelled on average 20.9 ± 1.6 m min^{-1}, or an average of 313.3 ± 23.9 m every 15 min. Mistletoebirds covered on average 0.69 ± 0.09 ha every 15 min. The mean distance (± s.e.) from the original tree that individual birds were located feeding did not vary significantly between time intervals (range = 76.9 – 138.1 m; $F_{5,72} = 0.62$, $P = 0.68$).

Table 3.1 Summary data from 14 individual Mistletoebirds radio-tracked between September and November 2004 in Aldinga Scrub, South Australia

ID	Sex	Tracking period	Body weight (g)	No of fixes	MCP (ha)	95 % kernel (ha)	30% kernel (ha)
1	F	14 – 20 Sep.	9.35	80	5.09	6.12	0.17
2	F	14 – 20 Sep.	9.72	52	13.77	15.30	0.39
3	M	14 – 20 Sep.	9.90	82	12.73	8.39	0.53
4	M	14 – 19 Sep.	10.35	56	5.69	3.09	0.13
5	M	15 – 21 Sep.	8.93	70	18.72	17.75	1.68
6	F	4 – 12 Oct.	7.95	156	83.59	83.23	1.14
7	M	5 – 9 Oct.	9.15	94	14.82	6.13	0.58
8	F	5 – 9 Oct.	9.23	87	43.84	43.79	0.41
9	F	5 – 9 Oct. / 31 Oct. – 2 Nov.	9.50	136	3.04	1.61	0.01
10	M	5 – 9 Oct.	9.19	80	8.96	5.84	0.28
11	F	31 Oct. – 3 Nov.	8.90	56	23.99	30.72	2.60
12	M	31 Oct. – 3 Nov.	9.40	50	23.00	14.74	1.67
13	Juv	31 Oct. – 5 Nov.	8.78	96	2.40	1.43	0.09
14	M	31 Oct. - 2 Nov.	8.80	44	13.35	17.47	1.28
Mean (± s.e.)		5.6 ± 0.45	9.2 ± 0.6	81.4 ± 8.7	20.8 ± 5.9$^+$	19.6 ± 5.9$^+$	0.8 ± 0.2$^+$

Home range size (based on 100% minimum convex polygons, MCP) and kernel areas (95% and 30%) were calculated in Ranges 6 software (Kenward *et al.* 2003). M = male, F = Female, Juv = juvenile. $^+$ Means given for MCPs and kernel areas are for adult birds only

Table 3.2 Percentage of differing levels of mistletoe infection available (as measured in 100 x 100 m cells; Fig. 3.1) at Aldinga Scrub, South Australia, and percentage of total Mistletoebird fixes, 95% and 30% kernel home ranges in each level of mistletoe infection intensity from radio-telemetry at Aldinga Scrub between September and November 2004

Infection level	% available	% of fixes	95% kernel	30% kernel
Very High	8.1	29.5	20.6	36.2
High	11.4	44.6	28.3	42.8
Moderate	7.2	4.6	3.9	4.5
Low	20.3	4.6	17.3	3.0
Minimal	53.0	16.7	29.9	13.6

Mistletoe seed shadow calculations demonstrated that the greatest probability of mistletoe seed deposition (combining gut passage time data) from an original mistletoe was within 150 m of the original tree with a 12.1%, 34.6% and 23.3% (total 70%) chance of mistletoe deposition at 0 m (same host tree), between 1 – 50 m and 51-100 m respectively (Fig. 3.2). Between 101 – 200 m, 201 – 300 m, 301 – 400 m, 401 – 500 m and greater than 500 m there was a 15.2%, 4%, 6.2%, 1.3% and 3.3% chance of mistletoe seed deposition respectively (Fig. 3.2).

Fruit abundance was recorded on 50 mistletoes of varying health (20 mistletoes in each of health categories '1' and '2', 10 mistletoes in category '3'), and of varying size (maximum diameter range = 60 cm – 270 cm, mean ± s.e. = 169.0 ± 7.9; host branch diameter range = 2.5 – 17.6 cm, mean ± s.e. = 9.5 ± 0.51). Fruit abundance ranged from 0 – 3753 fruit per mistletoe (mean ± s.e. = 391.2 ± 109.4). Therefore, the number of fruit per mistletoe plant was set at an average of 391 fruit per mistletoe in order to estimate the number of mistletoe seeds dispersed different distances. This was conservative, given that fruit abundance ranged up to 3753 fruit per mistletoe, and that 40 of the 50 mistletoes measured had either moderate or poor health. Our calculations suggested that of the 391 seeds dispersed from an individual mistletoe, 47 would be defaecated on the same tree, 226 on trees between 1 and 100 m from the original tree, 105 between 101 and 500 m, and 13 seeds beyond 500 m.

Seed rain

The number of seeds predicted to be dispersed to hectare cells in Aldinga Scrub ranged from 303 to 66 435 seeds per ha (mean = 13 857.2 ± 1026.7 per ha). In order to graphically demonstrate the spatial pattern of seed rain, five equal seed rain categories (with intervals of approximately 13 000 seeds) were determined using ArcMap 9.0 (ESRI 2004). The predicted pattern of seed rain across the landscape of Aldinga Scrub is graphically represented in Fig. 3.3, which demonstrates that the majority of seed rain would occur in areas where mistletoe infection levels were also highest (compare Figs 3.1 and 3.3).

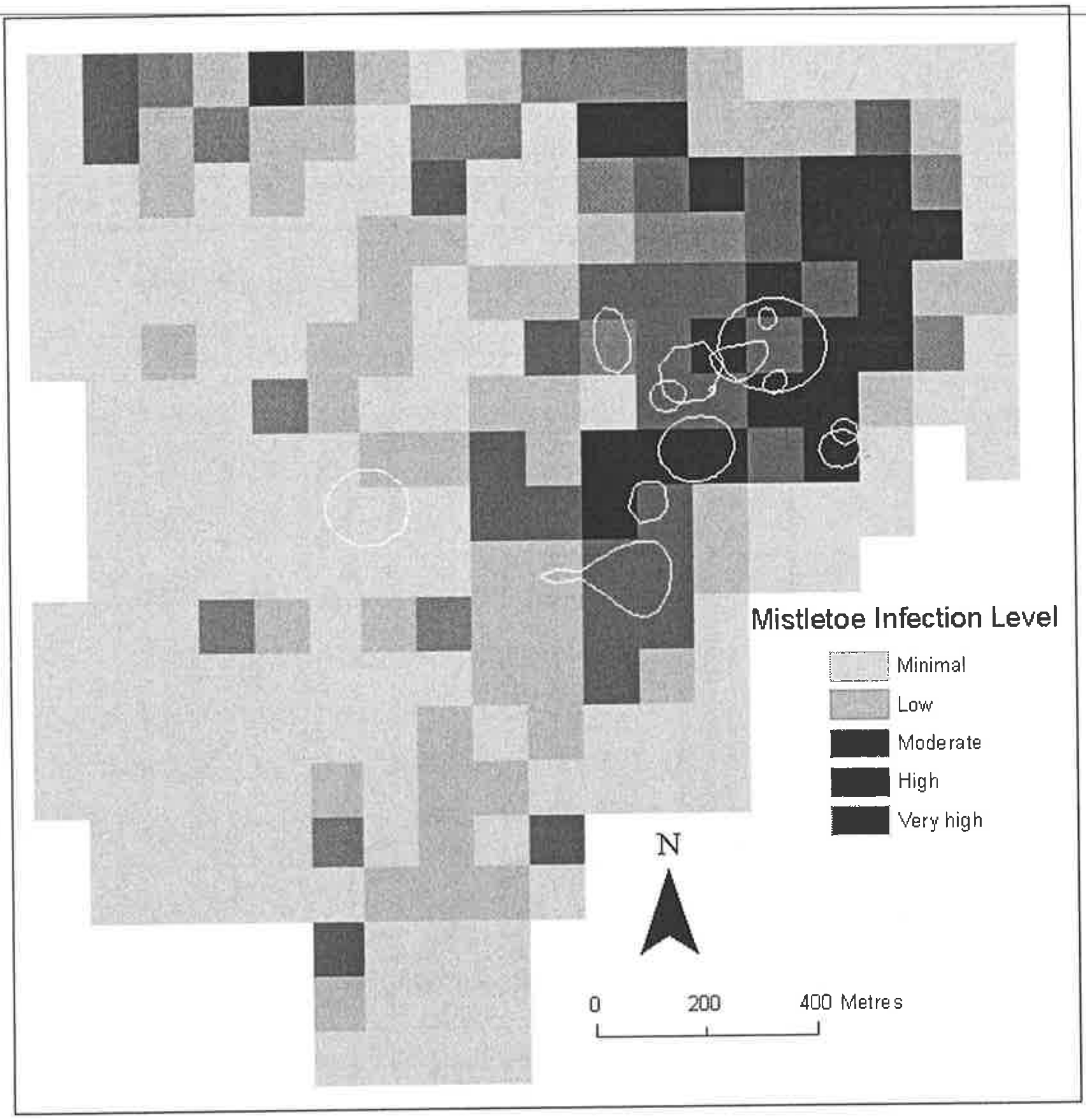

Figure 3.1. Grid of mistletoe infection levels in Aldinga Scrub, South Australia, and 30% kernels of 13 adult Mistletoebirds from radiotelemetry between September and November 2004. Note 95% kernels would have larger degrees of overlap. Each cell represents 1 ha. Mistletoe infection levels are: 'minimal', 0-10 mistletoes ha^{-1}; 'low', 10-50 mistletoes ha^{-1}; 'moderate', 50-100 mistletoes ha^{-1}; 'high', 100-250 mistletoes ha^{-1}; and 'very high', > 250 mistletoes ha^{-1}.

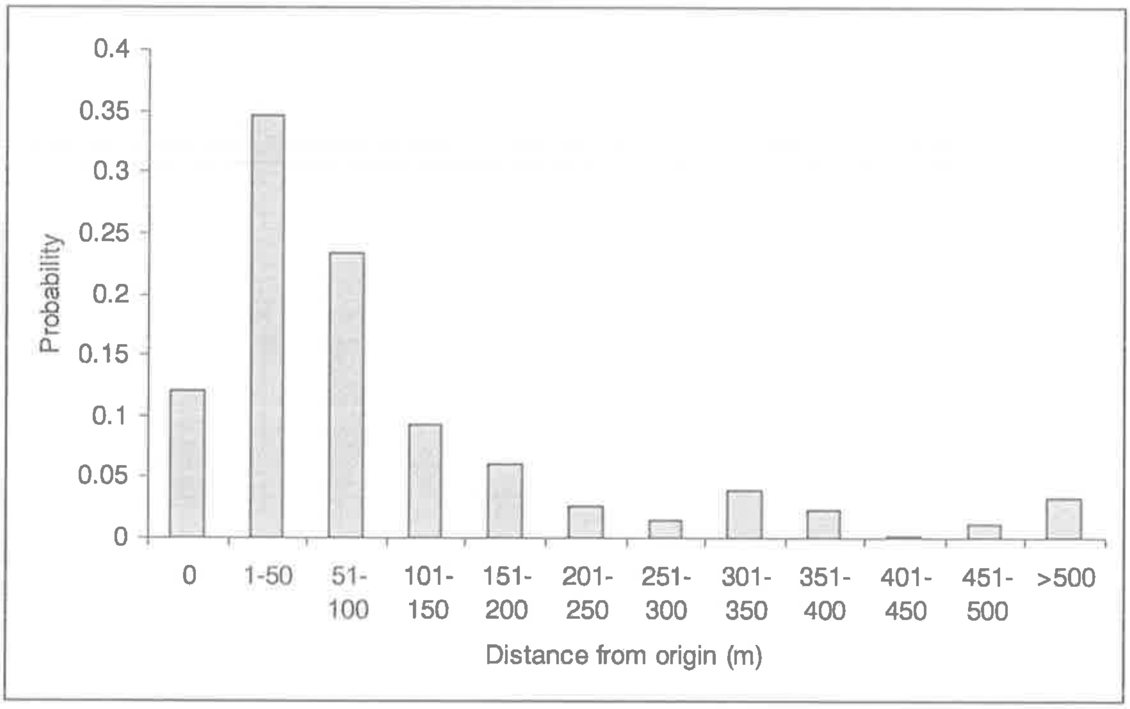

Figure 3.2. Seed shadow of box mistletoe *Amyema miquelii* as dispersed by Mistletoebirds *Dicaeum hirundinaceum* from a tree of origin in Aldinga Scrub, South Australia. Seed shadow probabilities are calculated by combining: 1) the probabilities of Mistletoebird presence at different distances from an original tree over different time periods (as calculated from radio-telemetry in the present study); and 2) the probability of Mistletoebirds passing seeds in different time intervals, as calculated from the data set of Murphy *et al.* (1993).

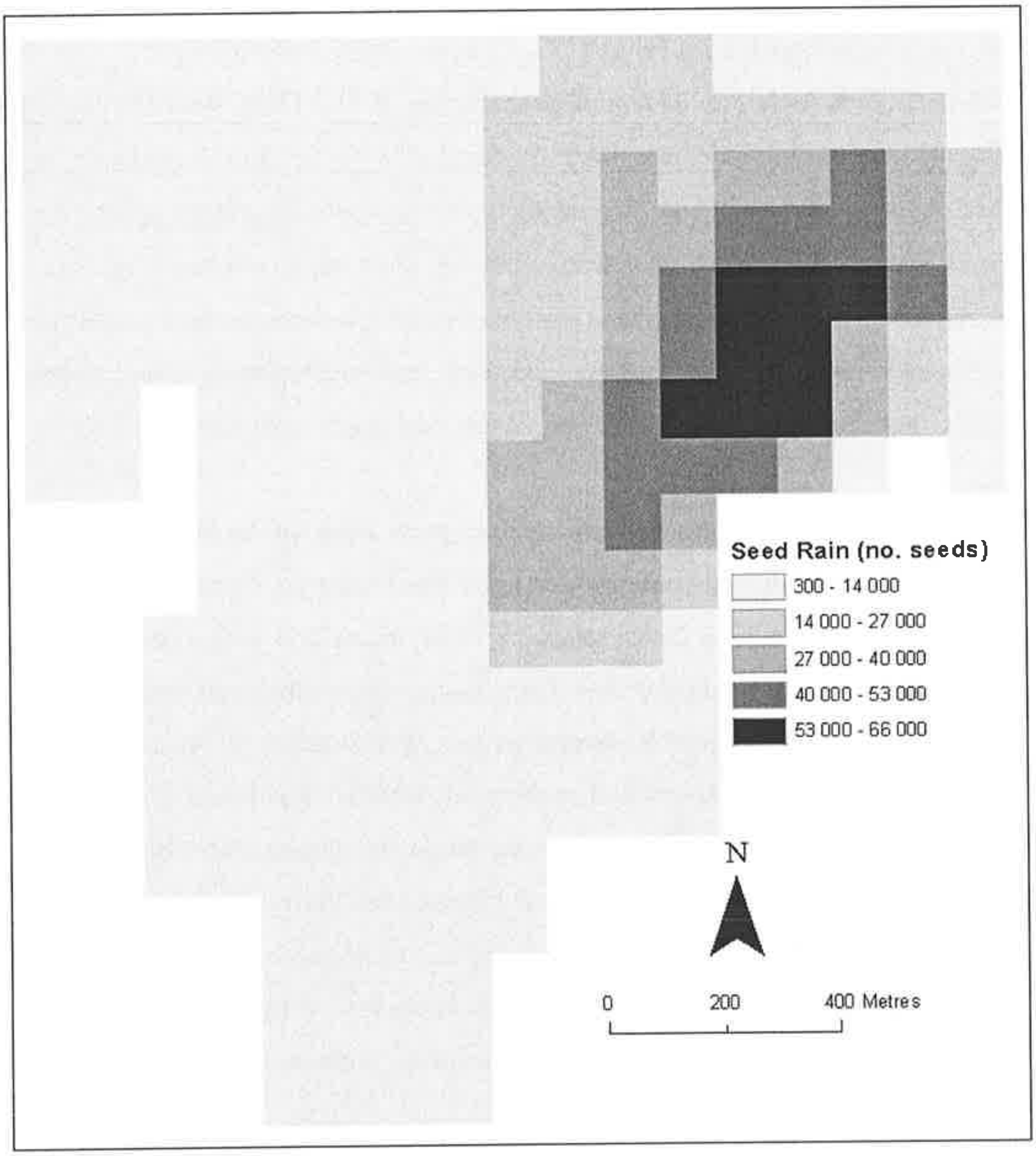

Figure 3.3. Grid of mistletoe seed rain in Aldinga Scrub, South Australia. Each square represents 1 ha. Categories of seed rain are approximately in equal intervals as defined in ArcMap (ESRI 2004), and represent the real estimate of the number of seeds dispersed to that cell based on: 1) the number of mistletoes in each cell; 2) an average of 391 fruit per mistletoe; and 3) seed shadow probabilities (Fig. 3.2).

3.5 DISCUSSION

Home range / habitat use

The mean MCP home range of Mistletoebirds at Aldinga Scrub was 21 ha (range 3 - 84 ha), which is within the range (13 – 25 ha) estimated previously for Mistletoebirds (based on incidental observations of four birds, Reid 1997a). Core activity areas, however, were much smaller (0.8 ha for the 30% kernel area, range 0.01 – 2.6 ha), indicating that the majority of Mistletoebird activity occurred within small areas of high mistletoe density, allowing home range overlap (Fig. 3.1). Analyses of habitat use supported this: Mistletoebirds demonstrated greater use of areas with higher levels of mistletoe infection, and smaller home ranges contained a higher percentage of habitat with 'very high' and 'high' mistletoe infection levels.

Mistletoebird home ranges and core activity areas were similar to those of the only other small frugivore of temperate Australia, the Silvereye, *Zosterops lateralis* (MCPs of approximately 20 ha, range 1 - 75 ha, mean 20% kernel core activity areas of 0.6 ha, Paton, unpublished data). Also, Mistletoebirds moved over areas comparable to similar sized frugivores in ecosystems outside of Australia, including potential mistletoe dispersers such as the toucan barbet *Semnornis ramphastinus* (Capitonidae, territory range 4 - 11 ha, Restrepo and Mondragon 1998), the ochre-bellied flycatcher *Mionectes oleaginous* (Tyrannidae, territories approximately 28 ha, Westcott 1997) and the scarlet tanager *Piranga olivacea* (Thraupidae, territory range 6 - 8 ha, Roberts and Norment 1999). However, no rigorous home range information is available on movement patterns for any other dicaeid or other mistletoe dispersers.

Seed shadow

The seed shadow for box mistletoe is a function of the simple alimentary tract that leads to short seed gut passage times (GPTs) in Mistletoebirds (Richardson and Wooller 1988; Murphy *et al.* 1993), and the movements of Mistletoebirds. Based purely on MCP home range estimates, the maximum area within which a Mistletoebird could potentially disperse a mistletoe seed is approximately 84 ha. However, the average distance of Mistletoebirds from the original tree in which they were located feeding, indicates that the majority of mistletoe dispersal will occur over a much smaller distance of less than 100 m from the parent plant. In addition, this distance did not vary across time intervals, indicating that variations in GPTs (within 0 – 30 min) will actually have little influence on predicted mistletoe seed shadows. When the movement path data are combined with the gut passage times, a more accurate prediction of seed shadow is gained.

The predicted seed shadow of box mistletoe is strongly leptokurtic, with a peak close to the original plant and a 70% probability that mistletoe seeds are deposited within 100 m of their parent plant / host tree (approximately 12% at the same host tree, 35% within 1 - 50 m, and 23% within 51 - 100 m of the original tree, Fig. 3.2). The long tail of the seed shadow distributions indicates that medium to long distance dispersal of box mistletoe (e.g. 200 – > 500 m) can also occur within the time a seed remains in the gut of a Mistletoebird. Indeed, estimates of the number of seeds dispersed more than 500 m from a tree would range from 13 for a tree with a single mistletoe, up to 255 for trees with 20 mistletoes, which are common in heavily infested eucalypt woodlands. This number would increase by orders of magnitude when one considers the amount of fruit dispersed from a hectare of woodland with medium to high levels of mistletoe infection. Although rarer, these long distance dispersal events are therefore significant for individual plant dispersal and have the potential to greatly affect plant community structure (Willson 1992).

The seed shadow for box mistletoe, as predicted in the present study, confirms previous assumptions that most mistletoe dispersal by Mistletoebirds occurs within 500 m (Reid and Yan 2000). It is also comparable with seed shadows of fleshy fruited plants dispersed directly or indirectly by other small frugivores (Godschalk 1985; Murray 1988; Stansbury 2001) and, when compared to seed shadows generated by larger birds, is in keeping with the relationship between body mass and mean dispersal distance, with seed shadows increasing with body mass of dispersers (Holbrook and Smith 2000; Westcott and Graham 2000). Further investigations in areas with lower mistletoe abundance are required, however, to determine whether these smaller seed shadows are a product of Mistletoebirds purposefully restricting their movements whilst processing fruit, or because they did not have to move large distances in the study site in order to find sufficient food.

Seed rain and mistletoe distribution

The present study has predicted that a contagious distribution of mistletoe seed rain will result from the landscape patterns of bird movement and habitat use of Mistletoebirds. Because bird movements were correlated with higher levels of mistletoe infection, it was predicted that the majority of mistletoe seed rain will occur in areas already containing high mistletoe infection levels (Figs 3.1 and 3.3), creating a positive feedback cycle which leads to an aggregated distribution of adult mistletoes (Aukema 2003; 2004). The presence of breeding birds will further promote this pattern, because the restricted home ranges of breeding adult (ID9 and ID10) and juvenile (ID13) Mistletoebirds, which results from nest attendance, feeding of young and long feeding periods in individual trees, will lead to continual deposition of mistletoe seeds across a limited number of trees.

Aggregated distributions and high abundances of mistletoe may also be enhanced by host tree susceptibility. Across the Mount Lofty Ranges pink gums are the most frequent hosts of box mistletoe (Ward 2005). They are more susceptible to mistletoe infection because establishment percentages are higher than on other eucalypt types (Chapter 5), and possibly because access to pink gum canopies for Mistletoebirds is enhanced through greater degrees of canopy dieback (Ward 2005). Pink gums will therefore host more mistletoe, provide a focus for Mistletoebird movements and reinforce the positive feedback of mistletoe dispersal and aggregation (e.g. Aukema and Martinez del Rio 2002).

The present study has clearly demonstrated that Mistletoebirds disperse a large quantity of fruit a range of distances from the parent plant. Effective dispersal is restricted, however, because: 1) Mistletoebirds rarely deposit mistletoe seeds onto live branches of suitable diameter for establishment (Reid 1989; Chapter 4); and 2) even on suitable branches, establishment percentages are low (Chapter 5; Yan and Reid 1995). Furthermore, up to 12% of seeds may be dispersed to the original host tree, and simulation studies have demonstrated that the mistletoe population is highly sensitive to post-dispersal seed survival (Lavorel *et al.* 1999). Although many mistletoes are thought to tend towards the ‘high investment’ dispersal strategy, whereby mistletoes produce a ‘small’ amount of fruit for specialised dispersers (McKey 1975; Howe and Estabrook 1977; Godschalk 1985), mistletoes must nevertheless produce sufficiently large numbers of fruit if they are to successfully recruit away from the parent plant, either close-by or to a more distant environment.

Implications for management

Management of trees with severe mistletoe infections commonly involves the partial or complete removal of mistletoes from individual hosts, and the simulation studies of Lavorel *et al.* (1999) indicate that control by disinfection would be most effective if removal targeted larger trees which host more mistletoes. The results of the present study support this strategy because Mistletoebird activity and seed rain, and hence mistletoe re-infection, are all strongly linked with mistletoe abundance. However, partial removal of mistletoes may only lead to a short term decrease in mistletoe abundance, because the relatively small seed shadow and aggregated pattern of seed rain of remaining mistletoes will contribute to more rapid reinfection of a host and its neighbouring trees. Detailed spatial modelling (e.g. Lavorel *et al.* 1999) of mistletoe dispersal from the results of the present study is therefore required to shed further light on the effectiveness of mistletoe removal strategies. Furthermore, the removal of mistletoe from a large number of host trees is expensive, logistically impractical and may have negative impacts on biodiversity (Watson 2001). The best long term, cost effective strategy for the management of mistletoe proliferations for temperate Australia includes strategic revegetation and habitat restoration, in order to address the underlying causes of mistletoe proliferations rather than just the symptoms.

Conclusions

To better understand the influence of mistletoe disperser movements on mistletoe seed shadows and seed rain, further research is required into the GPTs of mistletoe fruit in free-ranging Mistletoebirds and the movements of mistletoe dispersers in areas with lower levels of mistletoe infestation. However, the present study has demonstrated that Mistletoebirds have a home range of around 20 ha and that they more often use areas with higher levels of mistletoe infestation. Furthermore, the seed shadow predicted from these movements is leptokurtic and the predicted distribution of seed rain is contagious. Given the importance of mistletoes for animal diversity (Watson 2001; 2002) and the potential effects of mistletoes on host trees, the movements and habitat selection of mistletoe dispersers such as Mistletoebirds strongly influence animal and plant community structure.

Three box mistletoe *Amyema miquelii* seeds in a viscous chain following defaecation by a Mistletoebird *Dicaeum hirundinaceum*. These seeds have been deposited on the branch of a live box mistletoe. Chapter Four describes where Mistletoebirds most often defaecate seeds.

CHAPTER 4

HOST TREE SELECTION AND BEHAVIOUR OF MISTLETOEBIRDS

Chapter 4 Preamble

In order to better understand the dispersal of box mistletoe, information was also required on the behaviour of Mistletoebirds and the types of trees in which they forage. This initially caused some consternation, as Mistletoebirds are swift fliers and can move rapidly across the landscape, meaning a lot of detailed information would be lost whilst trying to follow the birds. This is also why foraging data were not collected simultaneously during the radio-telemetry study (Chapter 3). So, surveys were set up whereby I watched Mistletoebirds visit trees – for the first time in my ornithological career, I let the birds come to me. I conducted all of the field work and analyses for this chapter.

CHAPTER 4

HOST TREE SELECTION AND BEHAVIOUR OF MISTLETOEBIRDS *DICAEUM HIRUNDINACEUM* IN A EUCALYPT WOODLAND

4.1 ABSTRACT

In order to understand and predict the patterns of mistletoe distribution, we must also understand the behavioural patterns of their avian dispersers. We studied how Mistletoebirds *Dicaeum hirundinaceum* use host *Eucalyptus* trees and box mistletoe *Amyema miquelii*, during stages of a tree visit, including alighting, perch selection, mistletoe selection, feeding, defaecation and leaving behaviour. Trees which Mistletoebirds visited were taller, had greater mistletoe loads and had lower levels of surrounding canopy density. Mistletoebirds most often alighted in the upper and outer portion of tree canopy (59% of occasions), and most often on dead host tree branches (52%). Whilst in host trees, Mistletoebirds spent the majority of their time in live mistletoes (51%), and used large (56%) and healthy (59%) mistletoes more often than their relative abundance would suggest. However, the number of fruit consumed per mistletoe did not differ between mistletoe size and health classes. The attractiveness of a tree was a function of tree size, mistletoe crop size and accessibility. Also, the frequent use of dead branches for alighting, and the lower canopy density around visit trees, provides further support for the notion that dieback in woodlands may improve conditions for mistletoe dispersal by allowing more favourable habitat for Mistletoebirds.

KEYWORDS: box mistletoe *Amyema miquelii*, frugivore, seed dispersal, dieback, tree attractiveness.

4.2 INTRODUCTION

Mistletoes face a unique challenge amongst flowering plants, because the range of suitable sites for successful seed dispersal is extremely narrow: seeds must be dispersed on the small branches of a suitable host (Reid 1989; Aukema and Martinez del Rio 2002). Mistletoes of the Loranthaceae and Viscaceae meet this challenge by producing fleshy fruits with a sticky pulp that attract primarily avian vectors (Docters van Leeuwen 1954; Davidar 1983; Godschalk 1983b; Reid 1989; Lopez de Buen and Ornelas 1999). This ensures that upon defaecation or regurgitation of seeds, birds wipe their cloaca or beak on a perch in order to liberate themselves of a thread of sticky viscin, thereby transferring the seeds to a host branch, some of which might be suitable for successful establishment.

While this provides a mechanism for the transfer of seeds to host branches, it does not determine which branches are more likely to receive seeds and whether these branches will allow mistletoe recruitment. In other words, it does not ensure high dispersal 'quality' (the fraction of seeds which land in a safe site in germinable condition, Ladley and Kelly 1996). In order to understand the dispersal pattern of mistletoe seeds, therefore, we must also understand which trees mistletoe dispersers select to visit, which branches of trees birds choose to defaecate seeds on, and how dispersers behave within host trees.

The behaviour of dispersers within a host tree, such as how long they spend in a trees and how many fruit they consume, will influence how many seeds will be dispersed to that host tree and surrounding trees. In studies of detailed mistletoe disperser behaviour, little consistency has been demonstrated in behaviours such as the frequency of visits to host trees, length of mistletoe visits and mistletoe fruit consumption rates (Godschalk 1985; Reid 1989; Yan 1993c; Ladley and Kelly 1996; Lopez de Buen and Ornelas 1999). This is not surprising given intrinsic variation of parameters such as fruit availability between different mistletoe systems, and highlights that system specific research is required for a detailed and quantitative understanding of any particular mistletoe dispersal system.

The branches on which dispersers choose to perch and defaecate mistletoe seeds on is influenced by the mass and foot size of the bird (Reid 1991). Smaller mistletoe dispersers such as Flowerpeckers (Dicaeidae) have been shown to perch on small branches (e.g. 5 - 10 mm, Reid 1989) which are suitable diameters for the germination and establishment of mistletoe seedlings. However, seeds are frequently deposited on branches of incorrect host species or dead branches, and dispersal to branches which meet all criteria for successful establishment is seemingly rare (Reid 1989).

Host tree selection by mistletoe dispersers will influence which species of trees will potentially host mistletoes, as well as mistletoe distribution patterns on both an individual tree scale and a landscape scale (Aukema and Martinez del Rio 2002; Aukema 2004; Ward and Paton in press). Studies of host tree selection have revealed two consistent behavioural patterns amongst mistletoe dispersers. First, birds preferentially perch on plants which are already infected with mistletoe (Larson 1996; Martinez del Rio *et al.* 1996; Aukema and Martinez del Rio 2002). Second, mistletoe dispersers generally forage on larger and taller host trees with higher mistletoe loads (Martinez del Rio *et al.* 1995; Aukema and Martinez del Rio 2002). Such behaviour leads to the aggregation of mistletoe in space, and can also lead to severe mistletoe infections on individual hosts (Monteiro *et al.* 1992; Larson 1996; Aukema and Martinez del Rio 2002).

This consistency in host tree selection has been used by researchers interested in modelling the spread of mistletoes. In their model of the spread of mistletoes in fragmented Australian woodlands by Mistletoebirds *Dicaeum hirundinaceum*, Lavorel *et al.* (1999) defined the attractiveness of a tree to Mistletoebirds as a function of the size of the tree's canopy, the size of the mistletoe fruit crop on that tree, and the distance between the tree and the Mistletoebird. Although the mutualistic relationship between Mistletoebirds and mistletoes is well known (see Keast 1958; Liddy 1983; Reid 1986; see Simpson 1997 for reviews), and their effectiveness as dispersers has been discussed (Reid 1989; Yan 1993c), there are no quantitative data on Mistletoebird behaviour which support these assumptions.

This is surprising, given that across south-eastern Australia, severe box mistletoe *Amyema miquelii* infections are implicated in tree decline and are considered a major land management issue (Reid and Yan 2000; Ward 2005). Furthermore, severe infections may be in part a result of more effective dispersal in the contemporary eucalypt landscape. For example, the dieback of pink gums *Eucalyptus fasciculosa* and subsequent 'opening up' of the woodland canopy may provide easier access to trees for Mistletoebirds (Ward 2005).

In order to better understand the pattern of seed dispersal by Mistletoebirds, therefore, and to provide more rigorous data on which models of mistletoe spread can be formed, the following chapter addresses three questions regarding Mistletoebird behaviour:

1) What are the features of host trees that Mistletoebirds select for foraging?
2) What are the features of branches that Mistletoebirds choose to perch and defaecate on?
3) How do Mistletoebirds behave in the trees in which they choose to forage?

I address these questions by documenting the behaviour of Mistletoebirds in a temperate eucalypt woodland with high levels of mistletoe infection. I consider Mistletoebird behaviour to consist of a number of behavioural decisions, including: which host plant to visit; which mistletoe to visit on that host; how long it will spend in the host tree and / or mistletoe; how many mistletoe fruit it will consume; where does the bird defaecate; and finally, where does it subsequently travel to.

4.3 METHODS

Study and survey sites

The study was carried out from August to mid October 2004 in Aldinga Scrub Conservation Park (Aldinga Scrub hereafter, 138° 27′ E, 35° 18′ S), approximately 40 km south of Adelaide, South Australia. The climate is temperate, with maximum temperatures in winter and summer averaging 15° C and 27° C respectively. Mean annual rainfall is approximately 450 mm, with most precipitation occurring in the winter months (Bureau of Meteorology 2005). Aldinga Scrub, at 266 ha, represents the last remnant of native coastal woodland on the Adelaide plains. The park is surrounded by coastline and housing on the west side, and agriculture on all other sides. Almost all of the park contains *Eucalyptus* woodland, primarily pink gum *E. fasciculosa* and mallee box *E. porosa*. Surveys in 2003 and 2004 (Ward 2005; Ward and Paton in press) demonstrated that pink gums in Aldinga Scrub contain heavy loads of box mistletoe *Amyema miquelii*.

In order to document how Mistletoebirds use pink gums infected and not infected with box mistletoe, tree use 'surveys' were carried out in Aldinga Scrub. Survey sites were chosen by creating a theoretical 100 m x 100 m grid overlayed on approximately 25% of the park where mistletoes were abundant, and randomly choosing 20 sites from the grid intersection points (Fig. 1). At each survey site, each pink gum within a 20 m radius (henceforth 'survey trees') was marked with a unique combination of different coloured flagging tape. These trees formed the basis of recording visits of Mistletoebirds to trees, as well as Mistletoebird behaviour in these trees.

Survey trees

In each survey site, the following characteristics were measured for each survey tree: height (HEIGHT), canopy volume (CA.VOL), the extent of canopy dieback (DIEBACK), the overstorey canopy cover (%) surrounding each survey tree (CAN), the density of mistletoes within 5 m surrounding each survey tree (5m.DENS), and for each tree the total number of mistletoes (MTOE), and a 'mistletoe score' (a quantitative classification based on the number, size and health of all mistletoes on each tree).

HEIGHT was measured using a clinometer and tape measure. CA.VOL was determined using the volume of a sphere $4/3\Pi abr$ (where a and b are the north–south and east-west canopy radii respectively, and r: the vertical radius of the canopy). a and b were calculated by measuring and halving the north-south and east-west diameter for each pink gum canopy. r was calculated by measuring the height of the lowest canopy with a clinometer, subtracting this from the total height of the tree and halving. The density of mistletoes within 5 m radius surrounding each survey tree (5m.DENS) was calculated as $m/(A\text{-}T)$, where m is the number of mistletoes contained within 5 m around the canopy of the survey tree, A is the total area of both the tree canopy and the 5 m surrounding the canopy, and T is the tree canopy area. DIEBACK of individual trees was determined by visually estimating the proportion of canopy missing due to branch, limb and trunk death. The percentage overstorey canopy cover surrounding each survey tree (CAN) was determined using a 'spherical densiometer' (Model-A, Forest Densiometers, Forestry Suppliers Inc.), which measures what proportion of the overstorey contains foliage cover or free space and conversion to 'overstorey density' in percent (henceforth I will refer to this as 'overstorey canopy cover'). At a location 2 m from the north, east, south and west edge of the survey tree's canopy a reading was taken from the spherical densiometer and all four readings combined to obtain the estimate for overstorey canopy cover.

'Mistletoe score' for each tree was determined by giving a classification for the size, health and fruiting density of each mistletoe on each survey tree. Mistletoe size classes were 'small' (less than 30 cm maximum canopy diameter), 'medium' (30-80 cm diameter), 'large' (80-200 cm diameter) or 'extra large' (>200 cm diameter) and given a score of either 1, 2, 3 or 4 respectively. Mistletoe health classes were 'poor' (greater than 50% foliage dieback), 'moderate' (some signs of dieback but majority of mistletoe with healthy foliage), and 'good' (mistletoe vigorous with no signs of dieback), and given a score of 1, 2 or 3 respectively. Mistletoe fruiting density was scored as either 'low' (little or no fruit visible on the mistletoe), 'medium' (reasonable amounts of fruit visible) or 'high' (a lot of fruit visible relative to the size of the mistletoe), and given a score of 1, 2 or 3 respectively. 'Mistletoe score' was then calculated by adding all the scores for the size, health and fruiting density category (i.e. a minimum of 3 and maximum of 10 for each mistletoe).

Mistletoebird tree visitation

In order to examine the use of infected and non-infected pink gums by Mistletoebirds, each of the 20 survey sites were surveyed eight times over sixteen days in August 2004, and four times over eight days in October 2004, for a total of 240 surveys (160 in August 2004 and 80 in October 2004). A day of surveys involved starting surveys within 30 min of sunrise and conducting surveys at 10 of the 20 survey sites. Over a two day period, each of the 20 survey sites were surveyed once, and the sequence in which the 20 sites were surveyed was randomised for each two day survey period. Each survey lasted 20 min and involved vigilantly watching all trees within the 20 m radius survey area for use by Mistletoebirds. Therefore, each tree in each survey site was surveyed for a total of 240 min.

The use of trees and behaviour of birds in pink gum trees and mistletoes was recorded by watching birds through 10 x 42 binoculars and speaking into an electronic dictaphone which also recorded the length of each track. The duration in time of tree visits, mistletoe visits, and the specific behaviours of Mistletoebirds which were recorded could therefore be calculated post hoc. Dictaphone recordings began when a Mistletoebird alighted in a tree. All incidences of Mistletoebirds entering a survey site and using one of the flagged trees within the survey area was recorded as a 'tree visit'. Initially, the sex of the bird (male, female, juvenile, unidentified), whether the bird was banded or not (at the time of this study 96 Mistletoebirds had been banded from monthly trapping sessions begun in September 2003), and the unique flagging tape identifier of the tree it was visiting were recorded, and the detailed behaviour of the bird was described for the duration of the visit (see below). Each tree visit was classified as either a 'foraging visit', when the bird visiting that tree ate at least one mistletoe fruit, or a 'transitory visit', when the bird visited the tree but did not eat any mistletoe fruit. When more than one bird was using trees within the survey area, the unique identification mark of the trees was recorded for each of the birds, however the behaviour of only one bird was recorded at a time. This ensured that the measurements of bird behaviour of at least one bird were accurate, while still recording all initial tree visits within the survey area. When a bird using the survey area moved to a tree immediately outside a survey area, the observer (MJW) continued to record its behaviour, while being vigilant of any visits to other trees within the survey area by different Mistletoebirds. Behaviour recorded on these trees was used in analyses of bird behaviour, however not for tree visitation statistics. Trees which did and did not receive visits from Mistletoebirds during 240 min of observation were classed as 'visit trees' and 'non-visit trees' respectively, while those trees which did and did not receive foraging visits from Mistletoebirds were classified as 'forage trees' and 'non-forage trees' respectively.

Mistletoebird behaviour

In order to describe and analyse Mistletoebird behaviour in pink gums and mistletoes, the behaviour of Mistletoebirds was considered in six distinct stages: alighting behaviour; pink gum use; mistletoe use; feeding behaviour; defaecation behaviour; and leaving behaviour.

For each Mistletoebird alighting, the substrate and position on the pink gum where the Mistletoebird alighted were described. Substrates were classified as either live pink gum branches, dead pink gum branches, live mistletoe branches or dead mistletoe branches. Where Mistletoebirds alighted in the tree was classified in terms of both height and horizontal distribution. Height was classified as either upper third, mid third or lower third, and horizontal distribution as either 'core' for the inner half of the canopy, and 'edge' for the outer half.

During the remainder of the tree visit, the substrate on which the bird was perched and the distribution of this perch within the tree (using the same substrate and position categories as used for alighting behaviour) were recorded for each bird 'manoeuvre'. Each manoeuvre was considered to begin when a Mistletoebird moved distribution within the tree, moved to a different substrate, or whilst using mistletoes moved to a different mistletoe. For each manoeuvre the time spent using different substrates and differing distributions within a tree were later calculated from dictaphone recordings.

For mistletoe use, the size and health of all individual mistletoes visited by Mistletoebirds was recorded. Health classes were the same as used in calculating mistletoe 'score', however size classes were 'small' (less than 30 cm diameter), 'medium' (30 – 80 cm diameter) and 'large' (> 80 cm diameter). For feeding behaviour, all attempts to remove mistletoe fruit by Mistletoebirds were recorded, and classified as either 'cap removal', (when the bird removed the upper part of the mistletoe exocarp then squeezed out and swallowed the fleshy mesocarp and seed without detaching the base of the exocarp from its pedicel) or 'manipulation', (when a bird detached the entire fruit from the pedicel and manipulated the fruit against the branch to remove the fleshy portion of the fruit). Defaecation behaviour was also recorded each time mistletoe seeds were defaecated by Mistletoebirds. I also recorded the substrate on which the seeds were defaecated, whether the seeds immediately stuck to the substrate, and, where possible with binoculars, the number of seeds defaecated. When a Mistletoebird left a tree, the reason for the bird leaving was recorded as either 'no reason'; 'interspecific interaction' or 'intraspecific interaction'; and the distance travelled until perched or last seen was estimated.

Fruit density

Twenty mistletoes were chosen from 18 of the survey sites in order to track box mistletoe fruit abundance for Mistletoebirds over the fruiting season. Mistletoes chosen were healthy and accessible for measurements. For each mistletoe, all the leaves from approximately a quarter of the plant were chosen and counted. The number of ripe and unripe fruit was counted on this portion of the plant every two weeks between August and December, and fruit abundance was expressed as the number of ripe fruit per leaf (the number of leaves on the plant portion was counted only once when fruit was first counted, and is therefore representative of the size of the plant portion).

Analyses – Mistletoebird tree visitation

For all survey sites, the mean (± s.e.) height, canopy volume, overstorey density, mistletoe density within 5 m of tree canopy, dieback, mistletoe score and total number of mistletoes was compared using *t*-tests between infected and non-infected trees, between visit and non-visit trees, and between forage and non-forage trees.

All comparisons were pooled across survey sites. In addition, a range of parameters was calculated for individual tree and mistletoe visits (averaged over 240 survey minutes), including tree visitation rate (number of Mistletoebird visits / tree / 20 min); mistletoe visitation rate (number of individual mistletoe visits per 20 min); mistletoe visitation frequency (number of mistletoe visited per tree visit).

Logistic regression models were used to investigate the relationship between tree characteristics and whether or not a tree was visited by a Mistletoebird. Five independent tree variables which were likely to influence visits to trees by Mistletoebirds, MTOE, HEIGHT, 5m.DENS, DIEBACK and OS.DENS, were used as explanatory variables in the a priori development of a set of 15 models to compare the influence of tree variables on whether trees were 'visit' or 'non-visit' trees. CA.VOL and mistletoe score were not included as they were correlated with HEIGHT and MTOE respectively. Interactions among the variables were not considered, and post hoc analysis revealed interaction terms did not improve model fits. Models were fitted using generalised linear models (GLM) assuming a binomial error structure (1 = visit tree; 0 = non-visit tree) with a logit link function (logistic regression) using R 1.7.0 (The R Development Core R Development Core Team 2003). The proportion of variance explained by the chosen parameters was assessed by calculating, for the global models, the deviance ratio: [(null deviance - residual deviance) : null deviance].

Candidate models were ranked using Akaike's Information Criterion (AIC) model ranking techniques (Burnham and Anderson 2002). For all candidate models in the present study, model selection was based on a second-order bias corrected form of AIC (AICc) because n/K (sample size/number of parameters) was less than 40 (36.2). In addition, post hoc modelling was carried out using all possible combinations of parameters in models of different length (i.e. models with either one, two, three, four or five parameters). Each parameter was included in models an equal number of times. The relative importance of each individual variable (j) was then estimated by summing the Akaike weights w_i across all the models in the set where variable j occurs to give the sum $w_+(j)$. The larger the $w_+(j)$, the more important variable *j* is, relative to the other variables (Burnham and Anderson 2002).

Analyses – Mistletoebird behaviour

Descriptions and analyses of Mistletoebird behaviour were considered in the six behaviour stages. Alighting behaviour was described by comparing the proportion of Mistletoebird alightings and '2nd manoeuvres' (the first move made by a Mistletoebird after initial alighting) which occurred on different substrate types and, for alightings, at different height and horizontal distributions. Pink gum use was described by comparing the total number of manoeuvre records and total time on different substrate types. Also, the mean (± s.e.) time of individual bird manoeuvres on different substrate types was compared across substrate types with one-way ANOVA and post-hoc Tukey HSD Tests.

For mistletoe use, the proportion of manoeuvres was calculated for different mistletoe size and health classes, and the average mistletoe visit length compared using one-way ANOVA. Across all survey sites, the proportional use of mistletoes of different size and health classes was compared with the amount of mistletoe available in these classes using a Chi-squared goodness-of-fit test. Also, the amount of time that was spent in mistletoes at different height and horizontal distributions was compared. For mistletoe feeding behaviour, the percentage of fruits consumed in different manners was calculated, as well as the following parameters: fruit consumption frequency (no. fruit eaten per tree visit); feeding frequency (no. fruit eaten per mistletoe visit); feeding event fruit consumption frequency (no. fruit eaten per mistletoe visit in which fruit was eaten).

For defaecation behaviour, the proportion of defaecations on different substrate types was compared and the mean number of seeds per defaecation compared between substrate types using one-way ANOVA. The following parameters were also calculated: defaecation frequency (proportion of tree visits in which birds defaecated) and mean defaecation size (mean number of seeds defaecated per defaecation).

In order to meet assumptions of normality, transformations were conducted on all data used in ANOVA comparisons. ANOVA, however, is robust to considerable deviations from normality (Zar 1999). Therefore, when normality was not achieved, data were left in their original form.

4.4 RESULTS

Mistletoebird tree visitation

In total there were 217 survey trees across 20 survey sites, with a mean (± s.e.) of 10.9 ± 0.8 pink gums per site (range = 5 – 17, Table 4.1). The mean height, canopy volume and dieback of pink gums in survey sites was 7.6 m, 381.1 m^3 and 48.1% respectively. Across all survey sites there was a total of 1077 mistletoes, with a mean of 50.6 mistletoes $site^{-1}$ (7 – 93) and a mean mistletoe score of 314.7 $site^{-1}$ (20 – 622). 7% of survey trees had no mistletoes, while 29%, 34%, 15%, 12% and 3% hosted one, 2 - 5, 5 - 10, 10 – 20 and more than 20 mistletoes respectively (Fig. 4.1). There were positive correlations between canopy volume of survey trees and the number of mistletoe ($r^2 = 0.29$, $P < 0.001$) and the mistletoe score ($r^2 = 0.21$, $P < 0.0001$). Infected pink gums in survey sites were significantly taller than non-infected pink gums (mean 8.1 m c.f. 6.6 m, $t\text{-test}_{1,215} = -4.8$, $P < 0.0001$), had greater canopy volume (mean 232 m^3 c.f. 89 m^3, $t\text{-test}_{1,215} = -4.5$, $P < 0.0001$) and lower surrounding overstorey density (mean 28% c.f. 33%, $t\text{-test}_{1,215} = 2.3$, $P = 0.0239$, Table 4.2). However, the density of mistletoes within 5m of the canopy (mean 0.03 c.f. 0.02, $t\text{-test}_{1,215} = -1.4$, $P = 0.1722$) and dieback (mean 51% c.f. 41%, $t\text{-test}_{1,215} = -2.0$, $P = 0.0517$) did not differ between infected and non-infected pink gums in the survey sites (Table 4.2).

Each tree in each survey was surveyed for 240 min, for a total of 52080 tree survey minutes ('tree minutes' hereafter) and an average of 2604 tree minutes $site^{-1}$ (1440 – 4080, Table 4.1). I recorded a total of 439 individual tree visits by Mistletoebirds from 298 individual bird records. Of these, 150 birds were males, 52 were females, 5 juveniles, and for 91 records the sex was not determined either because the visit by the Mistletoebird was too short to determine sex or the bird was not the priority focus within the survey time. There were 27 records in which the bird was banded. Of the 490 visits, 290 were to uniquely identified trees within survey sites, 110 to trees adjacent to survey areas, and 39 erroneous recordings when the unique identifier of the tree was not recorded or incorrectly recorded (Table 4.3). The mean number of visits to uniquely identified trees per site was 14.5 (0 – 73, Table 4.1). From these data the following parameters were calculated for individual trees and mistletoes: *tree visitation rate* = 0.33 tree.visits tree.hour^{-1}; *mean tree visit length* (± s.e.) = 84.0 ± 6.0 seconds; *mistletoe visitation rate* = 0.44 mistletoe.visits tree.hour^{-1}; *mistletoe visitation frequency per tree* = 0.77 mistletoe.visits tree.visit^{-1}; *mean mistletoe visit length* 62.1 ± 4.6 seconds (Table 4.3).

Comparisons of tree features between visit and non-visit trees (Table 4.2) demonstrated that trees which were visited by Mistletoebirds had more mistletoes (mean 7.2 mistletoes per tree for visit trees c.f. 3.3 for non-visit trees, t-test$_{1,215}$ = -5.0, P <0.0001), had a higher mistletoe score (mean 49.1 c.f. 16.6, t-test$_{1,215}$ = -6.4, P < 0.0001), were taller (mean 8.1 c.f. 7.4 m, t-test$_{1,215}$ = -3.0, P = 0.003), had larger canopy volume (mean 226 c.f. 165 m^3, t-test$_{1,215}$ = -2.0, P = 0.046), had lower surrounding overstorey density (mean 26.0 c.f. 31.6 %, t-test$_{1,215}$ = 2.6, P = 0.0095), higher mistletoe density in the surrounding 5 m of canopy (0.04 c.f. 0.02 mistletoe.m^{-2}, t-test$_{1,215}$ = -3.4, P = 0.0008) and higher canopy dieback (57.2 c.f. 41.5 %, t-test$_{1,215}$ = -3.5, P = 0.0005). Similar trends were also demonstrated for forage and non-forage trees (Table 4.2). Forage trees had more mistletoes (10.7 per forage trees c.f. 3.8 per non forage tree, t-test$_{1,215}$ = -7.1, P < 0.0001), higher mistletoe scores (74.1 c.f. 21.4, t-test$_{1,215}$ = -8.4, P < 0.0001), were taller (10.7 c.f. 3.8 m, t-test$_{1,215}$ = -2.2, P= 0.0326), had larger canopy volume (605.0 c.f. 335.1 m^3, t-test$_{1,215}$ = -3.5, P = 0.0006), lower surrounding overstorey density (22.4 c.f. 30.6 %, t-test$_{1,215}$ = 3.0, P = 0.0035), higher density of mistletoes within 5 m of the canopy (0.04 c.f. 0.02 mistletoe.m^{-2}, t-test$_{1,215}$ = -2.5, P = 0.0121) and greater canopy dieback (63.8 c.f. 44.9 %, t-test$_{1,215}$ = -3.2, P = 0.0016).

Table 4.1 Summary of survey sites, including the number of trees in each site, total survey times, tree features, mistletoe numbers and scores, and the number of visits to mistletoes by Mistletoebirds. Mistletoe score is determined from a combination of the total number of mistletoes and the health and size of each mistletoe. Mistletoebird visits are visits to at least one identified *Eucalyptus fasciculosa* within each survey site. A further 149 visits were made to trees adjacent to survey areas

Site	Trees					Mistletoes		
	No. trees	Survey time (min)	Height (m)	Can Vol. (m^3)	Dieback (%)	No.	Score	Mistletoebird Visits
1	12	2880	7.8 ± 0.4	444.7 ± 87.3	70.3 ± 7.0	72	461	5
2	12	2880	8.4 ± 0.6	607.4 ± 234.0	47.5 ± 7.9	34	38	0
3	9	2160	6.8 ± 0.9	219.2 ± 87.3	61.8 ± 11.7	34	182	15
4	12	2880	8.9 ± 0.4	403.6 ± 96.2	67.7 ± 6.3	7	472	13
5	10	2400	9.1 ± 0.6	470.2 ± 99.3	49.7 ± 7.4	39	293	15
6	5	1200	7.5 ± 0.6	368.9 ± 70.4	80.0 ± 5.2	71	495	6
7	14	3360	8.2 ± 0.5	245.3 ± 54.0	75.3 ± 5.8	68	488	73
8	17	4080	7.6± 0.5	156.5 ± 24.6	41.9 ± 7.1	40	278	26
9	12	2880	7.2 ± 0.8	340.8 ± 188.4	46.3 ± 12.1	64	391	22
10	13	3120	5.3 ± 0.7	275.5 ± 137.0	44.2 ± 12.4	83	519	22
11	16	3840	7.0 ± 0.2	168.9 ± 29.8	20.6 ± 4.9	13	20	3
12	9	2160	8.4 ± 0.6	436.5 ± 86.6	25.4 ± 5.6	31	145	1
13	14	3360	6.4 ± 0.5	328.1 ± 101.9	73.9 ± 6.4	90	622	30
14	11	2640	7.6 ± 0.3	522.8 ± 106.7	73.8 ± 7.1	93	372	24
15	7	1680	8.3 ± 0.4	562.1 ± 290.3	10.7 ± 5.8	23	203	0
16	6	1440	7.3 ± 1.1	761.4 ± 366.2	25.2 ± 9.7	68	459	11
17	16	3840	8.3 ± 0.5	333.9 ± 72.0	36.0 ± 7.4	18	51	0
18	8	1920	7.1 ± 1.1	276.6 ± 94.1	53.1 ± 11.4	75	454	8
19	6	1440	8.2 ± 1.0	570.1 ± 148.5	16.5 ± 10.2	33	215	16
20	8	1920	8.1 ± 0.5	811.7 ± 231.2	16.9 ± 5.4	55	135	0
Mean	10.9 ± 0.8	2604 ± 191	7.6 ± 0.1	381.1 ± 30.1	48.1 ± 2.3	50.6 ± 5.9	314.7 ± 40.7	14.5 ± 3.8
(Total)	(217)	(52080)				(1011)	(6293)	(290)

Table 4.2 Summary of tree measurements of survey trees, including comparisons of infected and non-infected trees, trees which were either visited or not visited by Mistletoebirds (all visits), and trees which Mistletoebirds foraged at and did not forage at (foraging visits)

	Survey trees			All visits			Foraging visits		
	Infected	Non - infected		Visited	Not visited		Foraging Visit	Non - foraging visited	
No. mistletoe	6.6 ± 0.4	0		7.2 ± 0.6	3.3 ± 0.5	****	10.7 ± 0.9	3.8 ± 0.4	****
Mistletoe score	42.8 ± 2.8	0		49.1 ± 3.8	16.6 ± 3.3	****	74.1 ± 5.7	21.4 ± 2.6	****
Height (m)	8.1 ± 0.2	6.6 ± 0.3	****	8.1 ± 0.2	7.4 ± 0.3	**	8.3 ± 0.3	7.5 ± 0.2	*
Canopy Volume (m^3)	232.3 ± 17.1	88.5 ± 26.7	****	225.5 ± 22.9	164.9 ± 19.7	*	302.5 ± 35.5	167.5 ± 16.1	***
Surr. o/s density (%)	27.7 ± 1.3	33.0 ± 2.0	*	26.0 ± 1.6	31.6 ± 1.4	**	22.4 ± 2.5	30.6 ± 1.2	**
Mistletoe dens / 5 m (no. mistletoe.m^{-2})	0.03 ± 0.003	0.02 ± 0.004		0.04 ± 0.00	0.02 0± .00	****	0.04 ± 0.01	0.02 ± 0.0	*
Canopy dieback	50.9 ± 2.7	41.2 ± 4.2		57.2 ± 3.4	41.5 ± 2.9	***	63.8 ± 5.4	44.9 ± 2.4	**

* = P <0.05, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$

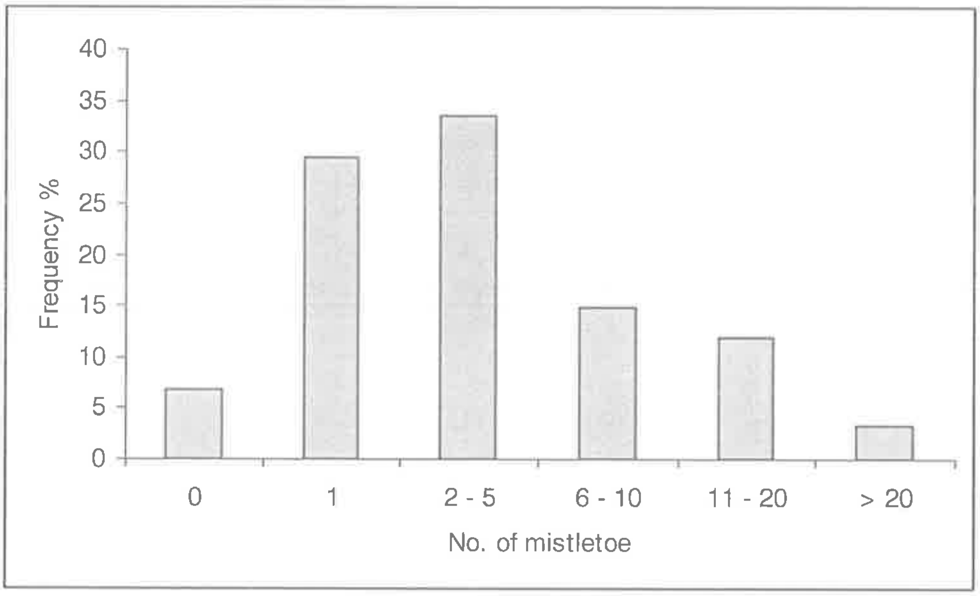

Figure 4.1. Frequency distribution of the number of mistletoes on 217 survey trees from which Mistletoebird behaviour was recorded in Aldinga Scrub, South Australia.

Table 4.3 Mistletoebird foraging and behavioural parameters

	Parameter	**Value**
Tree visitation	Tee visitation rate (tree.visits tree.hour^{-1})	0.33
	Tree visit length (secs), mean ± s.e. (n)	84.0 ± 6.0 (400)
Mistletoe visitation	Mistletoe visitation rate (mistletoe.visits tree.hour^{-1})	0.44
	Mistletoe visitation frequency (% of tree visits)	77%
	Mistletoe visit length (secs), mean ± s.e. (n)	62.1 ± 4.6 (379)
Fruit consumption	Fruit consumption rate (fruit tree.hour^{-1})	0.23
	Fruit consumption frequency (% of tree visits)	27.6 %
	Fruit consumption frequency (% of mistletoe visits)	31.9 %
	Feeding event fruit consumed, mean ± s.e. (n)	1.62 ± 0.08 (121)
Defaecation	Defaecation frequency (% of tree visits)	17.3%
	Defaecation size (no. seeds), mean ± s.e. (n)	2.41 ± 0.11 (63)

'tree hour' = an hour of watching a survey tree.

For logistic regression models of tree features and visited trees, model fit was reasonable with 16.5% of the variance in the model explained by the included parameters. AICc model ranking indicated that the model MTOE + HEIGHT + 5m.DENS was found to be the best fit model, having a 34% probability of being the best model of Mistletoebird visitation from the candidate set (as indicated by the Akaike weight, w_i; Table 4.3; Burnham and Anderson 2002). The next best models of Mistletoebird visitation were MTOE + DIEBACK + HEIGHT ($w_i = 0.29$) and MTOE + OS.DENS + 5m.DENS ($w_i = 0.24$). All other models were comparatively unlikely ($\Delta_i > 3$, Table 4.4). Estimation of relative parameter importance demonstrated that the two individual parameters with the highest estimated importance were HEIGHT (0.92) and 5m.DENS (0.92), followed by MTOE (0.85), OS.DENS (0.76) and DIEBACK (0.39). Pairs of parameters with the highest estimated importance were MTOE + HEIGHT (0.78), MTOE + 5m.DENS (0.78) and MTOE + OS.DENS (0.61). All other pairs of parameters had summed w_i of less than 0.4.

Fruit abundance in late August was 0.03 ± 0.004 ripe fruits per leaf. It peaked in mid October with 0.14 ± 0.02 ripe mistletoe fruit per leaf, and then decreased to 0.01 ± 0.003 in late November (Fig. 4.2).

Table 4.4 Ranking of logistic regression models of 'visit' and 'non-visit' trees using AICc model ranking procedures (Burnham and Anderson 2002) for 217 pink gums *Eucalyptus fasciculosa* in Aldinga Scrub Conservation Park, South Australia

	Candidate model	Log(Λ)	K	Δ_i	w_i
1	**MTOE + HEIGHT + 5m.DENS**	**-129.18**	**4.00**	**0.00**	**0.34**
2	**MTOE + DIEBACK + HEIGHT**	**-129.33**	**4.00**	**0.31**	**0.29**
3	**MTOE + OS.DENS + 5m.DENS**	**-129.51**	**4.00**	**0.66**	**0.24**
4	MTOE + 5m.DENS	-132.04	3.00	3.66	0.05
5	MTOE + DIEBACK	-132.82	3.00	5.22	0.02
6	MTOE + OS.DENS + DIEBACK	-132.01	4.00	5.67	0.02
7	MTOE + OS.DENS + HEIGHT	-132.22	4.00	6.08	0.02
8	MTOE + HEIGHT	-133.68	3.00	6.93	0.01
9	MISTLETOE	-136.20	2.00	9.92	0.00
10	MTOE + OS.DENS	-135.23	3.00	10.04	0.00
11	HEIGHT + DIEBACK	-135.87	3.00	11.32	0.00
12	DIEBACK	-141.92	2.00	21.37	0.00
13	5m.DENS	-142.18	2.00	21.87	0.00
14	HEIGHT	-143.27	2.00	24.05	0.00
15	OS.DENS	-144.46	2.00	26.44	0.00

A 'visit tree' is a pink gum which a Mistletoebird visited even if it did not forage within the tree, and 'non-visit tree' is a tree which a Mistletoebird did not visit at all. MTOE, number of box mistletoe *Amyema miquelii* on tree; HEIGHT, height of tree (m); 5m.DENS, the density of mistletoes within 5m of the tree's canopy (no. mistletoe / m^2); DIEBACK, percentage canopy dieback; OS.DENS, density of canopy surrounding tree. Log(Λ) is the log likelihood of the model; *K*, the number of estimated parameters; Δ_i, the difference between that model's second-order bias corrected form of Akaike's Information Criteria (AICc) and the minimum AICc value; and, w_i, Akaike weights. Candidate models with significant levels of empirical support (Δ_i, < 2) are shown in bold. Percentage of deviance explained by included variables = 16.5%.

Mistletoebird behaviour

The majority of Mistletoebirds alighted on dead pink gum branches and then moved to live mistletoes (68%, Table 4.5). Mistletoebirds more often (70%) alighted in the upper height distribution of pink gums, and in a horizontal plane, almost always (85%) in the outer portion of the canopy (Table 4.6). Accordingly, most alightings (59%) occurred at the 'upper-edge' of the canopy, followed by 21% at the 'mid-edge' of the canopy (Table 4.6).

Within pink gums, Mistletoebirds spent the majority of their time in live mistletoes (63% of total time), followed by dead pink gum branches (26%), dead mistletoes (9%) and live pink gum (2%) branches (Table 4.5). Post hoc Tukey HSD tests indicated there were significant differences in the average manoeuvre time for different substrates ($F_{3, 637} = 10.21$, $P < 0.0001$), with Mistletoebirds spending longer in dead (71 secs) and live mistletoe (62 secs) than on dead and live pink gum branches (34 and 26 secs respectively). The average time Mistletoebirds spent in individual trees was 84 seconds (Table 4.3).

When Mistletoebirds used live mistletoes, they used large mistletoes (56% of a total of 312 mistletoe records) more often than medium (36%) and small (8%) mistletoes, and healthy mistletoes (58.9%) more often than mistletoes with moderate (36.9%) and poor health (4.2%, Table 4.7). This was not in proportion to the relative availability of mistletoes in different size ($X^2 = 22.6$, $P < 0.001$) and health categories ($\chi^2 = 33.6$, $P < 0.001$), with large mistletoes in good health used considerably more often than expected (Table 4.7).

Mistletoebirds spent a greater percentage of their time in mistletoes which were located in the upper part of the canopy (51% of total time) followed by in the mid (38%) and lower (11%) parts of the canopy, and more time in mistletoes located in the outer half of the canopy (89%) than in the inner core half of the canopy (11%, Table 4.8). Accordingly, Mistletoebirds generally spent the majority of their time in mistletoes in the 'upper-outer' part of the canopy (45%) followed by the 'mid-outer' part of the canopy (34%, Table 4.8).

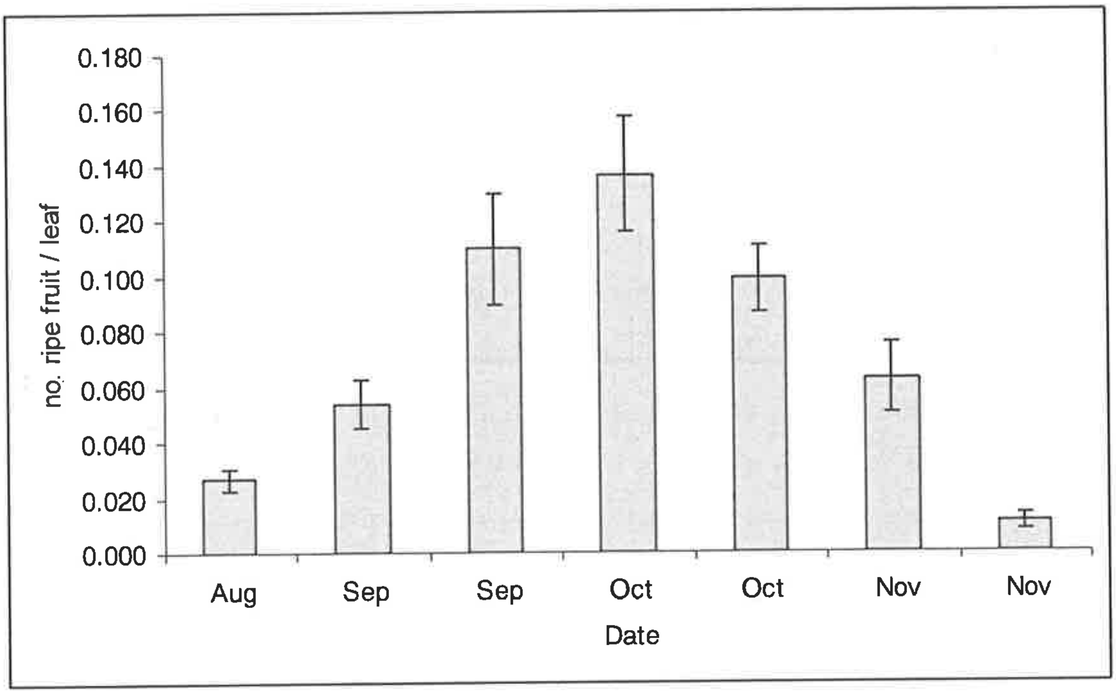

Figure 4.2. Box mistletoe *Amyema miquelii* fruit abundance from August to November 2004 in Aldinga Scrub, South Australia. For Sep, Oct and Nov, the first of each month category represents the counts taken from the first two weeks of the month, and the second month category represent counts in the latter two weeks of the month.

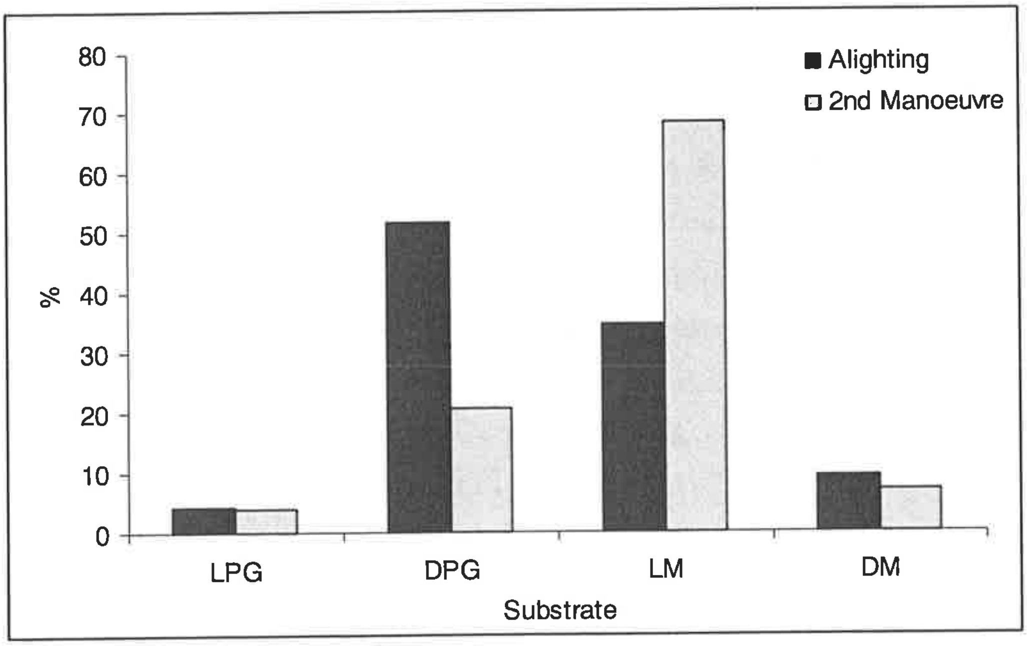

Figure 4.3. Percentage of alightings and second manoeuvres of Mistletoebirds on different substrates. LPG = live pink gum branch, DPG = dead pink gum branch, LM = live mistletoe branch, DM = dead mistletoe branch.

There were 121 individual records of Mistletoebirds eating mistletoe fruit, and a total of 196 mistletoe fruit eaten. Only one of these fruit was eaten by 'manipulation', all other 195 fruit were eaten by 'cap removal'. There was no difference in the number of mistletoe fruit eaten relative to mistletoe size ($F_{2,116}$ = 1.56, $P = 0.22$), with Mistletoebirds eating on average 1.8 ± 0.1 (n = 72), 1.4 ± 0.1 (39) and 1.5 ± 0.3 (8) mistletoe fruit every time they ate fruit in a large, medium or small mistletoe respectively. There was also no difference in the number of fruit eaten by Mistletoebirds when they visited a mistletoe of different health ($F_{2,112}$ = 0.48, $P = 0.62$), with Mistletoebird eating on average 1.7 ± 0.1 (n = 76) mistletoe fruit in healthy mistletoes, 1.6 ± 0.2 (37) in mistletoes of moderate health, and 1.0 ± 0.0 (2) in mistletoes of poor health. Parameters determined from feeding behaviour included: *fruit consumption rate* = 0.23 fruit tree.hour^{-1}; *tree fruit consumption frequency* = 0.45 fruit tree.visit^{-1}; *mean no. fruit consumed per feeding event* = 1.62 ± 0.08 (Table 4.3).

There was a total of 87 individual defaecation records (52 records on uniquely identified survey trees, 35 on trees adjacent to survey areas) and a total of 152 seeds defaecated. 100% of the survey trees on which Mistletoebirds defaecated were already infected with mistletoes. Mistletoebirds never defaecated whilst actively foraging for fruit or insects, and on nearly all occasions a bird would hold its abdomen away from the perch, pass seeds that remained suspended from the cloaca, and then press its cloaca against the branch a number of times in order to transfer the sticky string to the branch it was perched on (as described by Reid 1989). On no occasions did birds defaecate whilst sitting 'along the branch' (Kenneally 1973; Simpson 1997). The majority of seeds (43%) were defaecated on live mistletoe branches, followed by dead pink gum branches (38%), dead mistletoe (28%) and live pink gum branches (1%). 78 of 87 defaecations immediately stuck to the branch in the seconds following defaecation (89.7%), and the remaining 9 fell to the ground or onto lower branches. The following parameters were determined from defaecation behaviour; *defaecation frequency* = 0.20 defaecations tree.visit^{-1}; and *mean defaecation size* = 2.41 ± 0.11 seeds (Table 4.3).

Of the 390 records of Mistletoebirds leaving, 60% moved to outside the survey area to an unknown substrate, 16% left and alighted in a pink gum branch of another pink gum within the survey area, 16% left to a mistletoe in a different tree within the survey area, and 8% left to another tree outside the survey area. 13 % of birds left trees seemingly as a result of intraspecific interactions, 4 % left seemingly as a result of interspecific interactions, and the reason for 87 % of birds leaving was undetectable.

Table 4.5 Summary of substrates for Mistletoebird alightings, 2nd manoeuvres and all Mistletoebird manoeuvres in pink gums and box mistletoe in Aldinga Scrub

	Substrate type				
	Live Pink Gum	Dead Pink Gum	Live Mistletoe	Dead Mistletoe	Total
% Alighting records (n)	4 (16)	52 (194)	35 (130)	9 (35)	100 (375)
% 2nd manoeuvre (n)	4 (5)	21 (27)	68 (89)	7 (9)	100 (130)
% of manoeuvres (n)	4.4 (28)	38.5 (247)	50.9 (325)	6.3 (41)	100 (641)
% of total time (sec)	2.2 (724)	26.2 (8470)	62.5 (20186)	9.1 (2928)	100 (32308)
Mean time (sec) ± s.e (n)	25.9 ± 4.9 (28)	34.3 ± 3.0 (247)	62.1 ± 4.6 (325)	71.4 ± 11.5 (41)	50.4 ± 2.8 (641)

Data are percentages (actual no. in parentheses) of all manoeuvres recorded on different substrates, percentages of total time spent on different substrates, and average times for each recorded manoeuvre on each substrate.

Table 4.6 Summary of the percent of Mistletoebird alightings at pink gums (when Mistletoebirds initially arrived at a pink gum) in Aldinga Scrub

	Height			
	Upper	Mid	Lower	Total
Core	11.3 (38)	3.3 (11)	0.6 (2)	15.2 (51)
Edge	58.5 (196)	20.9 (70)	5.4 (18)	84.8 (284)
Total	69.9 (234)	24.2 (81)	6.0 (20)	100.0 (335)

Data are percentages (actual no. in parentheses) of all recordings of alighting location (number of alightings). Height distribution of alightings were categorised as 'upper' (upper third of canopy, assuming a cylindrical canopy), 'mid' and 'lower'. Horizontal distributions of alightings were categorised as 'core' (inner half of canopy assuming a cylindrical canopy) and 'edge' (outer half of the canopy)

Table 4.7 Summary of availability and use of mistletoes of different size and health classes

	Size			Health		
	Small	Medium	Large	Poor	Moderate	Good
% available (n)	16.2 (164)	36.4 (368)	47.4 (479)	16.0 (162)	36.6 (370)	47.4 (479)
% of records (n)	7.7 (24)	35.9 (112)	56.4 (176)	4.2 (12)	36.9 (106)	58.9 (169)
Mean time ± s.e., sec	44.4 ± 11.2	54.5 ± 6.6	72.2 ± 7.1	89.1 ± 41.5	54.0 ± 6.7	70.2 ± 6.9

Data are percentages (actual no. in parentheses) of mistletoes in different size and health classes, and all Mistletoebird records and average time of Mistletoebird manoeuvres in mistletoes of different size and health classes. The sample sizes 'n' for means are the same as for number of records. Size classifications are: 'small', < 30 cm diameter; 'medium', 30 – 80 cm diameter; and 'large', > 80 cm diameter. Mistletoe health classifications are: 'poor', greater than 50% foliage dieback; 'moderate', some signs of dieback but majority of mistletoe with healthy foliage; and 'good', mistletoe with vigorous foliage and no signs of dieback.

Table 4.8 Summary of the percent (actual no. in parentheses) of mistletoes used by Mistletoebirds which occurred in different locations within the canopy (total time recorded, seconds).

	Height			
	Lower	Mid	Upper	Total
Core	0.7 (163)	4.4 (962)	5.8 (1274)	10.9 (2399)
Edge	10.2 (2255)	34.1 (7538)	44.8 (9901)	89.1 (19694)
Total	10.9 (2418)	38.5 (8500)	50.6 (11175)	100 (22093)

The height of mistletoes was categorised as 'upper' (upper third of canopy, assuming a cylindrical canopy), 'mid' and 'lower'. Horizontal distribution of mistletoes was categorised as 'core' (inner half of canopy assuming a cylindrical canopy) and 'edge' (outer half of canopy)

4.5 DISCUSSION

Host tree selection

In deciding which host tree to visit, Mistletoebirds will be influenced by the 'attractiveness' of a tree. In their model of mistletoe spread, Lavorel *et al.* (1999) defined the attractiveness of a tree to Mistletoebirds as a function of the size of the tree's canopy, the size of the mistletoe fruit crop on that tree, and tree visibility. Each of these factors have influenced tree visitation by Mistletoebirds in the present study.

For example, the trees which Mistletoebirds visited and foraged in were taller, had a larger canopy volume, higher mistletoe abundances and hosted mistletoes of better size and health than trees which were not visited. Furthermore, logistic regression modelling indicated that tree height and mistletoe abundance both on the tree, and on surrounding trees, were the most important parameters in determining Mistletoebird visitation to trees. These patterns of host tree selection are consistent amongst mistletoe dispersers, with numerous studies demonstrating that the probability that a tree is visited increases with both tree height and mistletoe load (Martinez del Rio *et al.* 1995; Martinez del Rio *et al.* 1996; Aukema and Martinez del Rio 2002). Furthermore, it supports the notion that mistletoe dispersers can recognise the abundance of mistletoe plants on trees (Martinez del Rio *et al.* 1996; Lopez de Buen and Ornelas 1999), and mistletoe demographic studies which demonstrate that larger trees generally host more mistletoes (Lamont 1985b; Donohue 1995; Downey *et al.* 1997; Bannister and Strong 2001; Lopez de Buen *et al.* 2002; Ward 2005).

Prior to hosting any mistletoe, larger trees probably receive visits from Mistletoebirds simply because they occupy a larger proportion of the landscape and have a greater chance of being encountered. The subsequent establishment of mistletoes further increases tree attractiveness through an increase in the mistletoe fruit crop size, providing a positive feedback loop involving further visitation from Mistletoebirds and the aggregation of mistletoes on individual hosts.

However, a tree must also remain visible in the landscape if it is to receive visits from Mistletoebirds. Tree visibility is not only a function of tree size, but also the structure of surrounding trees. The present study has demonstrated that visit and forage trees had significantly lower percentages of canopy cover surrounding their own canopy and higher levels of canopy dieback than trees which were not visited. This is consistent with the patterns described by Ward (2005), who postulated this would result given that Mistletoebirds maintain direct flight paths between trees and would be more likely to visit canopies with easier access. The dieback seen in pink gums may therefore enhance access to tree canopies, and also suggest that Mistletoebirds would favour habitat edges. This raises questions about whether higher mistletoe abundances seen along habitat edges are primarily a function of better host quality (e.g. Norton and Stafford Smith 1999), or whether canopy access for Mistletoebirds contributes significantly to such trends. An experimental approach, involving artificial canopies with different mistletoe loads, is needed to shed further light on this.

Mistletoebird perch selection

If Mistletoebirds do prefer clear access to the canopies of trees, they should alight in the most open and accessible portion of the canopy. The results show that Mistletoebirds most often alight on the upper and outer portion of pink gum canopies. Furthermore, Mistletoebirds most often alighted on dead pink gum branches with little surrounding foliage, further supporting the notion that dieback of pink gums could enhance access for Mistletoebirds and hence mistletoe dispersal. The perching of Mistletoebirds in high branches will also enhance mistletoe dispersal quality (the fraction of seeds which land in a safe site in germinable condition, Ladley and Kelly 1996), by increasing the chances of defaecated seeds landing on a lower branch (e.g. Reid 1989; e.g. Ladley and Kelly 1996)

After alighting on dead pink gum branches, Mistletoebirds generally moved to live mistletoes, with 68% of all '2nd manoeuvres' occurring on live mistletoe. Optimal foraging theory would suggest Mistletoebirds would choose to visit mistletoes which provide the most reward for the least amount of effort, i.e. the closest mistletoe with the greatest amount of available fruit. On the surface, it appears that Mistletoebirds may follow this pattern: when birds used live mistletoes, they visited large and healthy mistletoes more frequently than medium and small mistletoes of moderate and poor health, and there was also a trend for Mistletoebirds to spend longer in large mistletoes than in medium and small mistletoes. In addition, Mistletoebirds foraged more often in easily accessible mistletoes, with 45% of all mistletoes visited in the 'upper-outer' category. While this is obviously a function of where mistletoes are located, it also reflects where Mistletoebirds frequently perch and deposit seeds.

Mistletoe dispersal quality will also be affected by the defaecation behaviour of Mistletoebirds, which has significant consequence for the resulting spatial distribution of mistletoes (Chapter 3; Ward and Paton in press). The defaecation rate calculated in the present study (0.16 seeds hour^{-1}) seems considerably lower than would actually happen, suggesting the method used to observe birds was not suitable to determine defaecation rate. In the present study, only 1% of defaecations occurred on live pink gum branches, with the majority of mistletoe seeds deposited on live mistletoe and dead pink gum branches (43% and 38% of occasions respectively). Although successful intraspecific hyperparasitism is documented in *Amyema miquelii* (Downey 1998), little information is available on the establishment success and resulting condition of adult mistletoes, although it is likely to be lower than for live host tree branches. If this is the case, defaecation patterns are consistent with the observation of Reid (1989), who noted that a large majority of branches on which Mistletoebirds deposited *Amyema quandang* seeds were dead or unsuitable for successful recruitment. This behaviour indicates that at some point the combination of the defaecation behaviour of Mistletoebirds and tree dieback may regulate the effectiveness of mistletoe dispersal, and hence mistletoe population growth.

Tree and mistletoe visit lengths

Mistletoe visit lengths and feeding rates of Mistletoebirds indicate that their foraging behaviour may not be strictly optimal, and yet may enhance the quality of mistletoe dispersal. Mistletoebirds spent on average only 62 and 84 seconds in each mistletoe and host tree respectively, which did not differ between mistletoes of different sizes or health categories, and they consumed only 1.6 fruits per visit (feeding occurred during 32 % of all mistletoe visits). Although these figures are consistent with other smaller mistletoe dispersers (Godschalk 1985; Ladley and Kelly 1996), they are considerably smaller than feeding rates (7.5 fruit per visit) and mistletoe visit lengths (around 5 min) by Mistletoebirds to *A. preissii* previously documented in a semi-arid acacia woodland (Yan 1993c). However, the large amount of fruit available to Mistletoebirds in the present study (based on number of fruit per mistletoe and number of mistletoe per tree) would indicate that Mistletoebirds could potentially remain feeding in trees and mistletoes far longer than they did. However during the present study Mistletoebirds were always 'on the move'.

So why do Mistletoebirds choose to leave mistletoes and trees when there is often an abundance of available food? It is highly likely that Mistletoebirds often left as a result of territorial behaviour, with 17% of birds leaving trees and mistletoes doing so as a result of intra- and interspecific interactions. The territorial nature of Mistletoebirds is well known (particularly males, Reid 1997a; Higgins *et al.* 2006) yet poorly quantified, however the frequency of such interactions is not surprising given the abundance of birds and spatial overlap of home ranges between birds in the study site (Chapter 3; Ward and Paton in press). Because of the small size of Mistletoebirds and the visual impedance they would encounter in the woodland, defence of their territories would rely solely on the active detection of intruders. Mistletoebirds, therefore, may forage and defend their territories simultaneously by continuously moving about their territory, similar to some nectar feeding birds which must forage frequently to maintain energy, yet simultaneously defend their territories to ensure food resources are not depleted (Paton and Carpenter 1984).

The continuous movement and short stopping times of Mistletoebirds in mistletoes and trees should, theoretically, improve mistletoe dispersal quality. Gut passage times of Mistletoebirds (Murphy 1991; Murphy *et al.* 1993) are far longer than the mean stopping time within individual trees, meaning most seeds would be defaecated away from the parent plant enhancing dispersal quality (Ladley and Kelly 1996; Lopez de Buen and Ornelas 1999). This would be limited, however, because Mistletoebirds frequently use the same individual trees, and up to 10% of seeds from mistletoes on an individual tree may be deposited on that tree (Chapter 3; Ward and Paton in press).

Conclusions

The present study provides a comprehensive quantitative description of the behaviour of Mistletoebirds in a heavily infected woodland. Host tree selection was consistent with assumptions used in models of mistletoe spread (Lavorel *et al.* 1999): in essence, taller trees with more mistletoe and accessible canopies are more attractive to Mistletoebirds. The frequent use of dead pink gum branches for alighting and the lower canopy density around visit trees, provides further support for the notion that dieback in pink gum woodlands may improve mistletoe dispersal quality by improving habitat for Mistletoebirds (Ward 2005). Mistletoe dispersal quality will be also be enhanced by the short visit durations to mistletoes and individual trees by Mistletoebirds. However, the recurrent defaecation of mistletoe seeds onto dead branches by Mistletoebirds is possibly the greatest regulatory influence on mistletoe dispersal.

Plate 4.1 The initial stages of canopy dieback of pink gum *Eucalyptus fasciculosa*. Note the browning of leaves and exposure of many small branches on the outer of the canopy. It is these branches on which Mistletoebirds often perched when alighting on pink gums in the current study.

I tagged more than 300 box mistletoes on 75 pink gums in Aldinga Scrub, with tie-wire and metal tags, in order to monitor the number of mistletoe recruits, survivors and deaths over a 24 month period (Chapter 5). This monitoring will be continued into the future for examination of longer term trends.

CHAPTER 5

ESTABLISHMENT AND RECRUITMENT OF BOX MISTLETOE

Chapter 5 Preamble

Chapter 5 describes a germination experiment and a mistletoe monitoring program, both conducted in Aldinga Scrub. The germination experiment was initially going to determine mistletoe establishment rates solely on pink gum. However, a stand of revegetated eucalypt woodland, which included three box mistletoe host species at approximately the same age, allowed an experiment to examine differences in establishment rates between different hosts. I conducted all field work and analyses for this experiment. The monitoring program was set up to determine the number of mistletoes recruited over the relatively short time period of the PhD program. Field work was conducted by myself and Colin Bailey. This chapter will be submitted to a scientific journal as a series of two manuscripts, part one describing the germination experiment, part two the mistletoe monitoring. Therefore, this chapter is slightly longer than preceding data chapters.

CHAPTER 5

AFTER DISPERSAL: ESTABLISHMENT AND RECRUITMENT OF BOX MISTLETOE *AMYEMA MIQUELII* IN A PINK GUM *EUCALYPTUS FASCICULOSA* WOODLAND

5.1 ABSTRACT

In the Mount Lofty Ranges, South Australia, box mistletoe infection is frequent and severe on pink gums *Eucalyptus fasciculosa*, raising concerns for tree health. In order to understand patterns of mistletoe host specificity and proliferation, I conducted a box mistletoe *Amyema miquelii* establishment experiment on three potential hosts. I also monitored mistletoe recruitment to determine whether recruitment rates reflected the behaviour of mistletoe dispersers.

Amyema miquelii seeds were inoculated on branches of different diameters and orientations on three species of eucalypt host: pink gum *E. fasciculosa*, mallee box *E. porosa* and red gum *E. camaldulensis*. Establishment success was highest on pink gum (42% of holdfast forming seeds), consistent with patterns of host specificity in natural eucalypt woodlands of temperate South Australia. Mistletoes on pink gums also had the greatest number of leaves (10 leaves per plant) and linear growth (average length of 6cm) after 13 months. Red gums had the lowest establishment success (22%) and smallest growth (1cm), because these trees had efficient methods of removing seeds (bark shedding), and probably because underlying chemical and physical defences prevented a functional xylem connection between host and mistletoe. Recruitment rates of box mistletoe were higher on taller trees with more mistletoe, reflecting the preference of Mistletoebird *Dicaeum hirundinaceum* to perch on these trees. Recruitment and establishment rates can now be used as parameters in modelling the spread of box mistletoe in pink gum woodlands.

KEYWORDS: germination, host specificity, mistletoe – host compatibility, infection.

5.2 INTRODUCTION

Successful recruitment of bird dispersed mistletoes has two key requirements – the dissemination of mistletoe seeds to appropriate branches of host trees by the bird disperser, followed by the germination and establishment of those seeds.

The dissemination of mistletoes to appropriate branches by birds is strongly influenced by the movements and foraging behaviour of the dispersers. Mistletoe dispersers generally prefer to perch and forage on larger, taller trees which host more mistletoe (Martinez del Rio et al. 1995; Martinez del Rio et al. 1996; Lopez de Buen and Ornelas 1999; Chapter 4). This subsequently leads to increased seed rain on the branches of individual trees (Aukema and Martinez del Rio 2002), and the aggregated distribution of seed rain at a landscape scale (Chapter 3; Ward and Paton in press).

The success of mistletoe seedling establishment is primarily dependent on the final resting place of the seed following dissemination. For example, seedling establishment is often low because birds disperse seeds to inappropriate sites such as dead branches or the branches of incompatible hosts (Chapter 4; Reid 1989, Ladley and Kelly 1996). For those that are dispersed to live branches of potential host trees, seedling establishment is influenced by the species of the host on which it is dispersed (Yan 1993a), the diameter of the branch (Sargent 1995; Yan and Reid 1995), and potentially micro-environmental factors such as light availability (Lamont 1983a; Yan and Reid 1995). Such variability in mistletoe establishment and recruitment can lead to mistletoe 'host specificity'.

Mistletoe host specificity is the non-random pattern of infection of potential hosts by mistletoes in a given area (Barlow 1981; Yan 1993a). Host specificity can result from herbivore avoidance (Barlow and Wiens 1977; Barlow 1981), the movement patterns and foraging preferences of bird dispersers (Martinez del Rio *et al.* 1996; Aukema and Martinez del Rio 2002; Ward and Paton in press), genetic compatibility of different hosts (Clay *et al.* 1985), and broader environmental influences such as poor recruitment in significantly altered habitats (Norton *et al.* 1997) and rainfall (Yan 1990).

The primary driver of mistletoe host specificity, however, is 'host compatibility' (Yan 1993a); that is, the ability of a seed to establish to maturity on a host branch. Host compatibility can be documented in studies where mistletoe seeds are inoculated on potential host species and their fate followed (Lamont 1983a; Salle 1983; Shaw and Loopstra 1991; Yan 1993a; Sargent 1995; Yan and Reid 1995; Ladley and Kelly 1996; Robinson and Punter 2001). In most of these studies, germination success of mistletoes are high and independent of host species, yet final establishment success varies and is strongly influenced by branch diameter and host species. In order to understand the link between establishment success and local patterns of host specificity in an area, deployment experiments are required.

In Australian Loranthaceous mistletoes, host specificity ranges from those that are seemingly specific to a single host (e.g. *Amyema pyriforme* on *Eucalyptus rupestris*), and those that are generalists such as box mistletoe *A. miquelii*, which is known to infect at least 111 *Eucalyptus* species (Downey 1998). However, even box mistletoe varies in patterns of infectivity on different eucalypt hosts. In the Mount Lofty Ranges (MLR), South Australia, for example, box mistletoe infects all *Eucalyptus* species present, yet the frequency and severity of infection on pink gum *E. fasciculosa* is far greater than other eucalypt types (Chapter 2; Ward 2005).

In the MLR, further examination of box mistletoe recruitment patterns and establishment success on pink gums is currently necessary for a number of reasons. Firstly, it has been postulated that the frequency of mistletoe infection in pink gums woodlands is higher because of more efficient dispersal by Mistletoebirds and reduced herbivory in degraded pink gum woodlands (Chapter 2; Ward 2005). However, it is also possible that germination and establishment success of box mistletoe may be higher on pink gums than other *Eucalyptus* species, and therefore, these need to be tested.

Secondly, although it is generally accepted that box mistletoe abundances are increasing across south eastern Australia, there is no evidence that mistletoe population growth is positive in these woodlands. Furthermore, testing patterns of recruitment on a variety of trees may provide a link between previously documented tree selection behaviour by dispersers (e.g. Chapter 4) and mistletoe recruitment.

Finally, determining establishment and recruitment success of box mistletoe in pink gum woodlands will assist in the development of models of the spread of mistletoe in these woodlands (e.g. Lavorel *et al.* 1999). Such models would help to predict the time frame over which mistletoes may infect a patch of woodland, as well as the effectiveness of mistletoe removal as a long term management tool. This is important because with box mistletoes infecting approximately 30% of all pink gums in the region, and pink gums demonstrating high levels of canopy dieback, there is the potential to manage mistletoe in the region (see Chapter 2; Ward 2005).

The following study aims to determine the establishment success of box mistletoe on pink gums and two other species of *Eucalyptus*, in order to determine the influence of host compatibility on the patterns of host specificity seen in natural eucalypt woodlands of the Mount Lofty Ranges. It also describes detailed demographic monitoring of box mistletoes in a pink gum woodland. Specifically, the study aims to answer the following questions:

1) Can variation of box mistletoe establishment success on different eucalypt species explain patterns of host specificity in the Mount Lofty Ranges?
2) Does branch size and orientation affect box mistletoe establishment on three eucalypt species (*E. fasciculosa*, *E. camaldulensis* and *E. porosa*)?
3) Do patterns of recruitment of box mistletoe reflect disperser behaviour?
4) What are the recruitment and mortality rates of box mistletoes on pink gums?

5.3 METHODS

Study site

Field work was carried out in Aldinga Scrub Conservation Park (Aldinga Scrub hereafter, 138° 27′ E, 35° 18′ S), approximately 40 km south of Adelaide, South Australia. The climate is temperate, with maximum temperatures in winter and summer averaging 15° C and 27° C respectively. Mean annual rainfall is approximately 450 mm, with most precipitation occurring in the winter months (Commonwealth Bureau of Meteorology 2005). Aldinga Scrub, at 266 ha, represents the last remnant of native coastal woodland on the Adelaide plains. The park is surrounded by coastline and housing on the west side, and agriculture on all other sides. Almost all of the park contains *Eucalyptus* woodland, primarily of pink gum *E. fasciculosa* and mallee box *E. porosa*. Surveys in 2003 and 2004 (Ward 2005; Ward and Paton in press) demonstrated that pink gums in Aldinga Scrub contain heavy loads of box mistletoe *Amyema miquelii.*

Germination trial

In the first week of September 2004, a large quantity of ripe *A. miquelii* fruit was collected from more than 50 healthy *A. miquelii* on different *E. fasciculosa* hosts in Aldinga Scrub. Ripe *A. miquelii* fruit are yellow to red-brown in colour, 8 – 12 mm in length (Reid 1986), soft to touch and swollen in comparison to unripe fruit. Fruits from different plants were mixed and kept overnight in paper bags in the shade. Over the next three days, seeds were placed (inoculated) on live branches of 29 pink gums *E. fasciculosa*, 29 mallee box *E. porosa* and 25 red gum *E. camaldulensis.* At the time of study, all trees were 10 – 15 year old and between 4 – 10 m in height, having been planted as part of a small revegetation scheme near the northern boundary of Aldinga Scrub.

On each tree, two branches with different orientations were selected to test the effect of branch orientation on mistletoe establishment. Orientation was classified as either North (315° - 45°), East (46° - 135°), South (136° - 225°) or West (226° - 315°). On each tree, ten seeds were inoculated along the length of each of two separate branches, from their thicker portion to their distal thinner portion (diameter range 5 - 74 mm). This was to test the effect of host branch diameter ('HBD') on mistletoe establishment. Seed deployment was similar to that of Yan (1993a) and Yan and Reid (1995), all seeds being removed from the surrounding pericarp and immediately placed on the upper side of branches to which they adhered. The location of inoculated trees was recorded with a GPS, and marked with a permanent aluminium tag and flagging tape. Inoculated branches were marked with tie-wire and metal tags, and the location of each and every seed was numbered with a paint pen (Plate 5.1). The diameter of the branch at the exact location where seeds were placed was measured using digital callipers, and the orientation of the branch classified as either north, east, south or west. On some trees there was only one suitable branch on which to place seeds, and to compensate seeds were deployed on three branches on some trees. Also, inadvertently, 11 seeds were placed along two branches. In total, 503 seeds were deployed on 51 *E. porosa* live branches, 501 on 51 *E. fasciculosa* branches, and 500 on 50 *E. camaldulensis* branches. In addition, 20 seeds were placed on a dead branch of each of a *E. fasciculosa* and a *E. porosa* in order to determine the longevity of free-living seeds (Yan and Reid 1995).

All seeds were censused one week after deployed, and seeds which were no longer present replaced with seeds using the same inoculation methods. Seeds were then censused 6 weeks (October 2004), 6 months (March 2005), 9 months (June 2005) and 13 months (October 2005) after deployment. During each census, seeds were scored as either alive, dead or missing. For live seeds, it was noted whether the seed had germinated, whether the hypocotyl had touched the host branch, whether a holdfast had developed, whether leaves had emerged and, if so, the number of leaves which had developed and the approximate length of the mistletoe seedling (from host branch to the apical meristem). Seeds were considered alive if they were present, not withered and were green in colour. Seeds were considered to have germinated when the radicle emerged from the seed and the hypocotyl had extended from the seed. A hypocotyl was considered to have touched the host branch only when its tip had made contact with the branch. A holdfast was considered to have developed when the tip of the radicle touching the branch had developed considerable contact with the branch, and had become swollen and circular in shape. Seeds were considered to have died when they were either missing, or had desiccated and turned brown.

The mortality of seeds was classified as either 'predated' (missing), 'bark-lift', 'host branch death' 'borer' or '*in-situ*'. As documented by Yan and Reid (1995), we found that missing seeds were often aggregated on particular branches or trees, yet there was no evidence that seeds had slipped off branches, indicating that animals were probably responsible for missing seeds. Therefore, missing seeds were classified as 'predated'. Many seeds were removed by the bark being shed from the host branch ('bark-lift'). This primarily occurred in the summer months after viable seeds had already developed haustoria and, when the bark lifted, the seed left a small cavity on the host branch. Some mistletoe seeds also died seemingly as a result of the death of the host branch (where no previous indication of mortality was evident; 'host branch death'). Many seeds also died as a result of parasitism, which was indicated by dead seeds on the host branch which, upon inspection, had either a small larva or pupal case within the endosperm of the seed that had damaged the inside of the seed ('larvae'). Several specimens of these larvae and pupal cases were taken for later identification. Lastly, mortality of seeds which died whilst still attached on the branch, with no evidence of predation, larvae, bark-lift or the host branch dying, were classified as '*in situ*'.

Analyses – germination trial

The differences in germination, branch contact and holdfast formation were compared for all deployed seeds between host species using contingency tables and Pearson's goodness-of-fit tests (χ^2). Differences in leaf emergence and establishment were compared for those seeds which developed holdfasts between host species, using contingency table and Pearson's goodness-of-fit tests (χ^2). Germination was defined as the percentage of the total number of seeds deployed that had germinated within 1 week or 6 weeks of deployment. Mortality was calculated as the number of seeds which died as a percentage of the total number of seeds deployed. Seeds were considered to have established if, by the 13 month recording period, seeds were present, had developed a holdfast and were still green in colour. The length of the newly established mistletoes with leaves and the number of leaves were compared between host species using one-way ANOVA and Tukey-Kramer HSD post hoc significance tests. Comparisons were also made across species of the establishment success of seeds deployed on different branch diameters, and 'optimal' host branch diameters (HBDs) were classed as those on which the majority of seeds established. Establishment of seeds was then compared across host species for those seeds which were deployed on 'optimal' branch sizes. In order to meet assumptions of normality, transformations were conducted on all data used in ANOVA comparisons. ANOVA, however, is robust to considerable deviations from normality (Zar 1999). Therefore, when normality was not achieved, data were left in their original form.

In addition, regression models were used to investigate the relationship between tree species (SPECIES), host branch diameter (HBD), branch orientation (ORIENT) and whether or not a seed established (was alive and had developed a holdfast). These three independent variables were used as explanatory variables in the *a priori* development of a set of seven models to compare the influence of these variables on seed establishment. Interactions among the variables were not considered. Models were fitted using generalised linear models (GLM) assuming a binomial error structure (1 = established; 0 = not-established) with a logit link function (logistic regression) using R 1.7.0 (R Development Core Team 2003). The proportion of variance explained by the chosen parameters was assessed by calculating, for the global models, the deviance ratio: [(null deviance - residual deviance) : null deviance].

Candidate models were ranked using Akaike's Information Criterion (AIC) model ranking techniques (Burnham and Anderson 2002). As a cautionary approach, model selection from candidate models was based on a second-order bias corrected form of AIC (AICc), even though sample size (1525) was large in relation to the number of parameters across variables (8). Because each variable was included in models an equal number of times, the relative importance of each individual variable (j) could be estimated by summing the Akaike weights w_i across all the models in the set where variable j occurs to give the sum $w_+(j)$. The larger the $w_+(j)$, the more important variable j is, relative to the other variables (Burnham and Anderson 2002).

Demography of A. miquelii

Using a GIS, a 500 m x 500 m grid was established in the south-eastern portion of Aldinga Scrub, which covered areas of high and low mistletoe abundance. For each grid intersection point (25 in total), a location between 0 and 100 m south of the grid was randomly selected. In November 2003, the closest three pink gums to each of these points were tagged, so that a total of 75 pink gums were selected. Only trees between 3 m and 8 m in height were selected, primarily to ensure adequate safety for subsequent searches of mistletoe by the authors. Using a 6 m ladder, the canopy of each pink gum was searched for box mistletoe *A. miquelii* by two observers (myself and Colin Bailey). All mistletoes, including juvenile mistletoes which were detected, were numbered and marked with aluminium tags and twist wire. On the several occasions that mistletoes could not be reached, notes were made of the size and position of the mistletoes so they could be located in the future. For each box mistletoe, the following variables were recorded: the maximum canopy diameter of the mistletoe, the vertical and horizontal distribution of the mistletoe in the tree canopy, the orientation of the mistletoe in the tree, and the minimum circumference of the host branch below the haustorium. The number of haustorial branches was counted but not used in analyses as it was thought to be too variable and difficult to record accurately. The diameter of the host branch (HBD) was then calculated from the circumference (HBD = circumference / π). The health of each mistletoe was classed as ‘poor’ (greater than 50% foliage dieback), ‘moderate’ (some signs of dieback but majority of mistletoe with healthy foliage), or ‘good’ (mistletoe vigorous with no signs of dieback).

The following characteristics were measured for each survey tree: height (HEIGHT), canopy volume (CA.VOL), the extent of canopy dieback (DIEBACK), the overstorey density of the canopy surrounding each survey tree (OS.DENS), the density of mistletoes within 5 m surrounding each survey tree (5m.DENS), and for each tree the total number of mistletoes it hosted in November 2003 (MTOE2003). HEIGHT was measured using a clinometer. CA.VOL was determined by measuring the height of the lowest canopy with a clinometer, subtracting this from the height of the tree and dividing by two to obtain *r*, measuring the north–south and east–west canopy diameter for each pink gum, and using the formula for the volume of a sphere ($4/3\Pi abr$, where a and b: the north–south and east-west diameters divided by two, respectively). The density of mistletoes within 5 m surrounding each survey tree (5m.DENS) was calculated as $m/(A\text{-}T)$, where m is the number of mistletoes within 5 m of the canopy of the survey tree, A is the total area of both the tree canopy and the 5 m surrounding the canopy, and T is the tree canopy area. DIEBACK of individual trees was determined by visually estimating the proportion of canopy foliage that had senesced. The overstorey density of the canopy surrounding each survey tree (OS.DENS) was determined using a 'spherical densiometer' (Model-A, Forest Densiometers, Forestry Suppliers Inc.). At a location 2 m from the north, east, south and west edge of the survey tree's canopy a reading was taken from the spherical densiometer and all four readings combined to obtain the estimate for overstorey density.

After 24 months, in November 2005, each tree was resurveyed for mistletoes. The same observers searched the canopy of each pink gum for each mistletoe which was originally tagged, and for any new mistletoe plants. Following Reid and Lange (1988), box mistletoes were therefore recorded as either 'survivors' (alive in 2003 and 2005), 'deaths'(alive in 2003 and dead in 2005) or 'recruits'(mistletoes that established between 2003 and 2005).

Analyses – demography of A. miquelii

A range of descriptive statistics was calculated for survey trees, mistletoes tagged in 2003 and for the mistletoe recruits tagged in 2005. The number of mistletoe 'survivors', 'recruits' and 'deaths' was determined, and from this the recruitment and mortality rates (no. mistletoes tree^{-1} year^{-1}) were calculated. The percentage of mistletoes in different health categories, including mortalities and recruits, was calculated. Linear regressions were performed on the number of mistletoe recruits on individual trees and each of the variables measured for the survey trees (HEIGHT, CA.VOL, OS.DENS, 5m.DENS, DIEBACK and MTOE). ANOVA and post-hoc Tukey-Kramer HSD tests were used to compare the Host Branch Diameter and Maximum Canopy Diameter between mistletoe survivors, deaths and recruits. In order to meet assumptions of normality, transformations were conducted on all data used in ANOVA comparisons. ANOVA, however, is robust to considerable deviations from normality (Zar 1999). Therefore, when normality was not achieved, data were left in their original form.

Poisson regression models were used to investigate the relationship between tree characteristics and the number of recruits on individual trees over 2 years. Five independent tree variables which were likely to influence visits to trees by Mistletoebirds and therefore recruitment rates, MTOE, HEIGHT, 5m.DENS, DIEBACK and OS.DENS, were used as explanatory variables in the *a priori* development of a set of 15 models to compare the influence of tree variables on whether mistletoes were recruited on trees. CA.VOL was not included as it was correlated with both HEIGHT and MTOE. Interactions among the variables were not considered, and post hoc analysis revealed interaction terms did not improve model fits. Models were fitted using generalised linear models (GLM) assuming a Poisson error structure with a log link function using R 1.7.0 (The R Development Core R Development Core Team 2003). The proportion of variance explained by the chosen parameters was assessed by calculating the deviance ratio for the global models.

Candidate models were ranked using Akaike's Information Criterion (AIC) model ranking techniques (Burnham and Anderson 2002), however, because the data were slightly overdispersed (variance inflation factor $c = 1.48$), a quasi-likelihood adjusted version of AIC_c, $QAIC_c$ was used (Burnham and Anderson 2002). The relative importance of each individual variable (j) was also estimated by developing models post-hoc including all possible combination of parameters, and comparing $w_{+(j)}$ for individual variables.

Plate 5.1. Example of a box mistletoe *Amyema miquelii* seed deployed on the branch of a pink gum *Eucalyptus fasciculosa*. Note the elongation of the hypocotyl and the tip of the radicle touching the host branch.

5.4 RESULTS

Germination trial

A total of 1526 *Amyema miquelii* seeds was deployed: 511, 514 and 501 seeds on *E. fasciculosa*, *E. porosa* and *E. camaldulensis*, respectively. Across all host species, growth of the hypocotyl or radicle was evident a few days after deployment of seeds, and across all hosts more than 90% of seeds germinated (Table 5.1). 75% of all seeds made contact with the host branch, with more hypocotyls managing to touch the host branch in *E. camaldulensis* (83.4%) compared with *E. porosa* (72.5%) and *E. fasciculosa* (69.9%; Table 5.1). However, significantly fewer seeds managed to develop holdfasts on *E. camaldulensis* (18.2%) in comparison with *E. porosa* and *E. fasciculosa* (31.4% and 27.4% respectively, $\chi^2_{2,1521} = 24.2$, $P < 0.0001$, Table 5.1). All of the seeds deliberately placed on dead branches of *E. fasciculosa* and *E. porosa* to determine the longevity of free-living seeds were alive 6 weeks after deployment, however all had died by the time of the next recording 20 weeks later.

Of those seeds which managed to form a holdfast, there was no difference in the number of seeds from which leaves developed between host species ($\chi^2_{2,389} = 2.48$, $P = 0.2890$; Table 5.1). However, significantly fewer seeds with holdfast attachments eventually established as viable mistletoes on red gums (22.0%) than on *E. porosa* (38.5%) and *E. fasciculosa* (42.1%, $\chi^2_{2,389} = 11.0$, $P = 0.004$; Table 5.1). For seeds which were deployed on optimal branch sizes (≤ 17 mm, see below) and which developed holdfasts, establishment was greatest on *E. fasciculosa* (73.5%), significantly higher than *E. porosa* (57%) and *E. camaldulensis* (29.4%; $\chi^2_{2,195} = 23.1$, $P < .0001$; Table 5.1). Of the established mistletoes, those on *E. fasciculosa* and *E. porosa* had significantly more leaves ($F_{2,1523} = 13.2$, $P < 0.0001$) and were larger in diameter ($F_{2,1523} = 10.9$, $P < 0.0001$) than those that had established on *E. camaldulensis* (Table 5.1).

There were significant differences in the percentage of seeds which died from different causes ($\chi^2_{8,1371} = 120.1$, $P < 0.0001$; Table 5.2). The majority of seeds were predated (range 43.5 – 56.0%) or died *in situ* (range 15.1 – 27.3%). 4% of seeds inoculated on *E. porosa* seemingly died because the branch on which they were placed senesced, however this was rare in the other eucalypt species (0.2%). Conversely, many seeds on *E. camaldulensis* (11.8%) and *E. fasciculosa* (7.2%) were lifted off the host branch when the branches shed their bark, however this was rare on *E. porosa* (0.6%). Across all species, the majority of seeds died between 6 and 26 weeks.

Insect larvae inflicted feeding damage and mortality in 13% of all seeds across all host species (Table 5.2). Samples of seeds affected by borers revealed the presence of two types of parasitoid wasp: one of the genus *Apanteles* (Braconidae: Microgastrinae), and one of the Family Eupelminae (Chalcidoidea: Eupelmidae). Both wasps were present within the pupal cases of Lepidoptera larvae (Fig 5.1). From what is known of their biology, both *Apanteles* and Eupelminae are endoparasitic of Lepidoptera, therefore the feeding damage and mortality of the seed would have resulted from the presence of the Lepidopteran larvae and not the wasp (N. Stevens pers. comm.).

Across all species, 74% of seeds deployed on branches less than 17 mm in diameter established. Maximum seedling establishment occurred on the branches less than 8 mm in diameter, with 22.7% of seeds deployed on such branches established (Table 5.3). Maximum establishment success for box mistletoe on *E. fasciculosa, E. porosa* and *E. camaldulensis* occurred on branches of 9–11 mm (27%), 15–17 mm (28%) and < 8 mm (15%) diameter, respectively.

Across all species, there was a slight yet difference in the establishment success between branches with different orientations ($\chi^2_{3, 1520} = 8.84$, $P < 0.03$). Establishment success was greatest with seeds placed on east orientated branches, with 13.6 % of all seeds placed on branches of this orientation establishing, compared with 8.1%, 9.3% and 8.0% for seeds placed on branches with North, South and West branches respectively.

For logistic regression models of establishment, model fit was reasonable with 15% of the variance in the global model explained by the explanatory parameters. $QAIC_c$ modelling indicated that the global model, including all variables measured (EUC + ORIENT + DIAM) was the best model of establishment from seeds, with a 70%

probability of being the best model in the candidate set (as indicated by the Akaike weight, w_i; Table 5.4; Burnham and Anderson 2002). The next best model of mistletoe establishment was EUC + DIAM ($w_i = 0.30$), and all other models were comparatively unlikely ($\Delta_i > 3$, Table 5.4). Estimation of relative parameter importance demonstrated that the two individual parameters with the highest estimated importance were DIAM (1.0) and EUC (0.99), followed by ORIENT (0.70; Table 5.5).

Table 5.1 Extent to which box mistletoe *Amyema miquelii* seeds became established on different eucalypt hosts, *Eucalyptus fasciculosa, E. porosa* and *E. camaldulensis*

	No. seeds	Germination (%)	Host branch contact (%)	Holdfast formation (%)	Dicotyledon emergence (%)	Leaf emergence (%)	No leaves / plant at 14 months (mean ± s.e.)	Mistletoes length, cm (mean ± s.e.)	Establishment (%)	HBD adjusted establishment (%)
E. fasciculosa	501	90.4	69.9	27.4	75.0 (20.5)	50.0 (13.7)	10.1 ± 1.3	5.8 ± 0.9	42.1 (11.5)	73.5 (25.4)
E. porosa	503	89.3	72.5	31.4	78.9 (24.8)	47.8 (15.0)	7.1 ± 1.1	4.5 ± 0.8	38.5 (12.1)	57.0 (22.2)
E. camaldulensis	500	91.8	83.4	18.2	74.7 (13.6)	42.9 (7.8)	2.1 ± 0.4	1.0 ± 0	22.0 (4.0)	29.4 (7.6)
Test		N.S.	****	****	N.S.	N.S.	***	***	**	****
All	1504	90.5	75.2	25.7	76.5 (19.7)	47.5 (12.2)	8.2 ± 0.9	4.8 ± 0.6	36.0 (9.3)	55.6 (18.4)

For germination, host branch contact and holdfast formation, data are percentage of *all* seeds deployed on branches. For dicotyledon and leaf emergence, number of leaves, mistletoe length, establishment and HBD adjusted establishment, data are percentage of those seeds that *formed holdfasts*, and parenthesised, percentage of all seeds deployed. HBD adjusted establishment is establishment success of seeds which were deployed on branches < 17 mm in diameter. Seeds were considered to have established if, after 12 months, seeds were present, had developed a holdfast, were still green in colour and had at least small dicotyledons present. Data were compared between host species using contingency table and Pearson's goodness-of-fit tests (X^2). Significance levels are $P < 0.0001$ (****), $P < 0.001$ (***), $P < 0.01$ (**) and $P < 0.05$ (*). N.S. = not significant

Table 5.2 Mortality of box mistletoe *Amyema miquelii* seeds inoculated on different eucalypt hosts, *Eucalyptus fasciculosa, E. porosa* and *E. camaldulensis*

	No. seeds	Died *in situ*	Predated	Bark lifting	Host branch died	Larvae
E. fasciculosa	511	15.1	56.0	7.2	0.2	9.8
E. porosa	514	22.4	44.6	0.6	4.3	16.1
E. camaldulensis	501	27.3	43.5	11.8	0.2	13.0
Total	1526	21.6	48.0	6.5	1.6	13.0

Data are percentage (%) of total number of seeds deployed on different host species.

Table 5.3 Establishment success of box mistletoe *Amyema miquelii* seeds on branches of different diameters on three different eucalypt host species

	No. seeds established (total deployed)	Branch diameter						
		< 8	9-11	12-14	15 - 17	18 - 20	20 - 30	> 30
E. fasciculosa	56 (511)	25.7 (1.8)	27.0 (3.9)	26.0 (2.5)	15.8 (1.2)	5.6 (0.8)	3.0 (0.6)	0.7 (0.2)
E. porosa	58 (514)	26.9 (1.4)	19.0 (3.1)	17.4 (1.6)	27.7 (2.5)	8.8 (1.0)	6.4 (1.4)	1.4 (0.4)
E. camaldulensis	21 (501)	14.8 (0.8)	9.0 (1.4)	4.2 (0.4)	6.8 (0.6)	0.0	0.8 (0.2)	3.7 (0.8)
Total	62 (1526)	22.7 (1.3)	18.2 (2.8)	16.0 (1.5)	17.1 (1.4)	4.6 (0.6)	3.2 (0.7)	1.8 (0.5)

Data are percentage (%) of seeds established of the total number inoculated on that branch diameter. Data in parenthesis are percentage of seeds established of total number of seeds deployed.

Table 5.4 Ranking of logistic regression models of seeds which did and did not germinate using AICc model ranking procedures for 1525 seeds deployed across three eucalypt species in Aldinga Scrub, South Australia

	Candidate model	$\text{Log}(\Lambda)$	K	Δ_i	w_i
1	**EUC + ORIENT + DIAM**	**-389.12**	7	**0.00**	0.70
2	**EUC + DIAM**	**-393.01**	4	**1.72**	0.30
3	ORIENT + DIAM	-400.39	5	18.50	<0.0001
4	DIAM	-405.88	2	23.45	<0.0001
5	EUC + ORIENT	-441.70	6	103.14	0.0
6	EUC	-444.94	3	103.57	0.0
7	ORIENT	-451.42	4	118.55	0.0

EUC, *Eucalyptus* species (*E. fasciculosa*, *E. porosa* and *E. camaldulensis*); ORIENT, orientation (N,S,E,or W) of branch on which seed deployed; DIAM, diameter of branch on which seed deployed, directly below seed. $\text{Log}(\Lambda)$ is the log likelihood of the model; *K*, the number of estimated parameters; Δ_i, the difference between that model's second-order bias corrected form of Akaike's Information Criteria (AIC*c*) and the minimum AIC*c* value; and, w_i, Akaike weights. Candidate models with significant levels of empirical support ($\Delta_i < 2$) are shown in bold. Percentage of deviance explained by included variables = 15.0%.

Table 5.5 Relative importance of each variable (*j*), estimated by summing the Akaike weights w_i across all the models in the candidate set (Table 5.4) where variable *j* occurs to give the sum $w_{+(j)}$. The larger the $w_+(j)$, the more important variable *j* is, relative to the other variables (Burnham and Anderson 2002)

Variable	$w_{+(j)}$
Branch diameter	1.00
Host *Eucalyptus* species	0.99
Branch orientation	0.70

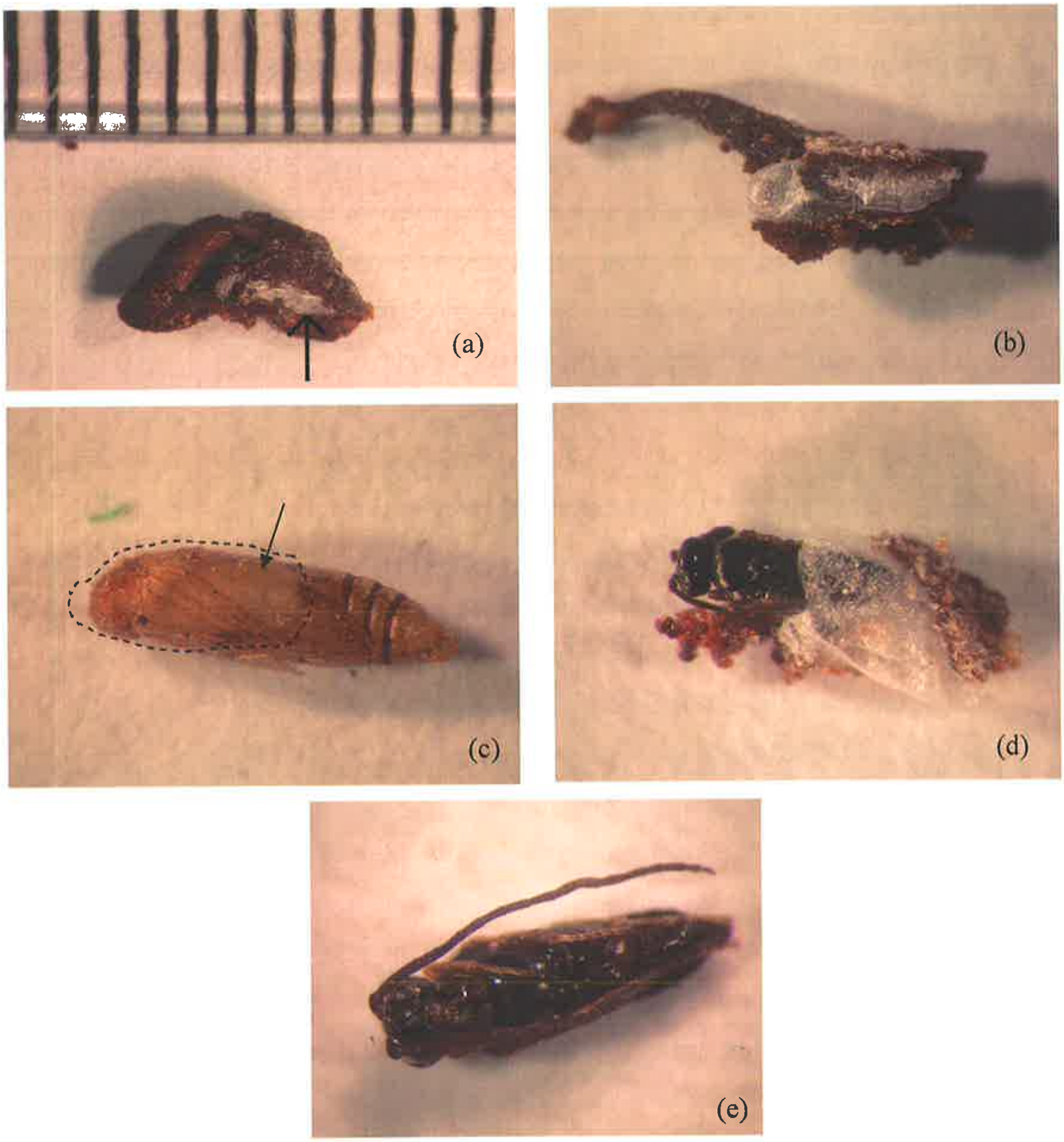

Fig 5.1. Various life stages of insects using box mistletoe *Amyema miquelii* seeds, which inflicted feeding damage and mortality in 13% of all seeds across all host species (Table 5.2). Samples of seeds revealed two types of parasitoid wasp: one of the genus *Apanteles* (Family Braconidae: Sub-family Microgastrinae), and one of the sub-family Eupelminae (Superfamily Chalcidoidea: Family Eupelmidae). Both wasps were present within the pupal case of a Lepidoptera larva. *Apantales* and Eupelminae are endoparasitic of Lepidoptera, and the mortality of the mistletoe seed results from the feeding damage inflicted by the Lepidopteran larvae. Photos are: a) wasp pupal case within endosperm of mistletoe seed (arrow), with mistletoe hypocotyl extended and holdfast (scale bars 1mm); b) wasp pupal case within endosperm of mistletoe seed; c) larva of parasitoid wasp (outlined with dashed line) of the Family Eupelminae (Chalcidoidea: Eupelmidae) within old Lepidoptera pupal case (length approx. 4 mm); d) parasitoid wasp of the genus *Apanteles* (Braconidae: Microgastrinae) emerging from pupal case (length approx. 4 mm); and e) fully emerged *Apanteles* wasp (length approx. 4 mm).

Demography of A. miquelii

In 2003, a total of 351 mistletoes were identified and tagged across 75 *E. fasciculosa* trees, with an average of 4.7 mistletoes per tree (Table 5.6). Over the 24 month study period, 43 mistletoes tagged in 2003 died, giving a mortality rate of 0.29 mistletoes per tree per year. Over the same period, 308 of the original mistletoes survived, and 111 new mistletoe recruits established, for a net mistletoe population growth of 68 mistletoes, or 0.45 mistletoes per tree per year. In 2005 there was an average 5.6 mistletoes per tree (Table 5.6).

For mistletoes, there were highly significant differences in the host branch diameter ($F_{2,377} = 33.0$, $P < 0.0001$) and maximum canopy diameters ($F_{2,383} = 63.4$, $P < 0.0001$) between 'survivors', 'recruits' and 'deaths' (Table 5.7). Tukey HSD tests revealed that the HBD and maximum canopy diameter of recruits were smaller than survivors and deaths. Survival of mistletoes between 2003 and 2005 was greatest (93%) on branches with HBD between 101 mm and 150 mm, and lowest (83%) on branches with HBD between 0 mm and 50 mm (Fig 5.2)

In 2003, a large number of tagged mistletoes (41.1%) were in poor health (Table 5.8), and 74.3% of the mistletoes that died over the study period, were in poor health in 2003 (Table 5.8). However in 2005, the majority of mistletoes were in good health (52%), as were the mistletoe recruits in 2005 (69%). As expected, new mistletoe recruits were smaller in diameter than established mistletoes (t -test$_{392}$ = 11.0, $P < 0.0001$), and the branches on which they grew were significantly smaller in diameter than branches on which established mistletoes grew (t -test$_{392}$ = 8.1, $P < 0.0001$; Table 5.7).

There were strong positive correlations between the number of mistletoe recruits and the canopy volume of trees ($r^2 = 0.3$, $F_{1,74} = 32.4$, $P < 0.0001$), and the number of mistletoes originally on that tree ($r^2 = 0.3$, $F_{1,74} = 39.8$; $P < 0.0001$, Table 5.9). However, there was no significant correlation between the number of recruits and the overstorey density ($r^2 = 0.004$, $F_{1,74} = 0.26$, $P = 0.62$) or dieback of the tree ($r^2 = 0.05$, $F_{1,74} = 3.64$, $P = 0.06$). There was a slight but highly significant correlation between the number of mistletoes on trees in 2003 and the number of deaths on those same trees ($r^2 = 0.15$, $F_{1,74} = 12.83$, $P = 0.0006$).

Table 5.6 Summary of the number of box mistletoes *Amyema miquelii* tagged in November 2003 and November 2005 in Aldinga Scrub Conservation Park, and the number of mistletoe 'survivors', 'deaths' and 'recruits', and net mistletoe population growth

2003	No. trees	75
	Total No. live mistletoes	351
	No mistletoes per tree (mean ± s.e.)	4.68 ± 0.65
2005	No. trees	75
	Total No. live mistletoes	419
	No. mistletoe 'survivors'	308
	No. mistletoe 'deaths'	43
	No. mistletoe 'recruits'	111
	Net mistletoe population growth	68
	No. mistletoes per tree (mean ± s.e.)	5.59 ± 0.75
Summary	Recruitment rate	0.74 mistletoes tree^{-1} year^{-1}
	Mortality rate	0.29 mistletoes tree^{-1} year^{-1}
	Population growth rate	0.45 mistletoes tree^{-1} year^{-1}

Table 5.7 Comparison of host branch diameter (HBD) and maximum canopy diameter of mistletoes which survived the 2003 – 2005 study period ('survivors'), those mistletoes which died ('deaths') and mistletoes which were recruited during this period ('recruits') in Aldinga Scrub

	HBD (mm)	Maximum Canopy Diameter (cm)
Survivors	33.8 ± 0.9^{a}	143.5 ± 4.2^{a}
Deaths	31.2 ± 2.7^{a}	118.0 ± 12.8^{a}
Recruits	19.2 ± 1.6^{b}	48.5 ± 7.3^{b}
Significance test	****	****

ANOVA was used to compare means. Significance levels are $P < 0.0001$ (****), $P < 0.001$ (***), $P < 0.01$ (**) and $P < 0.05$ (*). Significant differences between survivors, deaths and recruits, as determined by Tukey HSD tests, are indicated by 'a' and 'b'.

Table 5.8 Summary of the health of box mistletoes *Amyema miquelii* tagged in November 2003 and November 2005 in Aldinga Scrub Conservation Park

		Poor	Moderate	Good
2003	All mistletoes (333)	41.1	22.5	36.6
2005	2003 mistletoes	28.7	25.1	46.2
	Recruits (111)	9.9	20.7	69.4
	All mistletoes	23.7	23.9	52.4
	2003 mistletoes that died (43)	74.3	14.3	11.4

Table 5.9 Results of linear regressions between tree variables and the number of mistletoe recruits on 75 individual trees in Aldinga Scrub

	r^2	F	*P*
Height	0.13	11.01	0.0014
Canopy Volume	0.31	32.48	<0.0001
Overstory Density	0.004	0.26	0.62
Mistletoe density within 5 m	0.12	9.77	0.0025
% Canopy Dieback	0.05	3.64	0.0604
No. of mistletoe	0.27	27.47	<0.0001

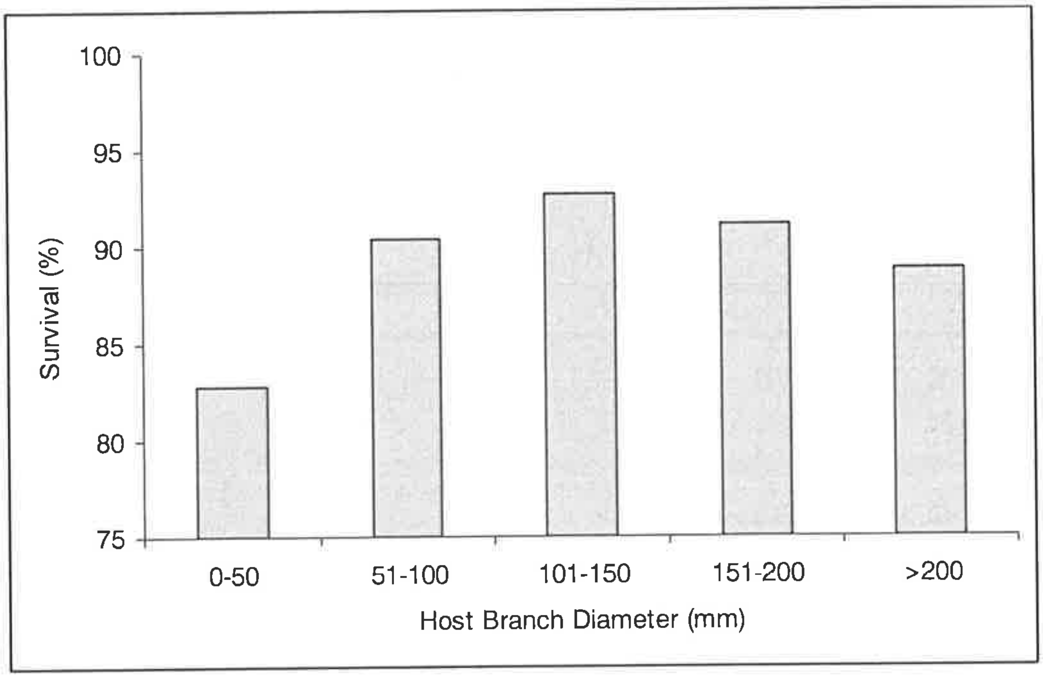

Fig 5.2. Percentage of mistletoes tagged in 2003 in Aldinga Scrub which survived through to 2005, relative to the diameter of the branch on which they were attached HBD).

For Poisson regression models of mistletoe recruitment, model fit was excellent with 44.2% of the variance in the global model explained by the included parameters. $QAIC_c$ modelling indicated that MTOE + HEIGHT + DIEBACK was the best model of the number of mistletoe recruits on trees, with a 77% probability of being the best model in the candidate set (as indicated by the Akaike weight, w_i; Table 5.10). The next best model of mistletoe recruitment was MTOE + DIEBACK ($w_i = 0.22$), and all other models were comparatively unlikely ($\Delta_i > 3$, Table 11). The parameter MTOE (the number of mistletoes present on each tree in 2003) was present in the best five models. Estimation of relative parameter importance demonstrated that the two individual parameters with the highest estimated importance were MTOE (0.93) and DIEBACK (0.92), followed by HEIGHT (0.83, Table 5.11). Given that MTOE was present in the top five models and also had far stronger linear regression model fit than dieback, it could be considered the most important variable influencing the number of mistletoe recruits on trees.

Table 5.10 Ranking of logistic regression models of seeds which did and did not germinate using AICc model ranking procedures (Burnham and Anderson 2002) for 1525 seeds deployed across three eucalypt species in Aldinga Scrub Conservation Park, South Australia

	Candidate model	Log(Λ)	K	Δ_i	w_i
1	**MTOE + HEIGHT + DIEBACK**	**-108.81**	**4**	**0.00**	**0.77**
2	**MTOE + DIEBACK**	**-112.36**	**3**	**2.54**	**0.22**
3	MTOE + HEIGHT	-117.59	3	9.58	0.01
4	MTOE + HEIGHT + OSDENS	-117.02	4	11.05	0.003
5	MTOE + MTOE5M	-122.43	3	16.10	0.0002
6	HEIGHT + MTOE5M	-125.70	3	20.50	<0.0001
7	HEIGHT + MTOE5M	-125.70	3	20.50	<0.0001
8	MTOE	-127.99	2	21.41	<0.0001
9	MTOE + OSDENS	-127.79	3	23.31	<0.0001
10	HEIGHT	-134.94	2	30.77	<0.0001
11	HEIGHT + DIEBACK	-133.45	3	30.93	<0.0001
12	HEIGHT + OSDENS	-134.87	3	32.84	<0.0001
13	MTOE5M	-137.84	2	34.67	<0.0001
14	DIEBACK	-142.37	2	40.77	<0.0001
15	OSDENS	-146.72	2	46.62	<0.0001

MTOE, number of box mistletoe *Amyema miquelii* on tree; HEIGHT, height of tree (m); 5m.DENS, the density of mistletoes within 5m of the tree's canopy (no. mistletoe / m^2); DIEBACK, percentage canopy dieback; OS.DENS, density of canopy surrounding tree. Log(Λ) is the log likelihood of the model; *K*, the number of estimated parameters; Δ_i, the difference between that model's second-order bias corrected form of Akaike's Information Criteria (QAIC*c*) and the minimum QAIC*c* value; and, w_i, Akaike weights. Candidate models with significant levels of empirical support (Δ_i, < 2) are shown in bold. Percentage of deviance explained by included variables = 44.2%.

Table 5.11 Relative importance of each variable (*j*), estimated by summing the Akaike weights w_i across all the models in the candidate set (Table 11) where variable *j* occurs to give the sum $w_+(j)$. The larger the $w_+(j)$, the more important variable *j* is, relative to the other variables (Burnham and Anderson 2002)

Variable	$w_+(j)$
MTOE	0.93
DIEBACK	0.92
HEIGHT	0.83
MTOE5M	0.70
OSDENS	0.03

5.5 DISCUSSION

Germination trial

The present study demonstrated that seedling establishment is higher on pink gum than on mallee box and red gum, and that establishment rates were consistent with previous studies of box mistletoe inoculation on eucalypts and for other Loranthaceae (Yan 1993a; Yan and Reid 1995; Norton and Ladley 1998). The findings also support the patterns of box mistletoe host specificity demonstrated in natural host populations in the Mount Lofty Ranges. Here, box mistletoe infection is most frequent on pink gum (almost 30% of all trees infected) compared to box eucalypts and red gum (Ward 2005), and the differences in seedling establishment demonstrated in the present study would therefore contribute to such trends. The present study has also shed some light on the possible causes of variation in establishment.

Germination of mistletoe fruits is triggered by excision from the parent plant, and in order to reach the host branch to form a holdfast, the excised seed immediately elongates the hypocotyl (Lamont 1983a). In the present study, almost all seeds (91%) germinated within the first few days regardless of host species, with the tip of the radicle of around 75% of all seeds making contact with the host branch within this time. This pattern is common for mistletoes, with previous studies demonstrating high germination rates (> 80%) independent of host species (Clay *et al.* 1985; Yan 1993a; Yan and Reid 1995; Ladley and Kelly 1996; Norton and Ladley 1998). Although fewer seeds made contact with the host branch on pink gums than red gums, this resulted from higher initial predation, and, like germination success, would have little bearing on final establishment success or the patterns of infection in natural host populations.

Once firm contact between the hypocotyl and host is established, the tip of the hypocotyl flattens and forms a 'bell' shaped holdfast (Yan 1993a). Despite more hypocotyls making contact with host branches in red gums, significantly fewer holdfasts were formed on red gums (18%) than on pink gum (27%) and mallee box (31%). These differences probably resulted from higher seed mortality on red gums through physical host defences, with almost 12% of seeds on red gum dying from being lifted off the host branch by the shedding of host bark.

After holdfast formation, the haustorium develops in the centre of the holdfast and grows towards the host. Its outermost cells digest, penetrate and replace host cells through a combination of enzymic action and the mechanical force of its growth, resulting in the close fit seen in mature haustoria (Kuijt 1969; 1977). Leaf emergence in seedlings reflects the success of the haustorium to penetrate the host bark and establish a functional connection with the host xylem (Yan 1993b; Norton and Ladley 1998). Unlike previous *Amyema* inoculation studies, no differences between host species were documented in leaf emergence in the present study (48% across all hosts, Yan 1993a; Yan and Reid 1995). Twelve months after inoculation, however, newly recruited mistletoes on red gums had significantly fewer leaves and were smaller in size than mistletoes on pink gum and mallee box, indicating haustorial connection in box mistletoe establishment on red gums is in some way hindered.

Closer inspection of mortality figures also reveals that despite having the lowest predation rates, red gums had the highest mortality through *in situ* deaths. It is difficult to determine the exact cause of *in situ* deaths, however histological evidence from previous studies has shown that, in such cases, the mistletoe haustorium penetrates through the host bark and reaches the xylem but fails to form a functional connection with the host tissues (Yan 1990; 1993b). This failure may result from host chemical defences (Frei and Dodson 1972 as cited in Clay *et al.* 1985), genetic incompatibility (Clay *et al.* 1985), the growth of abnormal host tissue around the haustorium (Yan 1990) or incompatible water potentials (Calder 1983).

Bark shedding was also a very effective mechanism in removing unwanted epiphytes such as mistletoe seeds, and its effectiveness in repelling mistletoe infection deserves further attention. For example, a delay in the onset of bark shedding by eucalypts in South Australia would allow mistletoe seeds dispersed in spring ample time to establish, and therefore also contribute to apparent increases in mistletoe abundance across temperate Australia.

Thirteen percent of seeds were affected by the feeding damage of Lepidoptera borers in the mistletoe endosperm, and although more seeds were affected on mallee box, this was probably independent of host species. Many mistletoes are known to suffer from leaf damage through feeding by Lepidoptera (De Baar 1985). Feeding damage at the seed stage, however, has been reported far less often (Carpenter *et al.* 1979). The present study has demonstrated that it can be a very effective biological control, and has raised questions about the effectiveness of such controls in the contemporary landscape. For example, have insect communities which provide effective biological control of mistletoes, suffered in the contemporary landscape where there are fragmentation-induced edge effects?

Branch size is also well known to have an influence on the establishment success of mistletoes (Reid 1987; Sargent 1995; Norton and Ladley 1998), and, given the potential variation in the branch size on which avian mistletoe dispersers may perch, provides an important link between dispersal by birds and mistletoe establishment (Reid 1989). In the present study, nearly 80% of all established mistletoe occurred on branches less than 20 mm in diameter, and logistic regression modeling indicated that diameter strongly affected mistletoe establishment rates. Similarly, Yan and Reid (1995) found that maximum establishment of box mistletoe occurred on eucalypt branch sizes of 7 – 20 mm.

High establishment rates on small branches are common in mistletoes, because in order to reach the host xylem, the haustorium is more readily able to penetrate the thinner layer of host bark present on thinner branches (Yan 1993a; Sargent 1995; Yan and Reid 1995; Norton and Ladley 1998). This effect was found across the three species tested in the present study, with all species having relatively smooth bark at these diameters. Also, these optimal branch sizes correspond with the most commonly used perch sizes of Mistletoebirds, and hence the most common perch size on which mistletoe seeds would be defaecated (Reid 1989; Yan and Reid 1995).

Demography of A. miquelii

Over the two year study period, the density of mistletoes on selected trees in Aldinga Scrub increased, with the number of new mistletoe recruits (111) more than double that of the number of mistletoes which died (43). Thus, in Aldinga Scrub, box mistletoe currently has a positive population growth rate of 0.45 mistletoes per tree per year.

The number of new recruits on pink gums was primarily influenced by the number of mistletoes originally on the tree, and the height of the tree. This reflects the behaviour of mistletoe dispersers, including Mistletoebirds, which restrict their movements to areas of higher mistletoe abundance and prefer to forage on taller trees with higher mistletoe abundance (Chapter 4; Larson 1996; Martinez del Rio et al. 1996; Aukema and Martinez del Rio 2002; Ward and Paton in press).

Canopy dieback was also important in determining mistletoe recruitment, with those trees with less dieback more likely to recruit mistletoe over the study period. However, Ward (2005) and Ward and Paton (Ward and Paton in press) postulated that increased dieback in a pink gum woodland would allow for more efficient movement by Mistletoebirds and higher quality mistletoe dispersal. While this may still be true, it is possible that at a certain level of dieback the probability of mistletoe recruitment may decrease because there are many dead branches on which Mistletoebirds defaecate seeds, or the tree is not healthy enough for successful recruitment on appropriate branches. Indeed, most trees which had dieback of 10 – 50% recruited more than two mistletoes, while only two with dieback above 50% recruited more than two mistletoes. Monitoring of these trees over a longer time frame would be required to confirm this pattern.

The established mistletoe plants which died during the study period were primarily of poor health in 2003, and tended to be smaller in diameter and occur on smaller branches than surviving mistletoes. Also, there was a slight correlation between the number of mistletoes which died and the number of mistletoes originally on their host. These findings are consistent with Reid and Lange (1988), who suggested that mistletoes which die are primarily young plants which face greater intraspecific competition on heavily laden trees, thus suffering density dependent mortality.

The health of mistletoes in Aldinga Scrub was dynamic over the study period. Most mistletoes in 2003 were in poor health, however this shifted over the two years and in 2005 the bulk of mistletoes were in good health. In fact, many mature mistletoes with only a few leaf shoots in 2003 were in very good health in 2005, indicating that that the condition of mistletoes can change quite readily.

Conclusions

The present study has demonstrated that differences in the establishment success of box mistletoe between pink gum, box eucalypts and red gum could explain patterns of host specificity seen in natural mistletoe and host populations. Establishment success was highest on pink gum, and box mistletoes that established on red gums were smaller, had fewer leaves and often died *in situ*. This resulted primarily from the better host defenses of red gums (in particular the shedding of outer layers of bark), and the failure of mistletoes to establish a truly functional haustorium, probably through underlying physical and chemical defenses. Branch sizes were also important to establishment, with greatest establishment on branches less than 20 mm in diameter, which coincides with branches of the size that Mistletoebirds frequently perch on. Monitoring of host trees revealed that recruitment of mistletoes over 2 years was more likely on trees with higher mistletoes densities, reflecting the preference of mistletoe dispersers for perching on such trees. Small amounts of tree canopy dieback may allow increased recruitment of mistletoe, however trees with considerable dieback (>50%) were less likely to recruit mistletoes. Continued monitoring of both the establishment experiment and natural mistletoe recruits will reveal more detail to mistletoe demographic patterns in pink gum woodlands.

An umbel of box mistletoe fruit. Only one fruit is ripe (the red fruit) – in general mistletoes stagger their fruiting in order to attract only specialised dispersers. Note also the small linear indentations at the top of the ripe fruit – these may be from the beak of a Mistletoebird testing to determine whether the fruit is ready to consume.

CHAPTER 6

GENERAL DISCUSSION

CHAPTER 6

GENERAL DISCUSSION

The preceding chapters aimed to provide quantitative descriptions on various aspects of box mistletoe *Amyema miquelii* demography and dispersal ecology, for temperate pink gum *Eucalyptus fasciculosa* woodlands of southern Australia. This was done by documenting the status of mistletoe infection in the Mount Lofty Ranges (MLR, Chapter 2), and then measuring and recording the salient stages of mistletoe dispersal, including: the local movement patterns of Mistletoebirds *Dicaeum hirundinaceum* (Chapter 3); host tree selection and foraging behaviour of Mistletoebirds (Chapter 4); and, mistletoe host compatibility and recruitment patterns (Chapter 5).

In the following discussion, the key findings presented in this thesis are summarised by considering the sequence of events, from fruiting to establishment, which lead to the successful dispersal of mistletoes within a pink gum woodland. This is appropriate, given few of the results presented in this thesis can be considered in isolation. In other words, the results discussed in each chapter in some way influence or respond to those from other parts of the dispersal system. For expanded discussion of individual results, the reader is directed to the relevant chapters. I have also taken the liberty of using this discussion to briefly consider some evolutionary trade-offs of the aggregated distribution of mistletoes. This is important, given that many of the traits of mistletoes and behaviours of Mistletoebirds described in this thesis promote mistletoe aggregation. Finally, a summary of the research required to complement this dissertation is presented.

6.1 CHRONOLOGICAL DESCRIPTION OF MISTLETOE DISPERSAL

Initially, let us consider a pink gum woodland. The frequency and severity of box mistletoe infection in this woodland will be far greater than in other woodlands which may be neighbouring, including blue gum *E. leucoxylon* and red gum *E. camaldulensis* woodlands (Chapter 2; Ward 2005). The evolutionary objective of any individual mistletoe on a pink gum within that woodland tree, is initially to be visited by a disperser, to then have its fruits consumed by a disperser, and finally, to have its fruits dispersed to an appropriate location for establishment.

Mistletoes, therefore, must have a strategy by which their fruiting display attracts the most efficient dispersers. To do this, box mistletoe in pink gum woodlands stagger the ripening of their fruit over a period of at least 4 months, with a peak in October (Chapter 4). This helps mistletoes attract specialist dispersers, such as Mistletoebirds, which are more likely to disperse seeds to appropriate locations. This 'high investment' fruiting strategy, by which fewer fruits are produced over a longer period of time, is also seen in other Loranthaceous mistletoes (McKey 1975; Howe and Estabrook 1977; Godschalk 1983b; 1985; Martinez del Rio *et al.* 1996).

Mistletoebirds foraging within a pink gum woodland are faced with the decision of which tree to visit, and they are presented with trees which vary in both architecture and level of mistletoe infection. Their decision is influenced by several non-exclusive factors, including the abundance of mistletoe on the tree, the height and size of the tree, and the structure and composition of the host's canopy and surrounding canopies. A Mistletoebird is more likely to visit a pink gum which is taller, has a greater canopy volume and hosts more mistletoes than surrounding trees (Chapter 4), a trait seen in most mistletoe systems (Martinez del Rio *et al.* 1995; Martinez del Rio *et al.* 1996; Aukema and Martinez del Rio 2002). Consistent with this, the number of mistletoes recruited on a pink gum correlates with the canopy volume of the tree and the number of mistletoes originally on the host pink gum (Chapter 5).

When alighting in a tree, a Mistletoebird will most often alight on a dead branch (Chapter 4). It is probable, therefore, that between two host trees with equal mistletoe loads, a Mistletoebird is likely to alight on the tree with greater availability of accessible perch sites, although this needs to be experimentally tested. Because of its swift and direct flight habit, a Mistletoebird will also more frequently visit trees whose canopies have clear access. Chapter 2 demonstrates that individual pink gums were more likely to host mistletoe when they had lower levels of canopy cover surrounding their own canopy (Ward 2005). In support, Chapter 4 demonstrates that trees visited by Mistletoebirds have lower levels of surrounding canopy cover than trees which are not visited.

After alighting in a tree, a Mistletoebird will most likely move directly to a live mistletoe – it must choose which mistletoe to visit, and, whilst there, how many mistletoe fruit to consume. The Mistletoebird will forage more often on larger and healthier mistletoes, and will typically spend longer in larger mistletoes than in smaller mistletoes (Chapter 4). Although a Mistletoebird might be presented with an abundance of fruit within a single mistletoe or within a single host tree, it will not remain in the tree for an extended period of time nor eat large numbers of fruit from a single mistletoe (Chapter 4). This is possibly because the territorial Mistletoebird must continue to move to defend its territory, or because it is chased out of a tree by another Mistletoebird.

Consuming mistletoe fruit has payload issues for a Mistletoebird, and will hinder its ability to fly (Liddy 1982) – to the next foraging site, to defend its territory, or to escape predators. A Mistletoebird, therefore, will often choose to defaecate prior to leaving a feeding tree. Because the average gut passage times of a Mistletoebird is considerably longer than tree visit times, the majority (90%) of seeds defaecated on a tree will originate from surrounding trees (Chapter 3; Ward and Paton in press). Many seeds are defaecated on the same host tree, however, through revisitation of that tree.

A Mistletoebird must also decide *where* to defaecate, which has a large consequence on the quality of mistletoe dispersal and on the distribution of mistletoes at a variety of scales. Because a Mistletoebird chooses to forage in trees with higher levels of mistletoe infection (Chapters 3 and 4), it will defaecate the majority of the seeds it consumes on pink gums already infected with mistletoe. This has been proven experimentally in other mistletoe systems (e.g. Aukema and Martinez del Rio 2002). As a result, mistletoes are aggregated on a smaller number of hosts, and the increased mistletoe loads on these trees then attract more visits from Mistletoebirds, providing a positive feedback loop (Aukema 2004; Medel *et al.* 2004).

At a landscape scale, a Mistletoebird will also choose to forage in areas with higher mistletoe loads. It may establish a territory within a heavily infected woodland of around 20 ha, but concentrate the majority of its activity within a much smaller core activity area (Chapter 3). As a result, the seed shadow of a mistletoe that a Mistletoebird creates is strongly leptokurtic, with 70% of seeds being deposited within 100 m of the parent plant, and the majority of seed rain across the pink gum woodland highly aggregated in areas with higher mistletoe infection (Ward and Paton in press).

The microhabitat in which a Mistletoebird chooses to forage is also of critical importance to successful dispersal. A Mistletoebird spends a large proportion of its time foraging within live mistletoes and perched on dead pink gum branches. Accordingly, it defaecates mistletoe seeds most frequently on either live mistletoe or dead pink gum branches (Chapter 4). Within a contemporary pink gum woodland with high mistletoe abundances and considerable canopy dieback, a Mistletoebird will, therefore, rarely effectively disperse a mistletoe seed onto a live pink gum branch. When a Mistletoebird does defaecate on a live pink gum branch, however, it is most likely they it is effectively dispersing the mistletoe seed. This is because its small foot size (Higgins *et al.* 2006) ensures it perches primarily on branches of small diameter (e.g. 5 - 10 mm, Reid 1989), which corresponds with the optimal branch size for seedling establishment on pink gums (< 17 mm, Chapter 5) and on other eucalypt species (< 20 mm, Yan and Reid 1995).

Having overcome many obstacles to be dispersed to a suitable location, the dispersed mistletoe seed must then overcome several more to become established as an immature mistletoe. Initially, the seed must germinate and extended its hypocotyl in order to make contact with the host branch and form a holdfast. A number of host defences are in place to then try and stop the mistletoe from developing a functional haustorium, including the shedding of bark, chemical defences or the growth of abnormal host tissue around the haustorium (Chapter 5). In addition, genetic incompatibility and inappropriate water potentials can also retard the development of a haustorium. Of those seeds dispersed to optimal branch sizes on host species, approximately 75% will become established as immature mistletoes after 12 months (Chapter 5).

6.2 MISTLETOES – WHY AGGREGATION?

The aggregation of parasites on a relatively small number of hosts is a general characteristic of host-parasite relationships (Medel *et al.* 2004 and references therein). Accordingly, many studies of the distribution and dispersal of mistletoes invariably draw on a similar theme – that mistletoes are aggregated in space on individual hosts (Godschalk 1983b; Donohue 1995; Martinez del Rio *et al.* 1995; Aukema and Martinez del Rio 2002) and at larger scales (Norton and Stafford Smith 1999; Aukema 2004; Ward and Paton in press).

The aggregation of mistletoes is dependent on heterogeneity in host compatibility, and the repeated use by dispersers of areas and trees already infected with mistletoe. For example, more compatible hosts have a greater probability of hosting mistletoe (Chapter 5; Yan and Reid 1995), leading to the aggregation of mistletoes on that particular host. Also, trees which host more mistletoes receive more visits from dispersers. These trees, therefore, also receive greater mistletoe seed rain and eventually host more mistletoes, leading to an aggregated distribution of mistletoes on individual hosts (Chapter 4; Aukema and Martinez del Rio 2002; Medel et al. 2004) and on a landscape scale (Chapters 3; Ward and Paton in press).

Most ecological studies on the evolutionary advantages of aggregation have focused on animal populations, such as the early detection of predators by large groups (Lazarus 1979), the energetic benefits of moving in large groups (Weihs 1973), and the benefits of mate selection seen in parasites on the gills of fish (Simkova *et al.* 2001). In plants, local or intraspecific aggregation is generated by limited seed dispersal, clonal growth and patchy environments (Stoll and Prati 2001). Evolutionarily, intraspecific aggregation promotes species coexistence and diversity by retarding competitive exclusion (Stoll and Prati 2001). The advantages to individual plants within an aggregation, however, have received little attention.

This is also the case for mistletoes, despite aggregation being a fundamental characteristic of their distribution and infection patterns in many different systems (e.g. Godschalk 1983b; Donohue 1995; Norton and Stafford Smith 1999; Aukema

2004). By understanding the advantages that aggregation confers on mistletoes, we might better understand the processes which lead to severe mistletoe infections. Below, I briefly consider the possible advantages of mistletoe aggregation for mistletoes and their dispersers.

Successful mistletoe dispersal is dependent on seeds being dispersed to safe locations on compatible hosts. Therefore, if aggregation poses evolutionary advantages for mistletoes, it should increase the chances of seeds being dispersed to compatible hosts. In Chapter 3, it was predicted that the vast majority of mistletoe seeds will be dispersed within 100 m of the parent tree (Ward and Paton in press). Given that conspecific hosts will be more common in the immediate surrounding area to a host tree, this will increase the probability that mistletoe seeds will be dispersed from one compatible host to another, particularly if genetic compatibility between mistletoes and host is important (Clay 1985) and the distribution of hosts is also patchy.

Aggregation of mistletoes may also play a role in attracting the services of dispersers and pollinators. Dispersers are more likely to visit trees with a larger number of mistletoes rather than trees with individual mistletoes (Chapter 4; Aukema and Martinez del Rio 2002). Therefore, this may increase the probability of an individual mistletoe on a tree with numerous mistletoes receiving a visit from a disperser than a single mistletoe on a tree – i.e. strength in numbers. This advantage would asymptote, however, as competition between mistletoes for the services of dispersers and pollinators increases through increased visitation.

Given the intricate relationship and coevolution between mistletoes and their dispersers (Reid 1991), the aggregation of mistletoes will also have evolutionary tradeoffs for dispersers such as Mistletoebirds. The primary consequence of mistletoe aggregation for dispersers is the concentration of food resources within a limited area. If mistletoes were randomly or uniformly distributed, dispersers may make many more trips between individual mistletoes to find food, however they may encounter individual mistletoes at a more consistent rate. When mistletoes are aggregated, however, mistletoe dispersers can learn the location of food resources and will spend longer in a single area with more available fruit, although the distance between mistletoe patches may be larger. With this in mind, aggregation would be an advantage to a dispersers if: 1) the energy gained from consuming fruit in the small area was greater than the energy expended moving to the next mistletoe patch; and 2) this was more energetically efficient than if mistletoes were randomly or uniformly distributed.

Of course, aggregation will also pose certain disadvantages, and perhaps the greatest threat to mistletoes from aggregation is an increase in the possibility of death to the host tree (and hence to mistletoes themselves). Mistletoes with 'ball and socket' haustorial structures, such as *A. miquelii*, suppress the activity of dormant buds and vegetative growth along the host branch distal and proximal to the haustorium (Reid and Yan 2000). Therefore, the aggregation of many mistletoes on a single tree progressively leads to the point where little or no host foliage remains. Although contrary to the adage that 'parasites never kill their hosts', the poor health of the host tree will directly affect the survivorship of mistletoes.

For dispersers, the aggregation of mistletoes will lead to increased competition for access to these food resources present only in a limited area, particularly when the number of ripe fruit is limited. This is especially critical for specialist mistletoe dispersers reliant on mistletoe fruit such as Mistletoebirds, and may contribute to the territorial nature of Mistletoebirds. Also, the aggregation of mistletoes increases the possibility that large quantities of food resources can be removed in single perturbations such as fires. Mistletoebirds, however, are able to traverse large distances and will therefore be able to search for new patches of mistletoe in which they can forage.

To summarise, mistletoe aggregation is one of the most conspicuous sights in temperature eucalypt woodlands. Given aggregation is also commonplace in mistletoes across the world, it must engender advantages for individual mistletoes and/or dispersers, rather than being an inadvertent result of the dispersal syndrome of mistletoes. It is also possible that by aggregating, mistletoes may evolutionarily act as a genetic group rather than just individuals. Although the above discussion is largely speculative, it provides a stream of thinking not previously addressed in the mistletoe literature. Of course, the hypotheses discussed above require experimental testing to determine whether aggregation is advantageous for mistletoes and their dispersers.

7.3 FUTURE RESEARCH

As with most ecological research, the current dissertation has raised far more questions than it has answered. Below is a list of potential areas for further research, required for advancement of both our theoretical and applied understanding of mistletoe ecology. The list also highlights areas of limitations of the preceding thesis.

- The research presented in this thesis was made possible because of the high mistletoe abundances in Aldinga Scrub, which allowed sufficient Mistletoebirds to be trapped for the radio-tracking study (Chapter 3), and to observe for the foraging behaviour study (Chapter 4). Much of the data, therefore, is constrained because to an extent, it only reflects the behaviour of a mistletoe disperser in an area with high mistletoe abundances. This is probably also the case for most studies of mistletoe dispersal (e.g. Liddy 1983; Aukema and Martinez del Rio 2002).

- Research of mistletoe disperser movements and behaviour in areas with lower mistletoe abundance, however, would help explain whether seed shadows are restricted because: dispersers quickly dispose of ballast seeds in order to aid manoeuvrability; dispersers purposefully limit their movements around a plant to increase the chance of a mistletoe fruit landing on a suitable host; or because high mistletoe abundance means birds do not have to travel as far to find suitable food resources.

- Also, an investigation similar to Chapter 4 in an area with lower mistletoe abundance could indicate whether the movements of Mistletoebirds between host trees and mistletoes, are driven by fruit abundance or territorial behaviour. In areas with limited mistletoe fruit, one might expect the behaviour of Mistletoebirds to more closely reflect optimal foraging principles than was documented in Chapter 4.

- Chapter 5 demonstrated that mistletoe seedling establishment was considerably higher on pink gums and mallee box *E. porosa* than on red gum *E. camaldulensis*. However, the patterns of mortality only give a small insight into why these differences might exist. Further research could aim to determine why pink gums are more compatible hosts, by examining the influence of host chemical defences (Frei and Dodson 1972), genetic incompatibility (Clay *et al.* 1985), the growth of abnormal host tissue around the haustorium (Yan 1990) or incompatible water potentials (Calder 1983).

- Chapter 3 predicted the seed shadow of *A. miquelii* and patterns of seed rain by combining recorded movements of Mistletoebirds with published gut passage time data for *A. quandang* (obtained from aviary trials, Murphy *et al.* 1993). A more accurate prediction of the seed shadow of *A. miquelii* would be obtained by using *A. miquelii* fruit in GPT trials, and, if possible, these trials should be conducted in as natural field conditions as possible.

- A recurrent theme in this dissertation is the potential effects of canopy dieback on the quality of mistletoe dispersal. Although Chapter 4 demonstrated the frequent use of dead pink gum branches for alighting, field experiments are required to determine whether Mistletoebirds do actually preferentially choose to visit trees which have many dead branches available as perches.

- A lack of herbivory by brush tailed possums has been cited as a probable cause of mistletoe increase for some time (Norton and Reid 1997; Reid 1997b), yet its influence on mistletoe control has yet to be proven or monitored. This is due to the fact that it would require an intrusive and logistically difficult experiment, involving the removal and/or introduction of possums to an area and long-term monitoring. Hence, this intriguing question may continue to be unanswered.

- The fundamental cause of the dieback of pink gums in the Mount Lofty Ranges, as documented in Chapter 2, urgently needs to be identified. Research should include investigating the use of ground water by pink gums, as well as the effects of mistletoe removal on the physiology of pink gums. This information could be used to assist in the management of pink gums in other parts of South Australia.

- Due to the time limitations placed on contemporary PhDs, there is limited scope for long-term monitoring of the dynamics of animal and plant populations. During the course of my PhD research, however, I have ensured much of my data collection will form the base of long-term monitoring (e.g. by using metal tags on eucalypt trees). It is only from such long term monitoring that we will be able to document whether mistletoes are currently in a state of increasing abundance, to understand the patterns of mistletoe recruitment, mortality and survivorship, and to monitor the populations of Mistletoebirds. The following components of this thesis should continue to be monitored into the foreseeable future:
    a) The abundance of mistletoes on individual pink gums across the Mount Lofty Ranges surveyed for Chapter 2 and Ward (2005).
    b) The recruitment, survivorship and mortality of mistletoes on pink gums in Aldinga Scrub initially monitored for Chapter 5.
    c) The patterns of site fidelity of Mistletoebirds in Aldinga Scrub, as trapping was conducted every month from September 2003 to November 2005. As of February 2006 I had trapped 141 new Mistletoebirds and had 105 recaptures.

6.4 FINAL REMARK

This thesis has highlighted the many obstacles that box mistletoe faces in having its seeds successfully dispersed and established on appropriate hosts. Despite this, box mistletoe is undoubtedly one of the few native organisms which has thrived within the contemporary temperate eucalypt landscape. This is particularly so in pink gum woodlands of the Mount Lofty Ranges.

The success of box mistletoe in eucalypt woodlands in Australia is habitually attributed to declines in canopy fires, decreased herbivory, and always ‘fragmentation’. However, at the culmination of writing this thesis and after hundreds of hours observing and mulling in the field, I feel it necessary to emphasise here an important point – that the *suitability* of mistletoe dispersal to the fragmented landscape is the fundamental cog in the wheel which drives mistletoe infections to proliferations. In other words, fragmentation will not drive an increase in mistletoe abundance, without a dispersal syndrome which suits such a landscape.

Mistletoe dispersal suits the open, fragmented and degenerating landscape in numerous ways; Mistletoebirds enjoy greater manoeuvrability between trees isolated by clearing; remnant woodlands which are selectively cleared or suffer from tree dieback provide easier access for Mistletoebirds between trees and to the canopies of trees; along fragment edges and in woodlands suffering dieback, many more perch sites are presented to Mistletoebirds in tree canopies; and, finally, in a landscape where so few trees and patches of remnant vegetation remain, there is little doubt where Mistletoebirds must concentrate their activity.

Where it all begins. Box mistletoe flowers from December through to April and the flowers are visited and pollinated primarily by Australian honeyeaters (Meliphagidae). A few fruit begin to ripen in late June and early July, with a peak in ripe fruit numbers occurring mid October (Chapter 4).

APPENDIX

Summary

Appendix A provides documentation from publishers that gives permission to reproduce chapters in this thesis that were published manuscripts (or accepted for publication) at the time of submission. This information applies for chapters 2 and 3. Chapters under peer-review with journals at the time of thesis submission do not require such information.

Chapter 2

Subject: Ward 2005 manuscript
Date: Fri, 24 Feb 2006 10:25:05 +1030
From: Matthew Ward <matthew.ward@adelaide.edu.au>
To: DickFisher@templeinland.com

Dear Dick

I am enquiring as to whether it is possible to obtain a statement from you in your capacity as editor in chief of Forest Ecology and Management, and on behalf of Elsevier, giving permission to include the following manuscript as a chapter in my doctoral dissertation.

Ward, M. J. (2005). Patterns of box mistletoe Amyema miquelii infection and pink gum Eucalyptus fasciculosa condition in the Mount Lofty Ranges, South Australia. Forest Ecology and Management 213, 1-14.

Thanks
Matt

Subject: Permission
Date: Fri, 24 Feb 2006 08:37:37 -0600
From: "Fisher, Dick" <DickFisher@templeinland.com>
To: "matthew.ward@adelaide.edu.au" <matthew.ward@adelaide.edu.au>

To Whom It May Concern:

I hereby grant permission for M. J. Ward to include the material previously published as "Ward, M. J. (2005). Patterns of box mistletoe Amyema miquelii infection and pink gum Eucalyptus fasciculosa condition in the Mount Lofty Ranges, South Australia. Forest Ecology and Management 213, 1-14" in his dissertation.

R.F. (Dick) Fisher
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Chapter 3

Subject: Permission
Date: Thu, 20 Apr 2006 18:35:15 +0930
From: Matthew Ward <matthew.ward@adelaide.edu.au>
To: Michael Bull <Michael.Bull@flinders.edu.au>

Dear Mike

I am enquiring as to whether it is possible to obtain a statement from you in your capacity as editor of Austral Ecology, and on behalf of Blackwell Publishing, giving permission to include the following manuscript, which has been accepted for publication, as a chapter in my doctoral dissertation.

Ward, M. J. and Paton, D.C. (accepted). Predicting mistletoe seed shadow and seed rain from movements of the Mistletoebird, *Dicaeum hirundinaceum*. Austral Ecology.

Many thanks
Matt

Subject: Re: Permission to include Austral Ecology paper in thesis
Date: Sun, 23 Apr 2006 15:12:30 +0930
From: Michael Bull <Michael.Bull@flinders.edu.au>
To: Matthew Ward <matthew.ward@adelaide.edu.au>
CC: peter.fairweather@flinders.edu.au
References: 1

Dear Matt

Copyright for Austral Ecology is owned by the Ecological Society of Australia. As managing editor of the journal I can assure you the ESA will have no objections to you using your accepted paper in the way you suggest. Since your thesis is a non-profit maker publication there is no problem with including a copy of your accepted manuscript as a chapter. Please let me know if you need more formal confirmation

Mike

The Washpool, on the southern boundary of Aldinga Scrub, after heavy rains in July 2004. Prior to the establishment of drainage lines in the region for agriculture, the northern and eastern boundaries of the scrub would have also been inundated with water during winter months.

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