

Spatial memory, search images and environmental cues: how do frugivores find ripe mistletoes fruits?

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Melinda Elizabeth Cook

BSc (Environmental Biology), University of Technology Sydney

Faculty of Science, School of Life Sciences

University of Technology Sydney

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Supervisors

Assoc. Prof. Andrea Leigh (UTS)

Prof. Dave Watson (CSU)

Dr. Brad Murray (UTS)

Certificate of original authorship

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

Signature of Student:

Date: 13th July 2017

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Abstract

Mistletoes in Australia are keystone resources that are patchily aggregated in space and with peak fruit production that varies in time. Understanding how seed dispersing birds find fruiting mistletoe and what visual or habitat-based characteristics may influence their searching decisions can shed light on potential bird-driven distributions of mistletoe. While mistletoe selection by foraging frugivores has been investigated in other mistletoe systems, none have explored their search strategies, specifically, the potential use of a search image and spatial memory. To determine the potential search strategies of frugivorous birds and the influences of those strategies when searching for mistletoe fruit, I designed a series of novel, manipulative experiments. These involved two approaches: 1) defoliation and 2) moving whole mistletoe plants to new locations. In Chapter 2 I compare bird visitation to defoliated and intact fruiting mistletoes to determine the visual effects of leaves on potential seed dispersing birds. Chapter 3 investigates the effects of mistletoe location in host *versus* non-host trees and the effects of visual characteristics of the host tree and manipulated mistletoe in a continuous forest. This was achieved by cutting mistletoe and either 1) replacing it (*In-situ*), 2) moving it to another tree of the same species or (*Same Species*) or 3) moving it to a tree species that does not host mistletoe (*Different species*). In Chapter 4, I repeat a modified version of the experiment conducted in Chapter 3, using only *In-situ* and *Same Species* treatments in a roadside habitat. The results of this experiment were then compared to the corresponding results from Chapter 3 to determine potential effects of habitat type on bird visitation of fruiting mistletoes. For each experiment I also explored potential differences in visitation patterns among birds grouped into three dietary guilds: mistletoe specialists, feeding primarily on mistletoe fruits and nectar; generalist frugivores, potential seed dispersers known to eat a variety of fruits and invertebrates; and opportunistic foragers that visit mistletoes but may be searching for invertebrates rather than fruits. Overall, birds showed a preference for intact, *In-situ* mistletoes in continuous forest habitat, preferences that were largely driven by the generalist frugivore guild. My research provides the first evidence of spatial memory in mistletoe-dispersing birds, linking foraging behaviour to aggregated seed dispersal patterns. As mistletoes are patchy fruiting resources with limited, specialised seed dispersers, the findings of this thesis may be transferrable and testable in other specialised fruit-frugivore systems.

Chapter 1: Introduction



Plague Soldier Beetle (*Chauliognathus lugubris*) feeding on the nectar of Grey Mistletoe (*Amyema quandang*).

1.1 Overview

Maslow's hierarchy of needs states that the physiological aspects of life must be satisfied before any other need can be met (Maslow 1987). The most basic physiological need is obtaining enough energy to allow growth and development, while also offsetting the energy spent to obtain that energy. Organisms have developed many strategies to assist them when obtaining energy from the sun, nutrients from the soil, or from consuming other organisms. For sessile organisms, such as plants, mycorrhizal associations increase potential to process nitrogen (van der Heijden *et al.* 1998), underground tubers store nutrients and water, fuelling growth after a fire or during drought (Burrows 2013), and tendrils allow upward growth towards sunlight (Friml and Sauer 2008). For animals capable of movement, they must find ways to capture other organisms by passive or active means (Kiørboe 2011). With the evolution of increasingly complex movement and the wider range of food resources, animals developed more sophisticated methods of foraging that required more cognitive advancements to maintain and hone (Janmaat *et al.* 2016). Some of these methods include the ability to predict and track the presence and peak availability of a food resource (Naniwadekar *et al.* 2015), the use of spatial memory to build a resource map and use it to re-locate food that has been hidden or is only seasonally available (Hadj-Chikh *et al.* 1996), and the ability to use visual or olfactory cues to locate high quality but cryptic food resources (Finelli *et al.* 2000, Ishii and Shimada 2010, Sulikowski and Burke 2015). The use of these strategies can have an effect on the population dynamics of the prey organism. For example, highly mobile animals such as birds searching for fruits can have influence the population dynamics and distribution of the fruiting plants by influencing their seed dispersal (Wang and Smith 2002, Levine and Murrel 2003, Carlo and Morales 2016).

Parasitic plants, such as mistletoes, evolved a life history strategy that reduced some of the challenges that other plants face when obtaining nutrients and water for growth (Watson 2009b). Mistletoes are stem hemi-parasites, growing in the canopy of their host tree, drawing on the host xylem and phloem for water and some nutrients, whilst producing much of their own photosynthates (Calder and Bernhardt 1983, Ehleringer *et al.* 1985). Unlike soil-rooted plants, many mistletoes form discrete attachments to their host tree via a root-like haustorium, thus they can be easily manipulated experimentally. For example, a tree rooted in the soil cannot be moved with ease unless it is in a pot or container, which may be visually prominent, whereas a mistletoe plant may be easily cut from its host and tied to a new host to visually and physically change its location. The fruits of mistletoes are attractive to birds, which are the primary seed dispersers, carrying viable seeds to new potential host trees (Calder and

Bernhardt 1983, Watson 2011b). As parasites, reliant on both a host and seed disperser for their distribution, mistletoes are patchy resources in the environment. Thus, they provide an excellent study system to investigate fruit-frugivore interactions, such as how frugivores find patchy fruit resources and what cues they use to guide their foraging. As mistletoes occur around the world and fruiting plants are often patchy resources in the landscape, the questions explored in this thesis are extended to other such fruiting systems. The findings may be transferrable to other frugivore-plant systems, and indeed to other patchy resources.

This introductory chapter considers animal foraging, specific search strategies and the conditions under which different strategies are employed. The strategy of particular focus is the use of search images to enhance foraging efficiency. I explore the interactions between frugivores and fruiting plants, some fruit-specific foraging strategies and the role of frugivores in dispersing the seeds of fruit-bearing plants and how dispersal patterns differ. I introduce mistletoe, its role in ecosystems, interactions with birds and the patterns of seed dispersal specific to mistletoes. Mistletoe distribution is especially abundant along roadside fragments and I discuss the increasingly important field of road ecology, with special focus on the role of roads in habitat fragmentation, use of roadside vegetation as corridors and discrete patches of habitat. Finally, I provide the framework for the remaining thesis chapters, which investigate the foraging strategies of frugivorous birds, the use of cues and the role of habitat characteristics and context in influencing those foraging strategies, with implications for seed dispersal and plant populations.

1.2 Foraging

Foraging is the act of searching for food. Food resources may be temporally predictable, such as, the seasonal migration of prey (Elbroch *et al.* 2013, Arriaza *et al.* 2015). Food resources may be spatially predictable, such as the foliage of a plant or nesting places of bird colonies (Bantle and Alisauskas 1998). Where resources are temporally or spatially stable or predictable, animals may develop and refine foraging strategies that rely on the predictability of their targeted food resource (Higginson and Ruxton 2015). However, food resources may be unstable and/or unpredictable in time or space; causing animals to develop more sophisticated, better informed foraging strategies, where adaptability or speciality may be equally rewarded (Vander Wall 2001, Garrison and Gass 1999).

Optimal foraging theory predicts that animals use the most efficient method to find food in order to get the maximum energy rewards from that food (Schoener 1971, Pyke 1984). Most models attempting to predict the foraging success of animals assume that the animal is able to assess the quality of the habitat or patch and use that assessment to estimate foraging success (whether or not foraging in that patch would be successful) (Eliassen *et al.* 2009). When food is scarce and/or finding that food becomes an inefficient use of the animal's energy, it is assumed that the animal will then move on to another patch (Eliassen *et al.* 2009). The point at which the animal moves on is the 'giving up density', describing the amount of food that is left unexploited by the animal when it moves on to another patch (Brown 1988). Animals in high quality habitat will often stay longer in that patch before moving on, presumably to take advantage of the good patch because the next patch may not be as good. In reality, foraging animals rarely have the complete knowledge of the patch or habitat they are in, hindering their ability to make an accurate assessment of the quality of the patch (McNamara and Houston 1985). Therefore, the cues or the foraging strategies that they use must optimise foraging success, offsetting their incomplete knowledge of the quality and quantity of food resources in the patch.

Food resources are often spatially patchy, or temporally sporadic. For example, 'masting' events in trees that produce bumper crops of nuts, seeds or flowers usually do so irregularly and unpredictably, producing a lesser crop in the intervening years (Pearse *et al.* 2016). Animals that consume food from these events, such as birds, squirrels and other rodents, are known to cache them, storing them for future consumption when that food source is less abundant (Vander Wall 2002, Zong *et al.* 2012). Small-bodied rodents may also scatter or larder hoard resources, storing the food in a single or series of locations for retrieval later. The hoards are usually scattered throughout the animal's territory which may indirectly contribute to the dispersal of those plants, thereby influencing plant population dynamics through seedling recruitment (Hulme and Hunt 1999, Brodin 2010, Shepherd and Ditgen 2013). Nectar is another resource that may be predictable in space but variable in time. Various species of bees and hummingbirds have developed a strategy to efficiently take advantage of the energy-rich but variable nectar resources. Trap-lining, is a foraging strategy whereby the forager develops and maintains a certain route to/between flowers (Gill 1988, Thomson 1996, Comba 1999, Saleh and Chittka 2007). This strategy uses spatial memory to allow the forager to not only build a map of the available resources (Saleh and Chittka 2007), but also annotate it with already visited (empty) flowers and nectar re-fill rates to produce the best route, avoiding empty flowers and re-visiting re-filled flowers (González-Gómez *et al.* 2011). These search

strategies must be remembered from season to season or foraging bout to foraging bout in order to take advantage of the temporally unpredictable resource. Another strategy to maximise foraging success, based on increasing detectability of cryptic food is a search image.

1.3 Search images

Foragers may tailor their searching to focus on some kind of cue that indicates cryptic or hidden food; for example, through use of variable search rates or a visual search image (Dawkins 1971, Allen 1989). Varying the rate of searching may allow the eyes to better adjust and recognise the cryptic food. Using a search image via visual cues to focus the search, may reduce searching time by using visual cues to focus the search. The original and commonly accepted definition of a search image refers to a mental picture resulting from a cognitive change in a predator that enhances their ability to perceive familiar cryptic prey (Dawkins 1971, Pietrewicz and Kamil 1979, Lawrence and Allen 1983). The search image is formed in the mind of the predator using specific visual characteristics of the prey species (Shettleworth 2010) and should increase the successful detection of common, but cryptic prey as compared to the more opportunistic searching without a search image. The search image may be retained for a limited time; for example, short term (minutes to hours) or long term (days) (Ishii and Shimada 2010). Only one image may be formed at a time (Dukas and Kamil 2001), allowing the predator to selectively and successfully detect one cryptic prey species with a decreased chance of detecting another prey that is equally common, cryptic and palatable (Guilford and Dawkins 1987, Dukas 2002).

There are a number of behaviours that are similar to or lead to similar results as the use of a search image (Lawrence and Allen 1983). To determine if a predator is using, has formed or can form a search image, other behaviours must be ruled out (Lawrence and Allen 1983). Six behaviours that must be rejected are: 1) learning to visit a particular place to find food, 2) learning to look in a particular type of place for food, 3) alteration of the search path to increase the chances of encountering prey, 4) learning to handle prey more effectively, 5) preference for, or avoidance of a particular prey that is independent of the predator's ability to see all available types and 6) the learning of specialised foraging techniques by particular individuals (Lawrence and Allen 1983). Early experiments designed to ascertain the existence of search images were focused on domestic chickens and their changing ability to find 'cryptic' coloured grains of rice against different coloured backgrounds. The chicks could learn to 'see'

or recognise the cryptically coloured grains of rice and therefore choose to forage for those grains of rice specifically (Dawkins 1971). The focus of experiments quickly moved on to more realistic applications of what appeared to be selective foraging. For example, captive-raised Blue Jays (*Cyanocitta cristata*) were shown to successfully detect cryptically coloured moths - as opposed to conspicuously coloured moths, only after they had encountered them several times (Pietrewicz and Kamil 1977, 1979).

As with all animal behaviour studies, our understanding is supported by assumptions about the way animals make decisions. These assumptions are constantly being challenged and modified based on experimental and observational results. To this end, identifying and confirming the existence of a true search image in the field is a challenging and complicated task. As a result, there have been a number of interpretations of the original definition of search image that have broadened the requirements to define it. For the purposes of the research presented in this thesis, a search image is defined as an image (visual, olfactory, tactile etc) in the mind of the forager of a specific food that enables the forager to search more efficiently and more successfully for that food item (Reid 1991b). This definition does not rule out the use of a variable search rate or behaviours 1, 2, 3, and 6 as set out by Lawrence and Allen (1983) (as listed above). As my research is focussed on detecting the possibility of proposed foraging behaviours and not with confirming, absolutely, the use of one or another, this wider definition is appropriate. Further experimental work may refine the observation techniques used in the current research to better detect and define the searching strategies as per the original, narrower definition.

When determining the possibility of an animal using a search image, questions might relate not to their specific mode of searching, but to what they are searching for. What are the visual cues being using to increase the efficiency of their foraging? Are animals cuing in to a common visual image, smell, or specific context of the food? For example, Redwings (*Turdus iliacus*) prefer Bilberries (*Vaccinium myrtillus*) that have a high UV reflectance than Bilberries that are less reflective (Siitari *et al.* 1999); could these birds be using a search image to select the berries with the highest UV contrast out of the available berries offered by the plant. What other aspects of ripening fruit or plant surroundings might play a role in attracting frugivores?

1.4 Searching for patchy resources: fruits and their associated frugivores

As with many food resources, fruits may be spatially patchy and/or temporally patchy. Animals, particularly frugivores have adapted to these patterns and developed foraging and searching strategies specific to these patchy resources (Carnicer *et al.* 2009). To inform on plant population dynamics and distribution much of the research to date, has attempted to uncover fruit preferences (Sallabanks 1993, Ctvrticka *et al.* 2016), the mechanisms behind the fruit tracking phenomenon (Blendinger *et al.* 2012) and the role frugivores play in seed dispersal (Chavez-Ramirez and Slack 1994, Smith and McWilliams 2014). Both fruiting plants and the fruits themselves influence frugivores searching strategies by their distribution, abundance and visual characteristics (Foster 1990, Carlo and Morales 2008). Fruiting plants attract frugivores with often large displays of small fruits, or smaller displays of larger fruits. The size of the individual fruits and colours are often good indicators of which frugivores consume a given fruiting species (Regan *et al.* 2001, Flörchinger *et al.* 2010, Lomáscolo and Schaefer 2010). For example, elephants (*Loxodonta* sp. and *Elephas maximus*) are known as the mega-gardeners of forests and rainforests, consuming large seeded fruits, (Campos-Arceiz and Blake 2011). Primates, such as chimpanzees (*Pan troglodytes verus*) prefer larger fruits that are found high in the canopy of fruiting trees (Flörchinger *et al.* 2010, Janmaat *et al.* 2013). Dwarf Cassowaries (*Casuarius bennetti*), large-bodied, flightless birds, also choose large, nutritious fruits preferring those that are temporally predictable (Wright 1998). Fruits consumed by mammals are often green in colour as opposed to bright reds or blacks of the fruits preferred by birds (Lomáscolo and Schaefer 2010). For example, the monitor del monte (*Dromiciops gliroides*) is a small marsupial attracted to the green fruits of the mistletoe, *Tristerix corymbosus* and is the mistletoes key seed disperser (Fontúrbel *et al.* 2012).

The phenomenon of fruit tracking — especially the fruiting of tropical trees— is known amongst frugivores of temperate and tropical forests (Saracco *et al.* 2004 and references within). In the Neotropics, seasonal fruiting events draw in a range of frugivores including rodents, marsupials and birds (Jansen 1983, Stevenson *et al.* 2000, Jansen *et al.* 2004, Wehncke and Domínguez 2007, Cortés-Flores *et al.* 2013). In temperate systems, some species of birds follow or ‘track’ the fruiting progression of fruit-bearing trees, descending during peak fruiting and following the peak across the landscape until the abundance of fruit decreases (Rey 1995, 2011). The mechanisms behind the ability to track variable fruiting progression across landscapes are still largely unknown (Blendinger and Villegas 2011). However, the roles of dietary specialisation and preference for specific characteristics of fruits have been

suggested (Rey 1995, Blendinger *et al.* 2015). Specialist frugivores that rely on a small range of fruits as the primary component of their diet may develop an enhanced ability to track fruiting patterns based on their close association with particular fruit-bearing species (Foster 1987). This form of species specialisation contrasts with generalist frugivores, which may include a wider range of fruits and other resources in their diet (Boyle *et al.* 2011).

Notwithstanding the above relationships, not all frugivores are seed dispersers and not all seed dispersers are obligate frugivores. Depending on the type of fruit being consumed, and the behaviour and preference of the forager, different patterns of seed dispersal may arise. These dispersal patterns may influence the physical distribution of the deposited seeds and the dynamics and genetic flow of the plant populations (Levine and Murrell 2003, McConkey *et al.* 2012, Carlo and Morales 2016). By their differing level of reliance on fruits, specialists and generalists vary in their effectiveness and efficiency of seed dispersal of these patchy resources (Howe 1993, Schupp 1993, Rawsthorne *et al.* 2011a, b).

1.5 Seed dispersal patterns

Understanding how frugivores find and interact with fruiting plants can provide insight into dispersing behaviour. The post-feeding behaviour of the frugivores usually determines where the ingested seeds are then deposited (García *et al.* 2009, Mellado and Zamora 2014, 2016). Forest Elephants (*Loxodonta africana cyclotis*) travel vast distances and can disperse seeds more than 10 km from the mother plant (Blake *et al.* 2009). Long distance dispersal such as this provides new opportunities for colonisation, spatially extending the gene pool by dispersing the seeds further away from parental competition and increasing the chances of growing to maturity and colonising a new patch (Nathan and Muller-Landau 2000, Levine and Murrell 2003). Short distance dispersal, for example via frugivores with preferred perches or latrines, may deposit all the ingested seeds under a perch in a clump, causing density-dependent mortality of the seedlings (Wenny and Levey 1998, Giombini *et al.* 2009, Spiegel and Nathan 2012, Vander Wall and Beck 2012, Sasal and Morales 2013, Gonzalez-Zamora *et al.* 2015). Alternatively, being deposited close to the mother plant may in fact may represent suitable habitat, creating a high density source of fruits that is attractive to frugivores, thereby increasing the local population (Carlo and Morales 2008). Gut processing time and foraging and searching behaviour, and other behaviours including territoriality, affect the seed rain or where the seeds are deposited (Male and Roberts 2002). Many frugivorous birds disperse

seeds in a leptokurtic pattern, aggregated at various spatial scales (Ward and Paton 2007, Carlo and Morales 2008). Understanding the different disperser behaviour can provide insight into not only the distribution of the deposited seeds, but also the dynamics and genetic flow of the plant populations (Levine and Murrell 2003, McConkey *et al.* 2012, Carlo and Morales 2016).

1.6 Mistletoe

Hemi-parasitic mistletoes present an ideal fruit-frugivore system in which to investigate the specific searching strategies and cues of both specialist and generalist avian frugivores. Mistletoes are a functional group of plant hemi-parasites that parasitise other plants, but that retain the ability to photosynthesise and produce their own photosynthates (Calder and Bernhardt 1983, Watson 2011b). They can be found all around the world, on all continents excluding Antarctica and in all terrestrial biomes excepting the most extreme (deserts and the poles) (Calder and Bernhardt 1983, Watson 2011b). As parasites, mistletoes form a physical and biochemical attachment to other plants using a specialised root called a haustorium. Only a few genera attach to multiple hosts underground while the majority of more evolutionarily advanced mistletoes attach to the aerial stem of a single host in the canopy (Calder and Bernhardt 1983). The haustorium penetrates the xylem and phloem of the host plant and draws up water and essential minerals (Calder and Bernhardt 1983, Ehleringer *et al.* 1985, Watson 2011b). This means that while the mistletoe relies on the host for all its water needs, it is also in competition with its host for sunlight (Pennings and Callaway 2002). Most mistletoes produce plentiful flowers and fruits (Kuijt 1969, Watson 2001, Guerra *et al.* 2013). The fruits contain a single seed that is surrounded by a sticky viscid layer, some of which is digested by seed-dispersing birds. As the seed is passed through the bird's gut, some of the sticky viscid layer is digested; the undigested viscin remains attached to the seed (Kuijt 1969). When the seed is passed by the bird, the remaining viscin usually sticks to the feathers of the bird's cloaca and forces the bird to actively remove the seed either by pecking it and wiping its beak on a branch or by wiping its cloaca along a branch to detach the sticky seed; thus, literally 'planting' the seed (Reid 1984, Sargent 1994).

Mistletoes are limited in their distribution by the need to parasitise other plants and therefore are bound in distribution by the foraging strategies of the seed dispersing birds visiting the host plants (Watson 2009b). Their physical existence is bound by the context of the host on

which they germinate and grow; for example, its foliage colour and shape, branch and canopy density. This host-context provokes a multitude of questions about the visual perceptions of the frugivores searching for ripe mistletoe fruits (Calder 1983). Such questions become particularly interesting with the knowledge that the birds that disperse mistletoe seeds are often different to those that disperse the seeds of the host plants, meaning that the former may often be searching specifically for mistletoe fruits (Barlow and Wiens 1977).

Both in Australia and worldwide, mistletoes are regarded as keystone species in woodland habitats, providing beneficial services disproportionate to their assumed influence relative to their abundance (Watson 2001, 2002, Watson and Herring 2012). Compared to other ecosystem facilitators such as mobile herbivores, which redistribute nutrients sometimes far from their origin (Pennings and Callaway 2002), these parasitic plants redistribute nutrients in just one highly concentrated spot. Mistletoes provide a large array of birds with nutritional resources over many months of the year, often when other resources are unavailable (Reid 1991a, Watson 2004a). The dense, stable branches of the mistletoes provide secure nest sites for birds and possums alike (Cooney *et al.* 2006) and concealment from predators in the dense mistletoe foliage (Martin 1988). However, arguably the greatest benefit of the mistletoes to the environment lies below the canopy in the enriched litter fall, which releases nutrients and soil elements previously unobtainable (March and Watson 2007, 2010, Ndagurwa *et al.* 2015, 2016), increasing soil health (Watson 2011a, Fisher *et al.* 2013, Ndagurwa *et al.* 2014, 2015), insect diversity and abundance (Braby 2005, Braby and Trueman 2006, Braby and Nishida 2010, Burns *et al.* 2011) and therefore insectivorous bird communities (Watson 2002, 2015).

As a food resource, mistletoes are attractive to a wide range of birds, providing nectar and fruits (Watson 1997, 2002, Oliver *et al.* 2003, Bowen *et al.* 2009, Napier *et al.* 2014) and increased arthropod diversity and abundance in the local surrounding habitat (March and Watson 2007, Burns *et al.* 2011). Australian Loranthaceae mistletoes produce fruits over an extended and variable fruiting season which can last for several months, often over the winter season (Kuijt 1969, Reid 1991a). This prolonged availability of fruit is of great benefit to the woodland birds of arid and semi-arid Australia, where there are often limited food resources during the winter season (Watson 2004a). The fruits of Loranthaceae mistletoes are usually nutritious and water-rich (Reid 1991a). These attributes are characteristic of plants that attract specialist frugivore dispersers (Herrera and Jordano 1981).

1.7 Mistletoe seed dispersal

Mistletoe seed dispersal is limited by the need for not only a host plant, but also for that host to be susceptible to infection by the mistletoe, i.e. compatible with the mistletoe haustorium, have adequate access to sunlight and appropriately thin-sized branches on which dispersers can perch to deposit the seed (Davidar 1983, Herrera 1985, Reid 1991a). These limitations dictate the effectiveness of the seed dispersers (Larson 1991, Rawsthorne *et al.* 2011a, b). For dispersers to effectively disperse seeds, they must transport many seeds and deposit them in suitable germination sites where they are likely to grow to maturity (Schupp 1993, Schupp *et al.* 2010). Not all mistletoe consumers disperse many seeds, nor deposit them in suitable germination sites (Larson 1991, Mellado and Zamora 2014). Indeed, in a number of systems, there are only a few effective dispersers of mistletoe seeds, usually generalist or specialist mistletoe consumers (Larson 1991, Sargent 1994, Watson 2012). Even the specialists may not be effective dispersers as they tend to deposit seeds on already infected hosts (Watson 2012, Watson and Rawsthorne 2013).

Despite high germination rates, mistletoes generally have a low establishment rate, influenced by the disperser species, the host species, and the quality or health of host, which facilitates the growth and maturation of the mistletoes (Watson 2009b, Luo *et al.* 2015, Moss *et al.* 2016). Some mistletoe seed dispersers prefer hosts containing lots of mistletoe fruits, as seen in Neotropical forests in Costa Rica, where the mistletoe *Phoradendron robustissimum* is visited by *Euphonia elegantissima*, *E. hirundinacea* and *Chlorophonia callophrys* (Sargent 1994). Also, some dispersers prefer taller plants, already hosting mistletoes; for example, in Chile where *Tristerix aphyllus* (Martínez del Río 1995) is dispersed by *Mimus thenca*; southern Arizona, USA, where *Phoradendron californicum* is dispersed by *Phainopepla nitens* (Aukema and Martínez del Río 2002c); and in *Acacia*-dominated savanna, southern Zambia, Africa, where *Phragmanthera dschallensis* and *Plicosephalus kalachariensis* are dispersed by *Pogoniulus chrysoconus*, *Lybius torquatus* and *Cinnyricinclus leucogaster* (Roxburgh and Nicolson 2005). Disperser preferences generally lead to more seeds being dispersed onto established hosts with multiple mistletoes, making dispersal away from the infected host or patch unlikely, except via opportunistic dispersal events (Green *et al.* 2009, Watson 2009b, Luo *et al.* 2015).

In Australia, mistletoes are dispersed by a select few avian frugivores, primarily the aptly named specialist Mistletoebird (*Dicaeum hirundinaceum*) and the Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*) (Reid 1990, Rawsthorne *et al.* 2011a, b). A number of other species are known to feed on the fruits, including the mistletoe specialist Painted Honeyeater

(*Grantiella picta*), which time their breeding to coincide with peak fruiting season (Barea and Watson 2007). Both the Mistletoebird and the Spiny-cheeked Honeyeater tend to disperse mistletoes in an aggregated pattern (Reid 1989). As the Mistletoebird is a mistletoe-obligate species, and its movements are centred on patches of infected plants, its seed dispersal services, while prolific, are unlikely to be advantageous to mistletoe gene flow as few seeds are dispersed beyond these patches (Rawsthorne *et al.* 2011b, Watson and Rawsthorne 2013). The Spiny-cheeked Honeyeater may be a better disperser as it supplements its diet with arthropods and the fruits and nectar of other species (Rawsthorne *et al.* 2011a). Therefore, the Spiny-cheeked Honeyeater is more likely to disperse seeds away from infected hosts, potentially leading to the creation of new infected patches (Reid 1989, Rawsthorne *et al.* 2011a). Where these important plants end up in the landscape and their subsequent ability to support other organisms therefore depends largely on the foraging behaviour of these few bird species. The nature of this foraging behaviour and what attracts mistletoe dispersers in Australian systems is essentially unknown.

1.8 Roadside Environments

Roads in rural or agricultural areas typically create long, roughly linear cuts through the landscape, facilitating human centred transport across distances (Davenport and Davenport 2006, van der Ree *et al.* 2015a). As the human population continues to grow, communication and technology increases and so does the number of roads, creating vast networks of linear transects through the landscape (Seiler 2001). While the effects of roads vary depending on the surrounding land use, type of road and flow of the traffic, the building of roads always catalyse changes on the biotic and abiotic components of the surrounding land (Spellerberg 1998, Seiler 2001). Vegetation along roadsides undergoes physical changes as a result of road construction and use through changes in microclimate, soil nutrients, water run-off, pollutants and substrate type (Reid and Dune 1984, Forman *et al.* 2003, van Bohemen and van de Laak 2003). Roads can also be barriers to animal movement, restricting dispersal through the landscape (Rosen and Lowe 1994, Aresco 2004, Kerth and Melber 2009), population gene flow, (Munguia-Vega *et al.* 2013, Ripperger *et al.* 2013, Garrido-Garduño *et al.* 2016) migrations (Sawyer *et al.* 2005, Brzeziński *et al.* 2012) and through vehicle-caused animal mortality (Spellerberg 1998, Seiler 2001, Lin 2016).

The combination of increased animal mortality through vehicle collisions and restricted animal migrations sparked the creation of a new area of research and policy planning into the effectiveness and design of animal road passes. Over- and under-road passes, along with stepping streams and species-specific barriers, are designed with the dual purpose of reducing animal-vehicle collisions and facilitating animal movement (Gardner *et al.* 2004). Over-passes are designed to facilitate movement for ungulates, other large mammals, and arboreal animals (Cramer *et al.* 2015, Donaldson and Cunneyworth 2015, Reck and van der Ree 2015, Smith *et al.* 2015). Under-passes are designed for nocturnal or elusive animals, e.g. Florida Panthers (*Puma concolor coryi*), bats, reptiles, and amphibians (Schwab 2006, Abbott *et al.* 2012, Berthinussen and Altringham 2012, Baxter-Gilbert *et al.* 2015). Tall barriers force birds to fly higher over the road (Kociolek *et al.* 2015), whereas tall solid barriers prevent ungulates and marsupial macropods (e.g. kangaroos and wallabies) from directly crossing the road (van der Ree *et al.* 2015b).

Vegetation on roadsides can play a large role in the risk of animal-vehicle collisions and facilitating movement (Orłowski 2008, Milton *et al.* 2015). Dense forest on roadsides increases the habitat of avian forest species, but also increases the risks of bird-vehicle collisions (Orłowski 2008). Complex vegetation along roadsides may be used as habitat (e.g. rodents) or may encourage animals to use it as a corridor to travel to other patches or better habitat (Ascensão *et al.* 2012, Carthew *et al.* 2013). Roadside vegetation also presents opportunities for foraging (Tanner and Perry 2007) and nesting. Nesting along roadsides can be a risky business with mixed results (Reijnen and Foppen 2006, Summers *et al.* 2011, Dietz *et al.* 2013).

Roadside vegetation that serves as habitat patches or corridors can facilitate dispersal (Arnold and Weeldonburg 1990, Haddad and Baum 1999). Roads can be corridors for seed dispersal via vehicles (Lonsdale and Lane 1994, Zwaenepoel *et al.* 2006, Herrmann *et al.* 2016) and dispersing or migrating animals. Seeds can travel hundreds of kilometres if caught in tyre tread, mud flaps or inside a vehicle (Zwaenepoel *et al.* 2006). Indeed, roads provide excellent corridors for the spread of early colonising or invasive plants. Early colonisers naturally colonise freshly-disturbed roadside areas and can be transported not only by vehicle, but also by wind, water or animal to other areas of suitable habitat (Damschen *et al.* 2014, Vakhlamova *et al.* 2016). Equally, roadside habitat can harbour remnant native vegetation and vegetation communities of conservation significance, especially in areas that have been historically cleared or consist of broadscale agriculture (van der Ree 2002, Milton *et al.* 2015). Current research investigates how effective vegetated roadsides are at maintaining or increasing

biodiversity and providing habitat in increasingly fragmented areas and their role in providing connectivity between patches (Escribano-Avila *et al.* 2014, de Torre *et al.* 2015).

Changed physical conditions of roadsides can be ideal for trees that mistletoes prefer as hosts. Roadsides generally have greater soil moisture, nutrient run-off and reduced competition for resources such as sunlight, all of which support healthy growth of potential mistletoe host trees (Norton and Stafford Smith 1999). Improved access to soil moisture and nutrients goes part-way to explaining why there appears to be greater numbers of mistletoes parasitising hosts in roadside habitats as compared to continuous or undisturbed forests (Norton and Stafford Smith 1999). This phenomenon has been observed multiple times, but rarely investigated empirically (Norton *et al.* 1995, Norton and Stafford Smith 1999, Downey 2004). Further, while the physical conditions of the roadside habitat and hosts has been offered to explain the apparent abundance of mistletoes, the role that frugivorous birds play in dispersing mistletoes to those environments has not been investigated. As keystone resources in Australia, with complex interactions with a range of organisms, including seed dispersing birds, this is an area of research that warrants further investigation. It is also not known the extent to which foraging behaviour of frugivorous birds differs in roadside patches relative to larger tracts of native habitat. The research presented in Chapter 4 takes the first steps into investigating the role of frugivorous birds in influencing the high abundance of mistletoes in roadside vegetation by quantifying the number of birds visiting fruiting mistletoe in roadside vegetation compared to continuous forest. It also explores which possible searching strategies may be used by birds searching for mistletoe in roadside vegetation as compared to continuous forest.

1.9 Significance and research context

Mistletoes hold complex relationships with a range of organisms, including leaf litter invertebrates, mammals and a wide range of birds. The influence of mistletoes on community interactions and functions is far reaching (Watson 2015, 2016). Woodland birds are declining in Australia. Their decline is attributed to a combination of factors including habitat loss, fragmentation and declines in habitat quality (Ford *et al.* 2001, 2009, Watson *et al.* 2003, Watson 2011a). Mistletoes may play a vital role in sustaining or enhancing bird communities. Through their fruit and nectar resources they may sustain or enhance the resources of an area for frugivorous and nectivorous birds, while their contribution to the nutrient cycle positively

affects the abundance and range of insectivorous birds which make up a large proportion of woodland avifauna (Briggs *et al.* 2007). Therefore, mistletoes may be a novel, largely untapped tool for improving degraded habitat through soil rehabilitation and maintaining or increasing avian community assemblages.

As discrete, aerial, stem-parasites, mistletoes can be easily experimentally manipulated by changing their visual appearance or moving them to different locations or hosts. Further, Australian mistletoes are dispersed primarily by only two species, one a mistletoe specialist and the other a generalist frugivore, both of which have vast distributions, coinciding with that of many mistletoe species. A few other bird species regularly feed on the fruits of various mistletoe species when they are available, but may not be effective dispersers (Reid 1986 and references within). These disperser relationships make for an ideal system to investigate the foraging strategies of birds searching for specific patchy food resources. Specifically, what strategies do they use? Do mistletoe-dispersing birds use visual cues such as the presence of fruits or the combination of mistletoe and host foliage to guide their search for mistletoe? Or do they use spatial cues or spatial memory to locate and relocate mistletoes? What influences those strategies and are they transferable to other habitats? Addressing such questions may not only have implications for the treatment of mistletoes in Australia as tools of conservation, but also provide insight into restricted or highly specialised fruit-frugivore systems. Furthermore, answers may help in predicting and mediating the impacts on populations affected by habitat loss and fragmentation.

1.10 Thesis structure

The research presented in this thesis aims to address some of the possible influences on and cues used by birds searching for mistletoe fruits. Chapter 2 presents a defoliation experiment exploring the visual cues used by frugivores, primarily asking if birds that specialise in consuming mistletoe fruits have equally specialised strategies of foraging using visual cues. With the expectation that birds use a search image of the whole mistletoe plant, rather than just the fruits I hypothesised that defoliated mistletoes would receive fewer bird visits than intact mistletoes. Chapter 3 presents a novel 'cut-and-paste' experiment addressing the role host identity plays on influencing searching behaviour in a continuous forest habitat. Specifically, this experiment asks a) if the searching birds recognise mistletoe in different hosts, b) whether there is evidence that visual cues influence their searching; and c) if they use

spatial memory to locate fruiting mistletoes. Here, I expected that birds would remember the location of a particular food source, leading me to hypothesise that the unmoved mistletoes would receive more visits than the mistletoes moved to new trees. Of the moved mistletoes I predicted those moved to a tree of the same species as the original host would receive more visits than those moved to a non-host tree species. Finally I predicted that birds of differing dietary specialisation (specialist or generalist frugivores) would show different visitation patterns, being influenced by different mistletoe or host tree characteristics. Chapter 4 compares selected visitation data from Chapter 3 with new data collected in roadside vegetation. Here I address how bird foraging strategies differ between remnant continuous forest and fragmented linear patches and what features of these different habitat types might be responsible. Because of the high abundance of mistletoes along roadside, I predicted that trees in roadside vegetation would host more mistletoe and that those mistletoes would receive more visits than the mistletoes in the continuous forest. In Chapter 5, I synthesise the findings of Chapters 2, 3 and 4 and discuss them in the context of current literature and research directions, suggesting new hypotheses for future investigation. Each of the three data chapters are written in the style of a manuscript for future publication; thus, there is some repetition of main concepts, which I have tried to keep to a minimum.

Chapter 2: The role of leaves in foraging strategies



Swamp Wallaby (*Wallabia bicolor*) feasting on freshly cut Grey Mistletoe (*Amyema quandang*) leaves.

2.1 Introduction

Foraging, the act of searching for food, is crucial to survival and there are almost as many foraging strategies as there are types of food. Sniffing out larvae (Floyd and Woodland 1981), listening for echoes bouncing off fluttering moths (Fenton *et al.* 2012), following large migratory herds and picking off stragglers (Elbroch *et al.* 2013), are all different strategies of foraging. Some strategies work best for resources that are stable in space, for example, gathering nectar resources using a trap lining strategy (Saleh and Chittka 2007). Other strategies are good for resources that are predictable in time, such as hunting prey that are available at the same time each year (annual migrations) (Middleton 2012, Arriaza *et al.* 2015) or tracking seasonal fruiting/flowering events (Saracco *et al.* 2004, Blendinger *et al.* 2012). However, some food resources are not obvious, and require specialised strategies. The use of a search image is one strategy that can improve the efficiency of animals searching for cryptic or hard to find food. For example, nectar feeding insects are confronted by a vast array of flowers offering varying qualities and quantities of nectar and pollen. Some solitary pollinators use 'nectar guides', coloured patterns on the petals of specific flower species to select individual flowers to feed from (Hansen *et al.* 2012). Likewise, birds are thought to cue in on the higher UV reflectance of high quality fruits to find patchy resources, such as fruiting plants, as they may reliably contrast with the leaves (Burkhardt 1982); although, whether UV forms part of the birds' search image has not yet been investigated.

Animals with a highly specialised dietary range are the most likely to employ search images to assist their foraging efforts. If the animal is highly restricted in dietary range then it is likely to have developed highly specialised search strategies that are more useful than generalised search strategies. Very few vertebrate species have highly specialised diets. Even species classed as specialists can consume a variety of foods. For example, Oilbirds (*Steatornis caripensis*) are classed as specialist frugivores, because they tend to only consume fruits, yet they have still been observed to include fruits from 33 fruiting species across three families (Bosque *et al.* 1995, Holland *et al.* 2009). By contrast, some specialists do indeed have very restricted diets. The Mistletoebird (*Dicaeum hirundinaceum*) is a specialist with a narrow primary diet of mistletoe nectar and fruit (Reid 1987). Indeed, because of the close mutualistic relationship between the seed dispersing Mistletoebird and the parasitic mistletoe, suggestions of co-evolution have been investigated (Reid 1987, 1991a). The Mistletoebird feeds on the fruits and nectar of various mistletoe species (Reid 1990, Ward and Paton 2007). Given their highly specialised diet, we might expect the specialists to use a range of specialised foraging strategies to help them find mistletoes, especially as their distribution is both spatially

and temporally patchy. One such strategy may be the use of a search image. To reduce the effort spent searching the Mistletoebird may have an image of the desired mistletoe fruit or whole plant in its mind to increase its chances of successfully spotting mistletoe in the canopy of a host tree species.

The use of a search image is especially advantageous if the desired food source is hard to find, or cryptic (Lawrence and Allen 1983). For example, there are a number of mistletoe species that visually mimic the foliage colour, shape and structure of their common host species; among suggestions as to why they are visually cryptic include increasing the chance for successful seed dispersal (Calder 1983). By mimicking the foliage of the host, the mistletoe foliage would become indistinct, leaving the fruits visually exposed to the seed dispersing birds (Calder 1983). Calder suggests these birds would form a search image for the fruits in the 'host' foliage and deposit the mistletoe seeds while searching through trees of the same species, thus increasing the chances of the seeds being dispersed to a suitable tree species that is susceptible to infection by the parasitic mistletoe. Calder's hypothesis has never been experimentally investigated. Therefore, one key question to be addressed in this thesis is what role the mistletoe foliage actually plays in influencing or attracting frugivorous seed-dispersers.

Few studies have investigated the mutualistic interactions between a plant and forager by manipulating part or all of the plant (but see Amsberry and Steffen 2008). Experimental leaf removal can affect the population dynamics of the defoliated plant species if it continues over a period of years because of reductions in seed set and fruit size, which reduce the attractiveness of the plant for seed dispersers (van Lent *et al.* 2014). In other words, the foraging strategies of seed dispersers can also affect the population dynamics of the manipulated plant because of the cues they use to find the plant (Howe and Smallwood 1982 and references therein). In Australia, the seeds of parasitic mistletoes are dispersed by only a small handful of frugivorous birds, primarily the Mistletoebird and the Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*), the latter being a generalist frugivore, including fruit other than mistletoes in its diet (Reid 1989, 1990). Most of the mistletoes in Australia are Loranthaceae mistletoes, many with a single haustorium connecting the mistletoe to the host. These relatively small, discrete woody parasites may be easily manipulated to experimentally investigate the foraging strategies of their seed dispersing frugivores.

In the case of the mistletoe-frugivore system, addressing how frugivorous birds find mistletoe fruits, and what role the foliage plays in that search, is critical to understanding the link between the foraging behaviour that precedes and potentially influences seed dispersal. The

strategies used by frugivores to track down fruiting mistletoes may help to not only explain, but also predict how this frugivore-plant system and other similar systems around the world may respond to changes in vegetation communities, such as increasing fragmentation or urbanisation.

To investigate the role of leaves in influencing frugivore searching strategies, I designed a novel experiment to alter on the visual appearance of mistletoes. This experiment aimed to test the hypothesis that mistletoe seed-dispersers use a search image of foliage to find fruiting mistletoes. I manipulated the visual appearance of Grey Mistletoe (*Amyema quandang*) by removing the most obvious contribution to the overall form of mistletoes, the foliage, leaving only the fruit on bare branches. I then compared bird visitation between un-manipulated mistletoes and defoliated mistletoes. Differences in the number of visits between these two treatments would indicate that the whole mistletoe plant, i.e. not just the fruits, influences the decision to forage at that mistletoe. The fruits on the defoliated mistletoes would be more visually exposed than those on intact mistletoes and visiting preferences would inform about the influence of the leaves *versus* the exposed fruit.

Grey Mistletoe hosted by Yarran (*Acacia homalophylla*) is not considered a host-mimic; therefore the use of this particular mistletoe-host combination investigates only the role of the mistletoe leaves in attracting birds. As demonstrated by van Lent *et al.* (2014), the defoliation of a fruiting plant can reduce the number of visits by frugivorous birds. Calder's hypothesis was that the mistletoe foliage would blend into the host foliage thereby exposing the fruits. If the fruits did form part of a search image for frugivores, particularly the specialist Mistletoebird, then I would expect these birds to visit the defoliated mistletoes more than the intact as the fruits would be more visually obvious. On the other hand, if frugivores formed a search image of the whole mistletoe or did not form one at all, I would expect the intact mistletoes to receive more visits than defoliated mistletoes because they would be recognised as their food source and/or appear healthy. I also predicted that smaller birds would preferentially visit intact mistletoes over defoliated as the former provide more protection from predators while feeding.

2.2 Methods

2.2.1 Site and species description

This study was carried out in Binya State Forest, 20km east of Griffith, 34°13'S, 140°16'E, with data collected in December 2015 and February 2016. Long-term average annual rainfall for Griffith is 396 mm; mean annual maximum temperatures are 24°C and minima average 10.0°C (Bureau of Meteorology 2016a, e, f). During the study period, Griffith received 116.2mm of rainfall 2016 (Bureau of Meteorology 2016b, c). The predominant vegetation type in this region is semi-arid woodland, with the canopy at the study site composed primarily of White Cypress Pine (*Callitris glaucophylla*, Cupressaceae), Yarran (*Acacia homalophylla*, Fabaceae) and Belah (*Casuarina cristata*, Casuarinaceae), with sub-dominant stands of Buloke (*Allocasuarina luehmannii*, Casuarinaceae) and Poplar box (*Eucalyptus populneus*, Myrtaceae). The native vegetation was extensively cleared ~120 years ago, now persisting only in protected areas and small remnants on private land and along roadsides. The dominant land uses in the area is irrigated rice, viticulture and cattle grazing. Grey Mistletoe (*Amyema quandang*, Loranthaceae) is the principal mistletoe in the area, growing almost exclusively on Yarran at the study site (Figure 1). In Binya State Forest there were four species of mistletoe including Grey Mistletoe, Box mistletoe (*Amyema miquelii*, Loranthaceae), Buloke Mistletoe (*Amyema linophylla*, Loranthaceae) and Harlequin Mistletoe (*Lysiana exocarpi*, Loranthaceae). Box, Buloke and Harlequin mistletoes were limited to a just a few individuals on a few host trees scattered throughout Binya State Forest, none were in fruit at the same time as Grey Mistletoe, which was the most common.

Grey Mistletoe is a woody, aerial hemi-parasite with chalky-grey foliage and cryptic greyish flower buds opening to reveal deep red coloured flowers inside the petals and pale yellow fleshy fruits (Watson 2011b) (Figure 2). As with many other mistletoes, Grey Mistletoe exhibits extended phenology, with flowers and fruit present in most months, but peak fruiting occurs in the Austral spring and summer (Barea and Watson 2007). Both pollen and seeds are bird-dispersed, the former primarily by honeyeaters (Meliphagidae), the latter primarily by two mistletoe specialist frugivores: Mistletoebird (*Dicaeum hirundinaceum*, Dicaeidae) and Painted Honeyeater (*Grantiella picta*, Meliphagidae) and two generalist frugivores, Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*, Meliphagidae) and Singing Honeyeater, (*Lichenstomus virescens*, Meliphagidae), with numerous other bird species opportunistically consuming the fruits and occasionally dispersing seeds (Barea 2008, Watson 2011b).

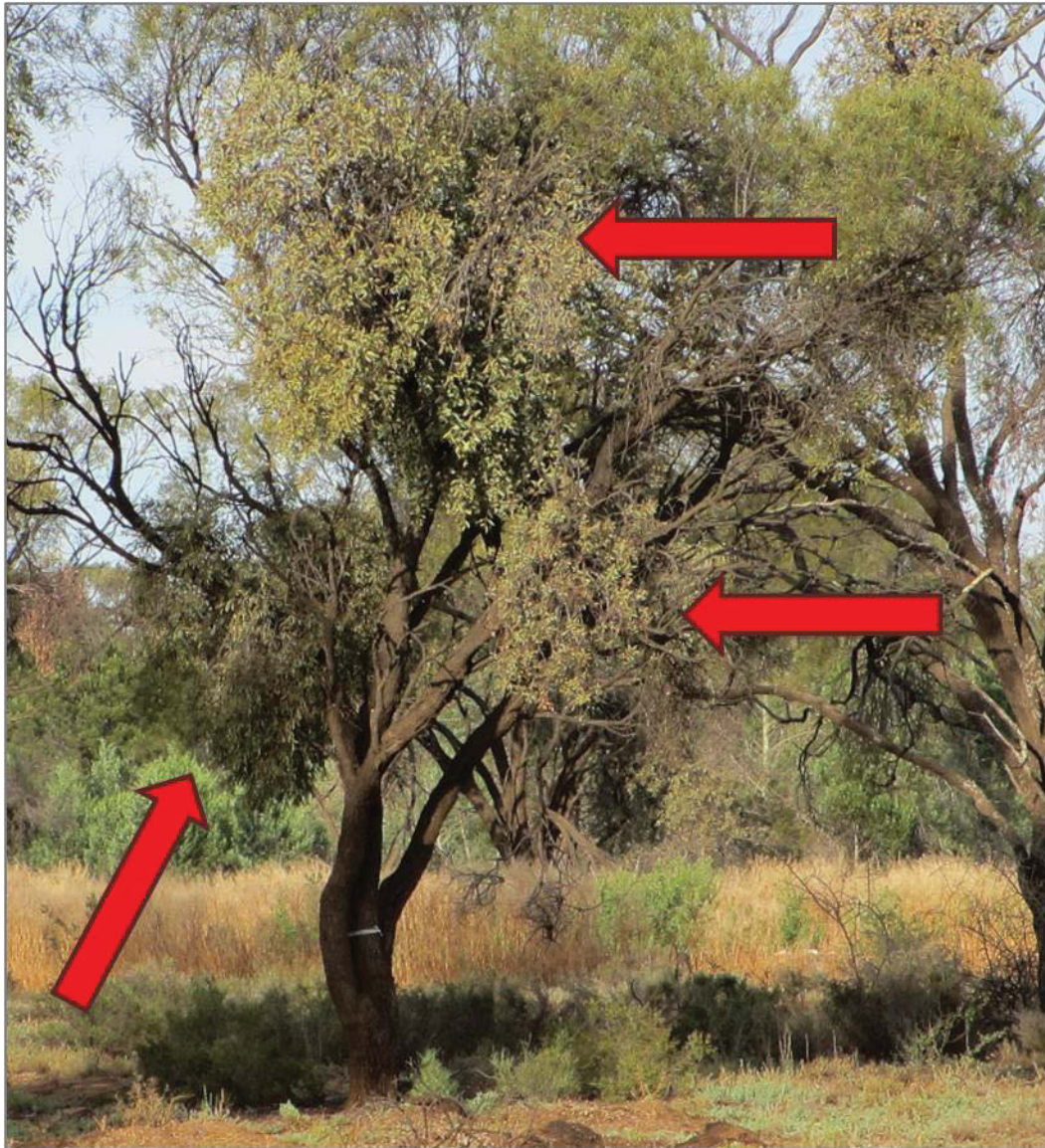


Figure 1. Typical Yarran (*Acacia Homalophylla*) hosting Grey Mistletoe (*Amyema quandang*) (mistletoes indicated by arrows), in Binya State Forest, NSW.

2.2.2 Experimental procedure

To investigate the foraging behaviour of mistletoe-eating frugivores and their potential use of a search image to aid their search for mistletoe fruits I designed a defoliation experiment. Manipulated mistletoes were selected from potential hosts in Binya State Forest based on accessibility, size and number of fruits. The mistletoes needed to be accessible by ladder (up to 4m high); of an adequate size to be considered mature and attractive to frugivores (no smaller than ½ m diameter at widest point) and to be fruiting, bearing no less than six fruits. From the

pool of plants fitting all of the above criteria 20 replicate host trees were randomly selected for this experiment. Experimental host trees were within an area heavily infected with mistletoes, such that a given mistletoe plant was generally within a few meters of another mistletoe plant, irrespective of whether that neighbouring mistletoe was in the same or a different host tree. Experimental mistletoes were in host trees no less than 10 m apart, each bearing between 1-23 mistletoes. One individual mistletoe plant per host tree was chosen for observation; these mistletoes were easily identifiable as mistletoe plants owing contrasting foliage density relative to the canopy of the Yarran host. Observations took place over two days per mistletoe. Experimental observations began no later than 7:30 am (AEST) and continued for 3 - 4 hours, then recommenced in the afternoon for a further 1 - 3 hours, ending by 6:30 pm. Variation in observation length depended on rain. The period of observation ranged from 5 hr 20min to 6 hr 30 min (with one exception of 4 hr 27 min due to rain) and averaged 5 hours across the 20 replicates.

On the first day of observation the target mistletoe was watched for bird visitation. On the second day of observation I defoliated that same mistletoe in the predawn light then commenced observations of bird visitation at the same time as the previous morning. To defoliate the selected experimental mistletoe I removed $\geq 90\%$ of leaves (Figure 3) using secateurs to cut individual leaves from the branch to which they were attached. Birds and mistletoes were watched from a distance of approximately 15 m depending on the density of vegetation between the observer and the mistletoe under observation, using 8 x 42 magnification binoculars. The observation distance of 15 m was used by Watson (2012) and found not to disturb the normal behaviour of foraging birds. Two observers recorded the visitation data for this experiment.

A visit was recorded if the bird perched in the experimental mistletoe; birds confining their movements to host branches or flying through the mistletoe without landing were not counted as a visit. All visits were considered potential foraging episodes by the birds as many searched the fruits and foliage while they perched or hopped through the mistletoe. Each visiting bird species was identified if possible and categorised as belonging to one of three dietary guilds based on their reliance on mistletoe fruits following dietary records in Barker and Vestjens (1990), diet and seed dispersal information in Rawsthorne *et al.* (2011a), augmented by personal observation. With an absence of Painted Honeyeaters, the 'mistletoe specialist' category comprised solely the Mistletoebird; 'generalist frugivore' comprised the Spiny-cheeked Honeyeater and Singing Honeyeater; 'opportunist' included all other birds that are

mainly insectivores and do not regularly consume fruit (Appendix 4, Table 14). Fieldwork was conducted under UTS ACEC 2013-745, NPWS Scientific License SL101337 and Forestry Corporation: Forest Permit - Research.

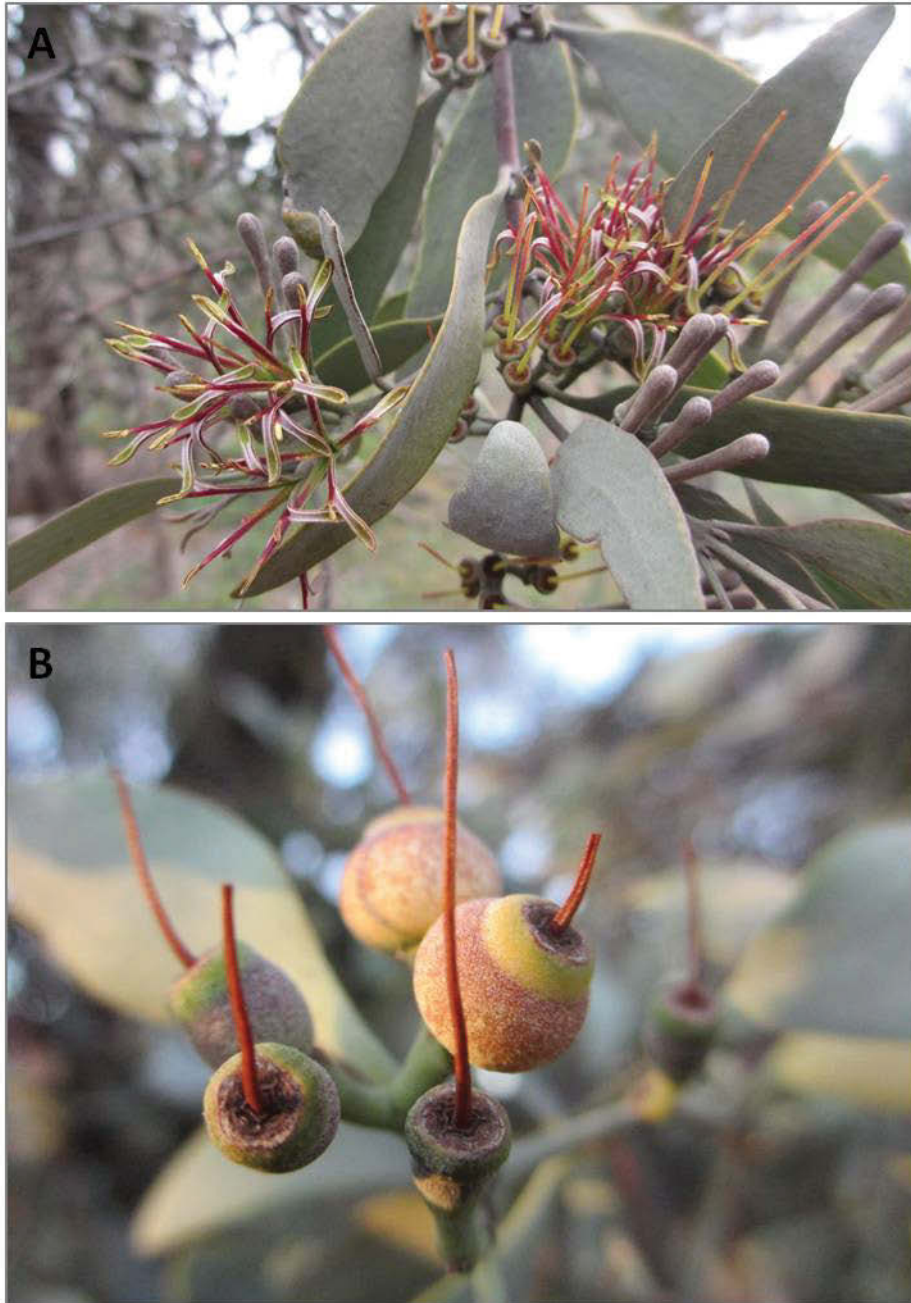


Figure 2. Grey mistletoe in flower and fruit. (A) Grey Mistletoe (*Amyema quandang*) in flower. Note the mix of mature flowers (centre left and right), unopened flower buds (right) and developing fruits with the stamens still attached (top and bottom). (B) Mature fruits of Grey Mistletoe. Note the two pale yellow swollen mature fruits and three immature fruits, all still bearing stamens.

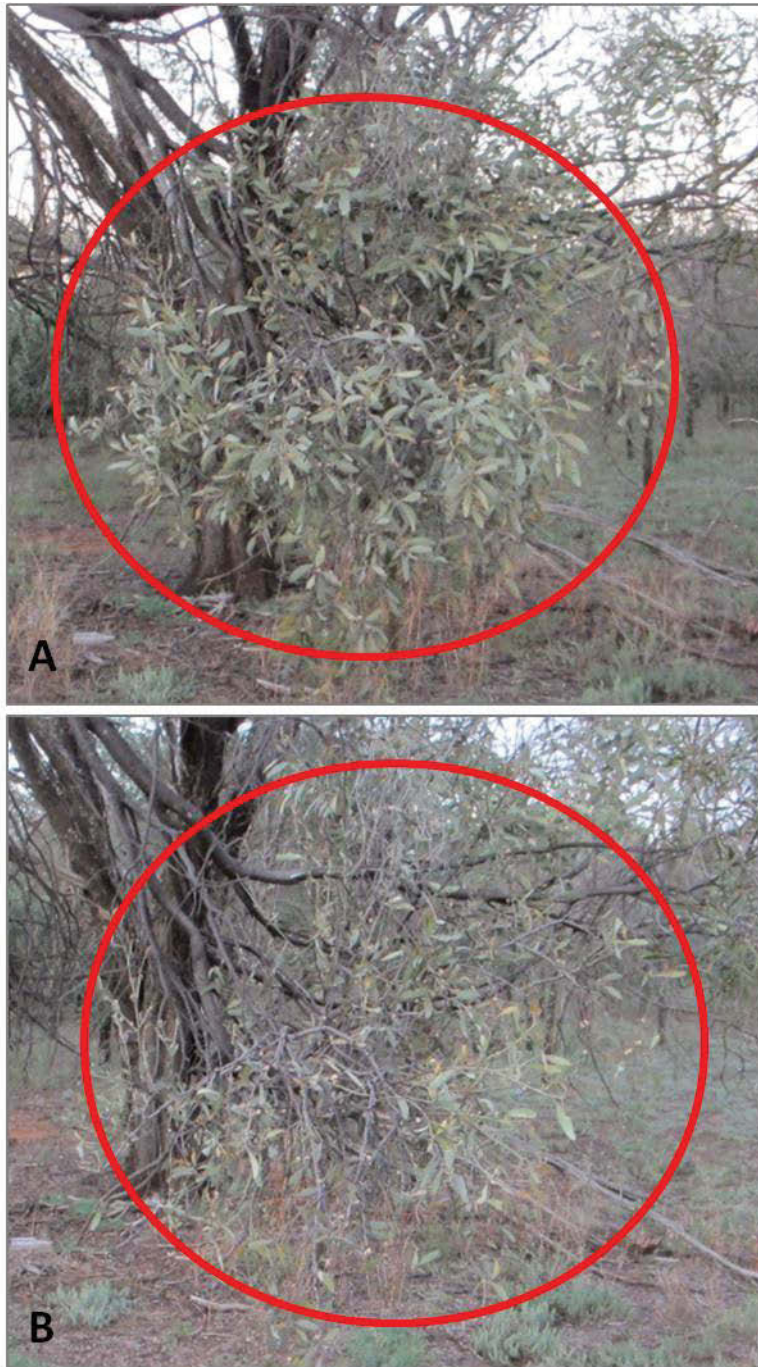


Figure 3. Example before and after of the defoliation of Grey Mistletoe (*Amyema quandang*). Mistletoes were observed over two days for bird visits to the manipulated mistletoes. The first day the mistletoe was intact and un-manipulated (A); on the second day, before observations commenced, $\geq 90\%$ of the foliage was removed, leaving fruits intact on the plant (B). Mistletoe is circled.

2.2.3 Data analysis

Each experimental mistletoe observed across two days (the day before and the day of defoliation) was counted as a replicate (n=20). For analysis the data were treated as related samples and were non-normally distributed with non-homogenous variance. Therefore, to test for differences in the number of bird visits to the treatment mistletoes before *versus* after leaf removal, a Sign test was conducted using SPSS (IBM SPSS Statistics v22, 2013). The next aim was to test for the effect of dietary guild (dietary specialist, generalist frugivore or opportunist) visitation to each treatment. However, due to insufficient visits to the experimental mistletoes for each guild, these analyses could not be run. Proportional graphs of the guild visitation are therefore presented in lieu of statistical analysis for a visual exploration of the data.

2.3 Results

A total of 226 hours of observation was recorded across the 20 replicates, with 33 visits to experimental mistletoes recorded in total. Eight species of birds were observed visiting the experimental mistletoes (Appendix 4, Table 14). For the twenty replicates, there were a total of 24 visits to seven mistletoes on day 1 (intact) and nine visits to four mistletoes on day 2 (defoliated) (Figure 4). Only four mistletoes were visited on both days. The number of visits to the mistletoes with and without leaves was significantly different ($n = 20$, $z = -2.041$, $P = 0.031$), with more visits to the intact mistletoes. Most visits to either intact or defoliated mistletoes were made by Mistletoebird ($n = 13$), followed by Yellow thornbill (*Acanthiza nana*) ($n = 6$), Southern Whiteface ($n = 5$) (*Aphelocephala leucopsis*), Spiny-cheeked Honeyeater ($n = 4$), Inland Thornbill (*Acanthiza apicalis*) ($n = 2$) with Eastern Yellow Robin (*Eopsaltria australis*), Red-capped Robin (*Petroica goodenovii*) and Singing Honeyeater (*Lichenstomus virescens*) each visiting only once. Grouped by dietary guild there were 13 visits by the specialist, Mistletoebird; a total of five visits by the generalist species, Spiny-cheeked Honeyeater and Singing Honeyeater, and 15 visits by the five opportunist species, Yellow Thornbill, Southern Whiteface, Inland Thornbill, Eastern Yellow Robin and Red-capped Robin. Visit length and visits per hour data included in Appendix 1, Figure 17, 18.

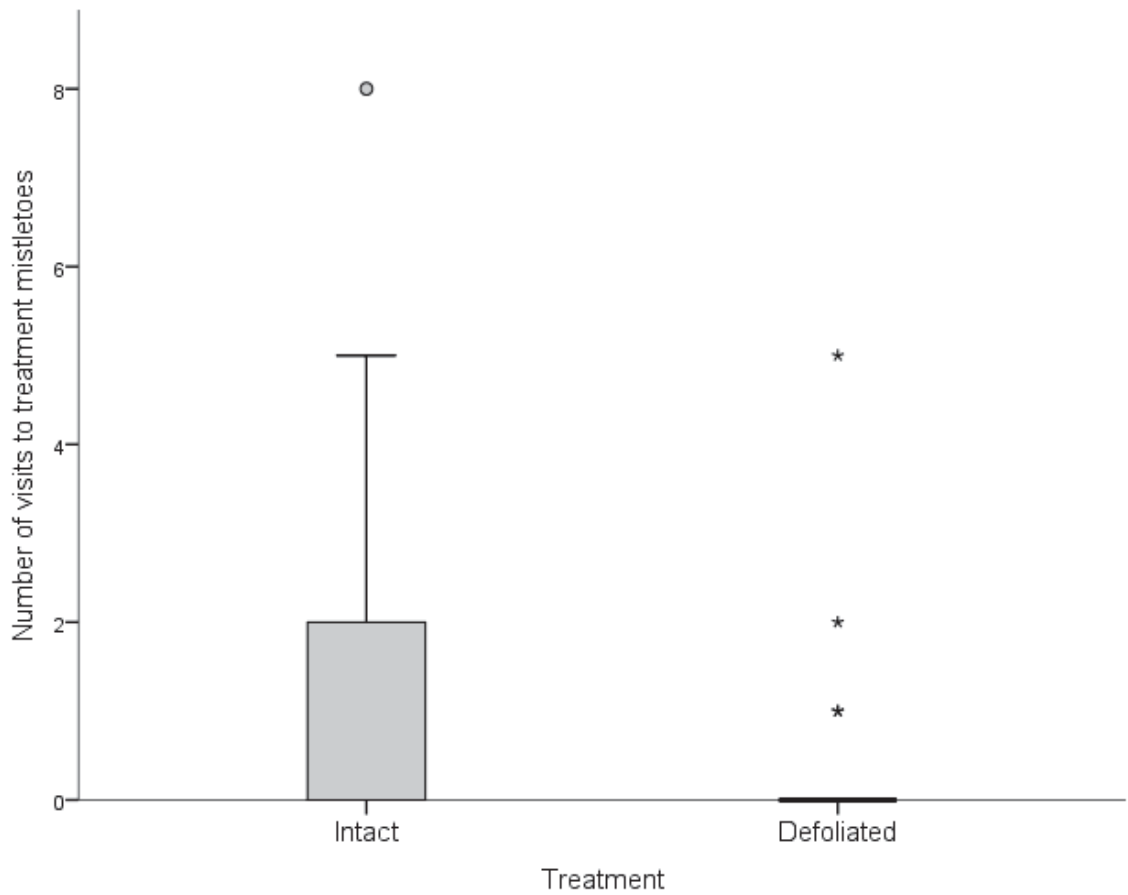


Figure 4. Total number of visits to experimental treatment mistletoes: intact mistletoes compared to the same mistletoes after being defoliated, leaving only the fruits on the plant (n = 20 replicates). Error bars are the standard error. Circles are outliers, stars are extreme outliers.

2.3.1 Proportional visits for dietary guild

The proportion of visits by each of the three dietary guilds was not statistically analysed due to low numbers of visits by each guild. However, a visual examination of the proportion of visits by each guild comparing visits to intact and defoliated mistletoes suggests that each guild responded differently to treatment, with the specialists visiting intact mistletoes only slight more than defoliated mistletoes; generalist frugivores visiting no defoliated mistletoes and the opportunists visiting the defoliated mistletoes notably less than the intact mistletoes (Figure 5).

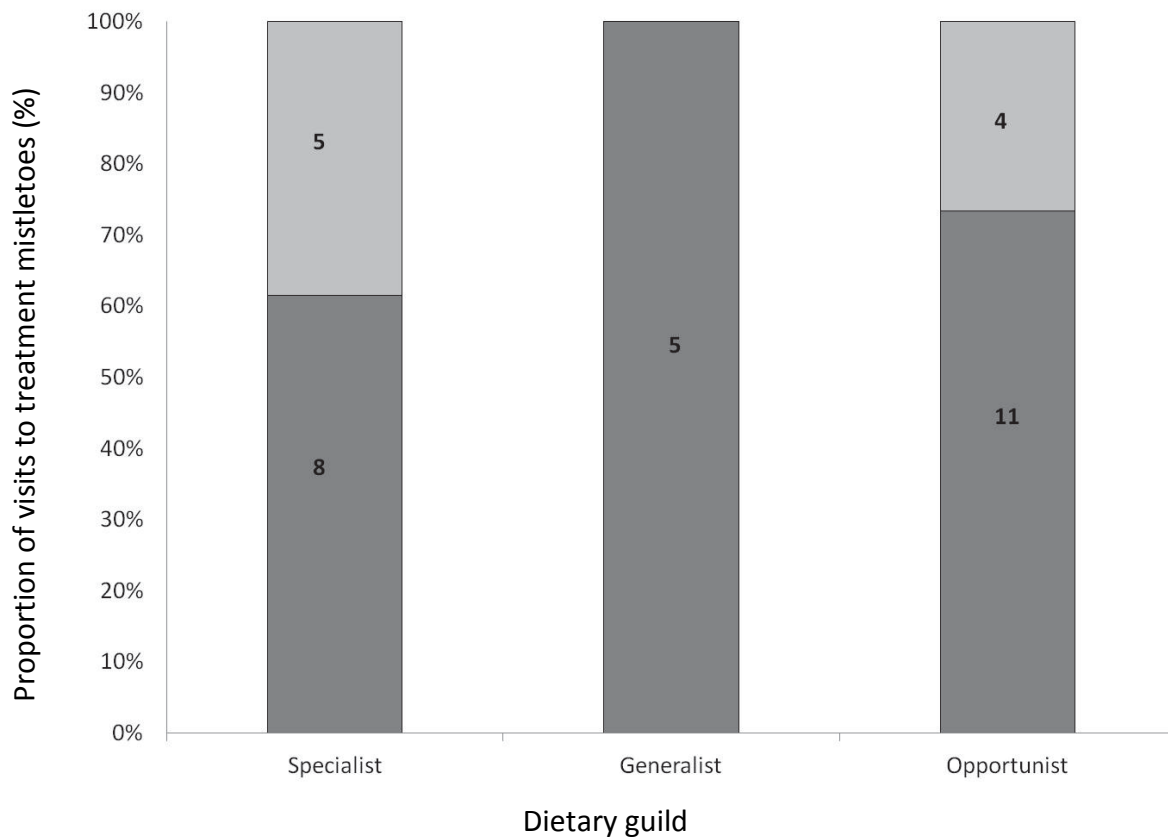


Figure 5. Proportional visits to intact (dark grey) and defoliated (light grey) mistletoe replicates, separated by dietary guild (mistletoe specialist, generalist frugivore and opportunist). Actual number of visits by each guild are indicated on the bars (n = 20 replicates).

2.4 Discussion

The visual role of leaves in attracting frugivores to fruiting plants is largely unknown. In this study I expected fewer visits to defoliated mistletoes than intact mistletoes due to the altered overall appearance of the mistletoes. I found that there were significantly fewer visits to defoliated mistletoes than those with leaves removed and fruits exposed. With more than double the number of visits to the intact mistletoes than the defoliated mistletoes, the birds do appear to be influenced by the visual appearance of the mistletoes. Defoliation may change the overall visual appearance e.g. shape, colour and density, of the mistletoes, as well as changing the visibility of the fruits by reducing the canopy density and exposing them. In spite of the fruits becoming more exposed through defoliation, the defoliated mistletoe may appear less healthy than intact mistletoes. Indeed, constant or repeated defoliation reduces plant reproductive fitness, which can be less attractive to foraging birds as the fruits may be fewer and smaller (van Lent *et al.* 2014). In this current study, all the mistletoes were defoliated once

but only some were visited on both days. This suggests that having previously been visually attractive the defoliated mistletoes were no longer considered so by the birds.

With mistletoe fruit having a different degree of importance for different fruit-eating birds, it is likely that not all species of bird perceive mistletoes in the same manner. The mistletoe specialist, Mistletoebird, relies on the fruits and nectar of mistletoes as its primary source of energy; therefore we might expect the Mistletoebird to have developed specialised strategies to find fruiting mistletoe. However, in the current study, this species did not appear to strongly discriminate between plants with leaves and those without. Although more observations are required for statistical support, this pattern suggests that the presence of foliage does not play a large role in its search patterns. The birds may have been visiting mistletoes that they remembered regardless of their visual condition. By contrast, both the generalist frugivores, consuming fruit along with nectar and invertebrates, and the opportunistic birds, consuming mostly invertebrates, did appear to show some preference for the intact mistletoes. Again, pending statistical support, I can only suggest that the presence of leaves acts as an attractant to these birds that search for other food sources within the canopy in addition to fruits. This experiment does not discriminate between the bird's use of a search image and learning to look in a particular place to find food (Lawrence and Allen 1983). The experiment in Chapter 3 investigates the potential that birds use spatial memory or a visual association between host species and mistletoe to locate fruiting mistletoes.

The natural partitioning of the dietary guilds is a reminder that all systems share a complexity that must be accounted for in experimental studies and analysis. The differences between foraging strategies of the specialist and generalists are probably intrinsically linked to their respective dependence on the fruits of the mistletoes as a nutritional resource, as are their seed dispersal patterns (Rawsthorne *et al.* 2011a, b). As such, their foraging strategies and cues used to inform their foraging warrant further investigation. For example, the role that the main host tree plays in informing the foraging birds of the probability of mistletoe being present in the habitat has not yet been investigated. This is the subject of my next chapter.

Chapter 3: 'Cut-and-paste' mistletoe relocation



Mistletoebird (*Dicaeum hirundinaceum*) perched in White Cypress Pine (*Callitris glaucophylla*).

3.1 Introduction

3.1.1 Foraging strategies

In order to recognise potential prey and assess an environment or patch for potential energy rewards, animals have developed many different searching methods, using multiple cues to inform their search behaviours. For example, different olfactory cues are used by elephants (Plotnik *et al.* 2014), albatrosses and fish (Nevitt *et al.* 2008, DeBose and Nevitt 2008) and macropods (Stutz *et al.* 2016). Other cues include chemical signatures (Clark 2004, Du *et al.* 2009), auditory (Shaw and Clayton 2014) and visual cues (Nawroth and van Borell 2015). The use of such cues can inform specialised searching strategies. For example, in Australia the Black-backed magpie (*Gymnorhina tibicen*) forage for larvae using their extremely sensitive hearing to detect the minute rustlings of the burrowing invertebrate (Floyd and Woodland 1981). Young magpies learn this technique by closely observing their parents and learning to associate the noises with food (Floyd and Woodland 1981). Three Spined Sticklebacks (*Gasterosteus aculeatus*), when placed in a foreign, experimental habitat, use featural cues e.g. body direction, to orientate themselves and to find food (Odling-Smee *et al.* 2008). The use of such cues may influence the formation of a search image (Reid 1991b).

Remembering where abundant food resources are is a valuable adaptive strategy, especially if that resource is predictable: temporally and spatially stable. For example, seed cachers or hoarders collect food and store it in a safe place for later retrieval (Vander Wall 2001). Arctic Foxes (*Alopex lagopus*) seasonally collect eggs of migratory geese and store them in hoards scattered throughout their territory for later retrieval and consumption (Samelius *et al.* 2007); Cape Ground Squirrels (*Xerus inauris*) hoard acorns from different oak species and retrieve them based on germination rates (Samson and Manser 2016a, b). The Corvid group of birds has some excellent cachers (Grodzinski and Clayton 2010), including Clark's Nutcrackers (*Nucifraga columbiana*) (Tomback 1982, Balda and Kamil 1992) and Western Scrub Jays (*Aphelocoma californica*) (Correia *et al.* 2007). Indeed, the cognitive abilities of Western Scrub Jays, combined with their spatial memory means that they can not only remember where their caches of food are hidden, but also notice when another jay watches them cache food and return later to re-cache the food elsewhere (Dally *et al.* 2006, Stulp *et al.* 2009).

Sometimes simply remembering where high quality food resources are may not be enough, particularly if the food is patchy, so a combination of strategies may be required. For example, Greenfinches (*Carduelis chloris*) can learn to associate colours with a particular location of food

rewards, and switch to spatial memory when that food is consistently found in the same location each time (Herborn *et al.* 2011). Trap lining is a foraging method used for resources that are stable in space but not time, as these can be depleted. To efficiently visit a group of flowers in a patch, individual bees and hummingbirds choose a path from flower to flower and feed from those flowers in sequence (Gill 1988, Thomson 1996, Comba 1999, Saleh and Chittka 2007). Some hummingbird species have extended this use of spatial memory to remember which flowers have already been visited in a given patch, only visiting flowers that have not already had their nectar depleted (Hurly and Healy 1996). Food resources that are spatially stable but temporally ephemeral, for example, seasonally, may include migrating prey (Arriaza *et al.* 2015), breeding invertebrates (Hunter and Dwyer 1998), masting nuts (Ostfield *et al.* 1996), nectar of mass-flowering plants or ripe fruits (Zimmerman *et al.* 2007). In this current study, Grey Mistletoe fruit, a food source that is spatially patchy, and seasonally predictable, was used to determine the searching strategies of birds foraging for fleshy fruits.

3.1.2 *Spatially aggregated, temporally variable mistletoes*

Mistletoes in the Loranthaceae family provide abundant nectar and fruits as inducements to attract birds that pollinate the mistletoes and spread their seeds (Calder and Bernhardt 1983, Watson 2001, 2011b). Some species of mistletoe offer fruits year-round, but have a peak fruiting season as well (Reid 1984). Many birds that are fully or partially frugivorous consume the fruits, but only a small number of them successfully disperse viable seeds (Murphy *et al.* 1993, Larson 1996, Aukema and Martínez del Rio 2002a, b, Okubamichael *et al.* 2011). These seed dispersers play a critical role in maintaining and spreading this keystone resource.

Mistletoes worldwide are generally known to grow in spatially aggregated patches in concert with the spatially aggregated seed dispersal patterns of their main dispersers (Overton 1994, Larson 1996, Aukema and Martínez del Rio 2002b, Aukema 2004, Green *et al.* 2009, Kavanagh and Burns 2012, Mellado and Zamora 2015). In Australia, the two species recognised as frequent mistletoe seed dispersers, the Mistletoebird (mistletoe specialist) and the Spiny-cheeked Honeyeater (generalist frugivore), each have slightly different dispersal patterns (Yan 1993, Ward and Paton 2007, Rawsthorne *et al.* 2011a, b, Wang *et al.* 2014). Although both have aggregated patterns of seed dispersal, commonly defecating in trees already hosting mistletoes, the generalist Spiny-cheeked Honeyeater is more likely to disperse seeds >700m away from the host tree, increasing the chances of spreading to a new location (Rawsthorne *et al.* 2011a). What is not known, is how the birds find the fruiting mistletoes to feed on. Results from Chapter 2 suggest that the generalist frugivores in particular may be influenced by the

overall visual appearance of the mistletoe. The use of other visual cues such as an abundance of fruits is still open to question. What search patterns do birds use to find the fruiting mistletoes and what visual characteristics of the mistletoes and/or host plants influence their foraging decisions? Further, to what extent does their reliance on mistletoe fruits or dietary guild influence the strategies employed by birds to find fruits? Answering these questions will help to clarify how the visual appearance and spatial location of food resources affects the variety of search strategies used by woodland birds seeking out mistletoe.

In the Riverina area of NSW, Grey Mistletoe (*Amyema quandang*) grows on only two hosts: Yarran (*Acacia homalophylla*) and Boree (*Acacia pendula*) (Milner 2014). In Binya State Forest, NSW, Yarran is the only host of Grey Mistletoe. Due to this host fidelity, I propose that birds searching for Grey Mistletoe fruits may use a number of different foraging strategies: a) they may use spatial memory to relocate previously visited fruiting mistletoes; b) they may associate the common host with fruiting mistletoe and forage preferentially in potential hosts in search of mistletoe fruits; c) they may use a search image of the mistletoe fruits/ overall plant to locate the mistletoes; or d) they may simply randomly encounter the mistletoes and fruits as they forage for a variety of food resources in the woodland canopy (e.g., invertebrates and nectar). To determine which strategies were being employed, I manipulated the location of fruiting Grey Mistletoes in Binya State Forest and recorded bird foraging visits to the mistletoes. I tested the concept of spatial memory by cutting and replacing a mistletoe plant in its original host tree (strategy a). I tested recognition via host-mistletoe association by removing a mistletoe plant and relocating it to another tree of the same host species (strategy b). Finally, I tested the concept of search image formation (strategy c) *versus* random encounter (strategy d) by removing a mistletoe plant from its host tree and relocating it to a tree of a different species – one that does not host Grey Mistletoe. I hypothesised that 1) birds would visit mistletoes cut and reattached in their original location more than mistletoes relocated to new trees; 2) for relocated mistletoes, birds would visit mistletoes placed in the same host species more than mistletoes placed in a non-host tree; 3) dietary breadth would influence which bird species visit mistletoes in host *versus* non-host trees i.e. mistletoe specialists would diverge from the generalist frugivores and opportunists; 4) birds of different dietary guilds would be influenced by different vegetation and mistletoe characteristics. If no visitation pattern to the different mistletoe locations were found, then I would expect this to be evidence of a random encounter strategy in use by all the birds.

3.2 Methods

3.2.1 Site and species description

This study was carried out in Binya State Forest, 20km east of Griffith, 34°13'S, 140°16'E, with data collected from November 2014–February 2015. During that period Griffith received 193.4 mm of rain and temperatures ranged from 14.2°C to 34.4°C (min-max) (Bureau of Meteorology 2016b, c, e, f). The tree canopy at the study site composed primarily of White Cypress Pine (*Callitris glaucophylla*, Cupressaceae), Yarran (*Acacia homalophylla*, Fabaceae) and Belah (*Casuarina cristata*, Casuarinaceae), with sub-dominant stands of Buloke (*Allocasuarina luehmannii*, Casuarinaceae) and Poplar Box (*Eucalyptus populnea*, Myrtaceae). Grey Mistletoe (*Amyema quandang*, Loranthaceae) is the principal mistletoe in the area, growing exclusively on Yarran (*Acacia homalophylla*) at the study site (Figure 1, 2.2.1).

Grey Mistletoe is a woody, aerial hemi-parasite with chalky-grey foliage and pale yellow fleshy fruits (Watson 2011b). Seed dispersal services are reliably provided by two species, the mistletoe specialist: Mistletoebird (*Dicaeum hirundinaceum*, Dicaeidae) and the generalist frugivore: Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*, Meliphagidae). Occasional seed dispersal services may be provided by the mistletoe specialist: Painted Honeyeater (*Grantiella picta*, Meliphagidae), and the generalist frugivores: Silveryeye (*Zosterops lateralis*, Timaliidae), Singing Honeyeater (*Lichenstomus virescens*, Meliphagidae) and Striped Honeyeater (*Plectorhyncha lanceolata*, Meliphagidae). Numerous species opportunistically consume the fruits and may rarely disperse the seeds (Barea 2008, Watson 2011b).

3.2.2 Experimental procedure

To determine how birds locate fruiting mistletoe plants I devised a novel experimental approach. To uncouple the influence of host identity, context and mistletoe location on bird visitation, mistletoes were assigned to different treatments. Whole plants of fruiting Grey Mistletoe (*Amyema quandang*) were cut from their hosts and affixed to one of three different types of host location: 1) *In-situ* (IS, Figure 7A), where mistletoe was cut and reattached in its original position, thereby keeping spatial location and host identity constant while controlling for the effects of cutting; 2) *Same Species* (SS, Figure 7B), where a mistletoe plant was cut from its original host, moved and attached to a different individual of the same species as the original host i.e., Yarran (*Acacia homalophylla*) but with few to no existing mistletoes, enabling the roles of spatial memory *versus* host-association to be distinguished; and 3) *Different Species* (DS, Figure 7C), where a mistletoe plant was cut from its original host tree, moved and

attached to an individual of a different tree species, White Cypress Pine (*Callitris glaucophylla*) (a conifer that does not act as a host for mistletoes in this region) to determine if there is any evidence for mistletoe fruit consumers using a search image of the mistletoe in isolation of its host setting, and if visiting birds in general (e.g. opportunists) randomly encounter the mistletoes regardless of which host they are attached to. Twenty mistletoe plants were selected for each of the three treatments, with each mistletoe plant considered a replicate.

3.2.2.1 Selection of plants and their relocation

Entire individual mistletoe plants were cut from their host using an arborist's handsaw and secateurs and moved to the selected new 'host' where they were reattached using black cable ties (Figure 6). Mistletoes in the *Same Species* and *Different Species* treatments were attached to an accessible branch with the cable ties as inconspicuously as possible, the mistletoe foliage hanging as naturally as possible. The extent to which foliage wilt after cutting affected attractiveness to foraging birds was tested by comparing relocated mistletoes with and without the ends sealed with glue. There was no significant difference in the number of visits to sealed or unsealed plants (one-way ANOVA: $F_{(1,10)} = 0.445, P > 0.05$). Therefore, as visitation data were collected on the day of cutting, to make the experimental procedure more time-efficient and commence observations as early as possible each day, I chose to not seal the cut end of the mistletoe.



Figure 6. Typical cable tie re-attachment, here shown for an *In-situ* mistletoe.

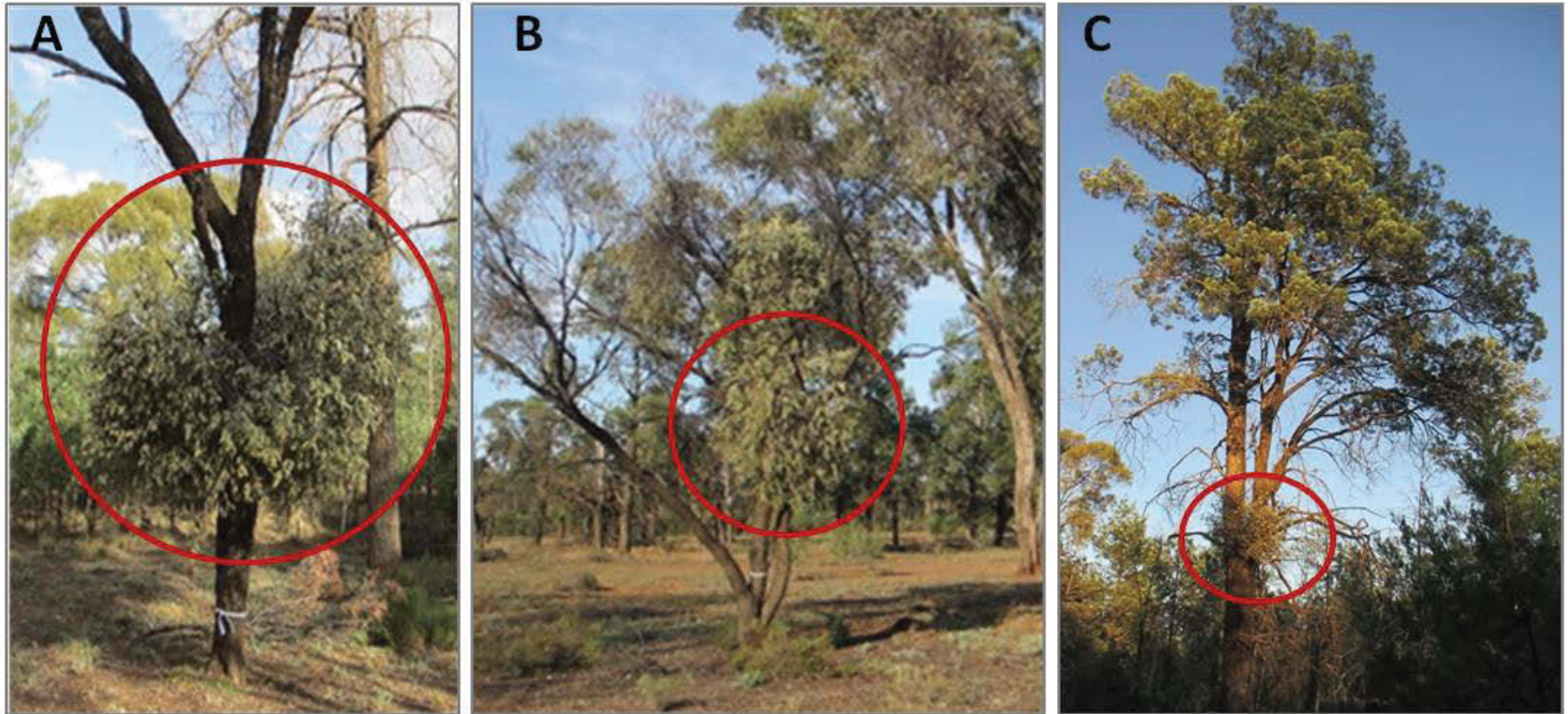


Figure 7. Grey Mistletoe (*Amyema quandang*) in Yarran (*Acacia homalophylla*). *In situ* mistletoe before being removal from the host and then reattached in its original location (A); *Same Species* mistletoe after being removed from its original host and relocated to another Yarran tree (B); *Different Species* mistletoe after being removed from its original host and relocated to a White Cypress tree (*Callitris glaucophylla*) (C). Experimentally relocated mistletoes circled.

Experimental mistletoes were randomly selected from potential hosts fulfilling certain criteria. Mistletoes were deemed suitable if accessible (up to 4 m by ladder), of adequate size to be attractive to birds (larger than ½ m diameter at widest point), yet not too big that I could not cut, lift or move the mistletoe, and to be fruiting. Mistletoes selected for the *Same Species* and *Different Species* treatments were also selected with relocation in mind – they were of a manoeuvrable size and with a single discrete haustorium. Both Yarran and White Cypress Pine trees used for *Same Species* and *Different Species* treatments were selected for accessibility by ladder (up to 4 m). In most cases, the Yarran hosts used for treatment were not heavily infested.

3.2.2.2 Observations

Replicate mistletoes were cut and relocated in the pre-dawn light with all bird observations beginning by 7:30 am and ending by 6:30 pm. Each day the observations were conducted during the times of peak foraging activity (Stanley and Lill 2002, Zuria *et al.* 2014). In the morning observations lasted 4 - 5 hours, beginning no later than 7:40 am and up to 3 hours in the evening ending by 6:30 pm (AEST). There was some variability in observation length due to inclement weather. The period of observation ranged from 5 hr 21 min to 7hr 45 min with four exceptions (4 hr 10 min, 4 hr 10 min, 4 hr 25 min and 4 hr 35bmin) which were shortened due to rain, and averaged 6 hr 30 min across the three treatments. *In-situ* treatment observations average 6 hr 30 min, *Same Species* observations average 6 hr 36 min and *Different Species* observations average 6 hr 30 min. One-way ANOVA and Levene's homogeneity of variances tests were conducted to account for variation in observation lengths among the three treatments. Observations were not significantly different across treatments (One way ANOVA, $F_{(2, 57)} = 0.055$, $P = 0.947$) and variances were homogenous (Levene's homogeneity of variances test, $F_{(2, 57)} = 1.802$, $P = 0.174$). Therefore, it was not considered necessary to further standardise the lengths of observations for this experiment.

Experimental mistletoes were watched from a distance of no less than 5m and up to 15 m depending on the visibility and density of vegetation, using 8 x 42 magnification binoculars. Four observers recorded visits for this experiment. The primary observer conducted 43 observations, a second observer, seven observations, a third, six observations and a fourth, four observations. As per 2.2.2, a visit was recorded if the bird perched in the experimental mistletoe; birds confining their movements to host foliage or flying through the mistletoe without landing were not counted as a visit. All visits were considered potential foraging episodes by the birds as many searched the fruits and foliage while they perched or hopped through the mistletoe. Visiting bird species were divided into three diet-based functional

groups following 2.2.2: 'mistletoe specialist', comprising solely the Mistletoebird; 'generalist frugivore', comprising the Spiny-cheeked Honeyeater, Singing Honeyeater, Striped Honeyeater and Silvereye; 'opportunist', which included all other birds, which are mainly insectivores and do not regularly consume fruit (Appendix 4, Table 15).

In addition to the observations recorded for the experimentally manipulated mistletoes, and to control for the effects of manipulation, observations were concurrently recorded visits elsewhere in the host tree and its un-manipulated host mistletoes as well to adjacent, non-experimental trees and their mistletoes (Figure 8). These non-experimental trees were defined as the mistletoe-hosting tree nearest to the host tree (nearest-host tree and nearest host mistletoes). Visits to the branches of the nearest host tree and pooled visits to any mistletoe hosted by that nearest host tree were recorded concurrently.

To contextualise the influence of each mistletoe treatment on bird behaviour and discern a possible suite of factors determining visitation, four vegetation characteristics that best represented the 'attractiveness' of the mistletoe and the host tree to potential visitors were measured for each replicate. The characteristics were the height of the host (m), host canopy cover (%), number of fruits on the relocated mistletoe, the number of pre-existing/un-manipulated mistletoes in the treatment host tree. These vegetation characteristics were included as covariates in the analyses below.

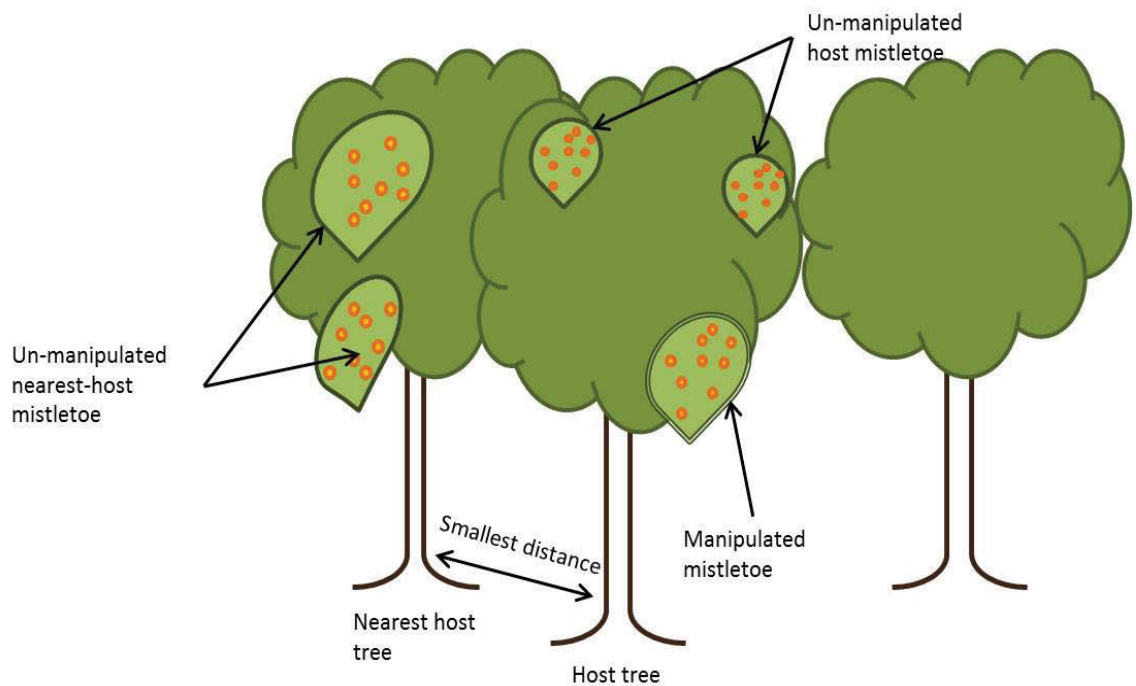


Figure 8. Diagrammatic representation of manipulated and un-manipulated mistletoes and host and nearest-host trees and their spatial relationship.

3.2.3 Statistical analysis

Generalized linear models (GzLMs) were used to quantify the effect of treatment on bird visitation using SPSS (IBM SPSS Statistics v22, 2013). As the data were zero inflated, the use of Poisson *versus* negative binomial distributions were compared during model building, the latter provided a better fit to the data (using 'lower is better' Akaike's Information Criterion, AIC) (Richards 2005, Symonds and Moussalli 2011); therefore, negative binomial models were used in GzLMs, unless otherwise specified. Parameter estimates obtained through the GzLMs were used to indicate the direction and strength of the significant main effects and interactions. First, to determine if the number of mistletoes on the treatment host tree may have played a role in influencing any differences in visitation to *In-situ versus Same Species* manipulated mistletoes, the number of visits to un-manipulated mistletoes on the host and nearest-host trees of these two treatments were compared. (*Different Species* host and nearest-host mistletoes were excluded from this analysis because White Cypress Pine does not host Grey Mistletoe). In this model, treatment (*In-situ/Same Species*) and un-manipulated mistletoes (host/nearest-host) were predictors and the number of visits to those mistletoes was the response. A further three sets of models were created to compare the number of visits to the manipulated mistletoes between treatments. The first aimed to detect any effects

of experimentally manipulating the mistletoes; it included the number of visits to the manipulated mistletoes as the response variable, treatment (*In-situ*, *Same Species* and *Different Species*) as the predictor variable and two covariates: the number of visits to host mistletoes (un-manipulated) and the number of visits to nearest-host mistletoes. Because the focus of this study was on bird's searching patterns and not on the difference of visitation between manipulated and un-manipulated mistletoes, the second model removed the covariates and focussed on the effects of treatment (predictor variable) on the number of visits to the manipulated mistletoes (response variable). The third set of models included habitat variables which were added to the second model (above) in every possible combination without interactions and the model with the lowest AIC score and Pearson's Chi Square value was selected.

The four vegetation characteristics representing the attractiveness of the mistletoe and the host tree to foraging birds were included as covariates: host height, host canopy cover, number of un-manipulated mistletoes on the host and number of fruits on the manipulated mistletoe. Before including these covariates, to check for potential bias in selecting host and mistletoe specimens for the study, I conducted one-way ANOVA's comparing differences in each variable across treatments. If any of the variables differed among treatments and could not be explained by species-based variation (e.g. inherent average variation in height between the two host species, Yarran and White Cypress Pine) then it would be evidence of experimenter bias in selecting treatment trees and the variable would have to be included in all subsequent models to account for potentially confounding interactions between treatment host trees. I expected significant differences between treatments in host height, host canopy cover and the number of mistletoes on the host tree. These differences are expected because of the inherent differences between the two host species in morphology and susceptibility to mistletoe infection (the commonly infected Yarran is shorter, with a less dense canopy than White Cypress Pine which is tall and dense and not susceptible to mistletoe infection). A significant difference is also expected between the *In-situ* and *Same Species* Yarran hosts in the number of mistletoes they host, due to the design of the experiment.

To determine whether the dietary breadth of birds influenced their search strategy to locate fruiting mistletoe, I included dietary functional guild (mistletoe specialist, generalist frugivore and opportunist) as a second predictor alongside treatment. Further analyses were then conducted separately for each functional group using a Poisson GzLM with a loglinear link. Models for the three guilds were created initially including all combinations of the four

selected variables as covariates and selecting the best fitting model as per the information theoretic approach as described above.

3.3 Results

3.3.1 Bird visitation

A total of 392 hours of observation was collected over 38 days across the three treatments (3 x 20 treatments = 60 person observation days). Of the 44 species of bird observed during the observation period, 15 species visited manipulated mistletoes (Appendix 4, Table 15). Across the three treatments, 26 mistletoes received visits. Most visits were by Mistletoebird, followed by Splendid Fairy Wren (*Malurus splendens*) and Spiny-cheeked Honeyeater. Visits ranged from one second to 17 minutes 30 seconds (for visit durations and over time see Appendix 2, Figures 19, 20).

3.3.2 Mistletoe and vegetation characteristics

As predicted, host height, host canopy cover and the number of pre-existing mistletoes on the host tree all differed significantly across the three treatments (Table 1). Tukey's post-hoc tests determined that the *Different Species* hosts significantly differed from the other two hosts with respect to host height and canopy cover, while the *In-situ* hosts had more un-manipulated mistletoes than *Same Species* hosts (Table 1). The number of fruits of the manipulated mistletoes did not significantly differ across treatments (Table 1).

Table 1. Results of one-way ANOVAs comparing vegetation characteristics among treatments (*In-situ*, IS; *Same Species*, SS; *Different Species*, DS) (n = 20 replicates for each of the three treatments). Significance is shown in bold.

Vegetation characteristic	Mean (IS, SS, DS)	Degrees of freedom (within, total)	F statistic	Significance (P - value)	Direction of significance
Host height (m)	5.3, 6.4, 8.9	2, 59	22.035	< 0.001	DS > IS, DS > SS
Host canopy cover (%)	44, 49, 64	2, 58	7.714	0.001	DS > IS, DS > SS
Number of un-manipulated mistletoes on the host tree	8, 3, 0	2, 59	15.685	< 0.001	IS > SS

Number of fruits on the manipulated mistletoes	42, 39, 34	2, 56	0.266	0.768	-
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3.3.3 Treatment effects

To account for the influence of mistletoe infestation on *In-situ versus Same Species* host trees, the number of visits to host and nearest-host un-manipulated mistletoes was compared between the *In-situ* and *Same Species* treatments. There was no significant difference between treatments in the number of visits to the un-manipulated mistletoes to host or nearest-host trees ($\chi^2 = 0.955$, $df = 1$, $P = 0.328$). Neither was there any difference in visitation to host *versus* nearest-host un-manipulated mistletoes ($\chi^2 = 0.955$, $df = 1$, $P = 0.328$). To further, account for the effects of experimental manipulation, the number of visits to un-manipulated host mistletoes and nearest-host mistletoes were initially included as covariates in the basic model comparing the number of visits to manipulated mistletoes across treatments. For this model, the *In-situ* treatment received significantly more visits than the *Same Species* and *Different Species* mistletoes (Table 2A). The number of visits to un-manipulated host- and nearest-host mistletoes did not significantly differ (Table 2A), suggesting that bird visitation to experimental trees was not affected by early morning human handling of mistletoe. Therefore, the next model did not include the number of visits to mistletoes other than the manipulated mistletoe of interest. When only treatment was included in the model, again there was a significant difference in the number of visits by birds to each of the mistletoe relocation treatments (Table 2B). The number of visits to *In-situ* mistletoes (45 visits) was significantly higher than the number of visits to either mistletoes relocated to hosts of the *Same Species* (11 visits) or hosts of *Different Species* (16 visits) (Table 2B). The most parsimonious model investigating the effects of the vegetation characteristics on visits to treatment mistletoes included host canopy cover and the number of fruits on the manipulated mistletoe. When these covariates were included in the model, the difference between the three treatments remained significant, but the covariates were not themselves significant (Table 2C).

Table 2. Generalised linear models exploring the influence of Grey Mistletoe relocation treatment on the number of bird visits to each treatment: *In-situ* (IS) cut from the original host tree and reattached exactly where it was; *Same Species* (SS), moved to another tree of the same species as the original host and *Different Species* (DS), moved to a species that never hosts Grey Mistletoe. Three models included different covariates: model A includes visits to un-manipulated host and nearest-host mistletoes (AIC = 179.449); model B does not include covariates (AIC = 176.027); model C is the most parsimonious of

models comparing different combinations of four habitat variables as covariates the final model included host canopy cover and the number of fruits on the manipulated mistletoes (AIC = 174.155), (see Appendix 2, Table 7 for other models). Models used a negative binomial error distribution with a log link. Significance is shown in bold.

Source of variation	Wald chi-square	Degrees of freedom	Main effects (P - value)	Direction of relationship
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A. Number of visits to the three treatments, including visits to un-manipulated mistletoes as covariates

Treatment	8.735	2	0.013	IS > SS; IS > DS; SS = DS
Host mistletoes	0.003	1	0.955	-
Nearest-host mistletoes	0.488	1	0.485	-

B. Number of visits to the three treatments

Treatment	11.246	2	0.004	IS > SS; IS > DS; SS = DS
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C. Number of visits to the three treatments including two vegetation characteristics as covariates

Treatment	9.086	2	0.011	IS > SS; IS > DS; SS = DS
Host canopy cover	1.759	1	0.185	-
Number of fruits	0.189	1	0.664	-

3.3.4 Dietary guilds, resource use and influences over foraging strategies

The specialist dietary guild included one species: Mistletoebird; the generalist frugivore guild included four species: Spiny-cheeked Honeyeater, Silvereye, Singing Honeyeater and Striped Honeyeater the opportunist guild included nine species: Splendid Fairy Wren, Inland Thornbill, Yellow Thornbill, Rufous Whistler, Australian (Mallee) Ringneck, Double-barred Finch, Grey Shrike-thrush, Noisy Miner and Red-capped Robin (see Appendix 4, Table 15, for scientific names and dietary guild designation).

The specialist Mistletoebird was recorded visiting manipulated mistletoes 19 times, with 19 visits by generalist frugivores and 34 by opportunists. Visitation to each treatment differed

significantly among the three guilds and there was a significant interaction between the diet guilds and the treatments (Table 3A). The generalists visited the *In-situ* mistletoes significantly more than they visited either *Same* or *Different Species* mistletoes (Table 3A).

Table 3. Generalised linear models exploring the influence of Grey Mistletoe relocation treatment on the number of bird visits by dietary guild to each treatment: *In-situ* (IS) cut from the original host tree and reattached exactly where it was, *Same Species* (SS), moved to another tree of the same species as the original host and *Different Species* (DS), moved to a species that never hosts Grey Mistletoe. Model A includes visits by the dietary guilds to treatment mistletoes as the response variable. Models B – D were the most parsimonious of models comparing the effects of habitat variables on individual dietary guilds (see Appendix 2, Tables 8 - 10 for non-parsimonious models). Model B used mistletoe specialist visits as the response variable; model C used generalist frugivore visits; and model D used opportunist guild visits. Models used a Poisson error distribution with a log-linear link, unless otherwise indicated. Significance is shown in bold.

Source of variation	Wald chi-square	Degrees of freedom	Main effects (P - value)	Interaction (P - value)	Direction of relationship
A. Number of visits to the three treatments by different dietary guilds (specialist, generalist and opportunist)*					
Dietary guild	6.469	2	0.039	-	Gen > Spec; Gen > Opp; Spec = Opp
Treatment	11.685	1	0.001	-	IS > SS; IS > DS; SS = DS
Treatment x dietary guild	8.301	1	-	0.016	Gen DS < Gen IS, SS
B. Specialist visits (response) to the three treatments (predictor) influenced by the number of fruits on the manipulated mistletoe (covariate)					
Treatment	2.743	2	0.254	-	-
Number of fruits	11.086	1	0.001	-	-
C. Generalist visits (response) to treatments (IS/SS) (predictor) influenced by the number of un-manipulated mistletoes on the host tree on the manipulated mistletoe (covariate)					
Treatment	13.764	1	< 0.001	-	IS > SS
Host canopy cover	5.883	1	0.015	-	-

Number of un-manipulated mistletoes on the host tree	9.679	1	0.002	-	-
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D. Opportunist visits (response) to the three treatments (predictor) influenced by the number of fruits on the manipulated mistletoe (covariate)

Treatment	9.719	2	0.008	-	IS > SS; IS > DS, SS = DS
Host height	4.203	1	0.040	-	-
Host canopy cover	5.212	1	0.022	-	-

* negative binomial with log link

The individual model examining the number of visits made by the mistletoe specialist to the different treatments (no covariates) was invalid (GzLM, Poisson log linear, Omnibus test $P = 0.135$) (Appendix 2, Figure 21A). When the number of fruits on the manipulated mistletoe was added as a covariate, specialist visits did not significantly differ among treatments; however, they were positively influenced by the number of fruits ($P = 0.001$; Table 3B). The number of fruits on manipulated mistletoes was not significantly different across treatments (one-way ANOVA: $F_{(2, 56)} = 0.266$, $P = 0.768$; Table 1). The final individual model for generalist frugivores excluded the *Different Species* treatment as no visits by generalists were recorded at those mistletoes (Table 3B; Appendix 2, Figure 21B). The best model for the generalist visits included host canopy cover and the number of un-manipulated mistletoes on the host tree as covariates. Generalist frugivores visited *In-situ* mistletoes significantly more than they visited *Same Species* mistletoes (Table 3C; Appendix 2, Figure 21B). The percentage of host canopy cover and the number of un-manipulated mistletoes on the host tree significantly influenced the visiting generalist frugivores (Table 3C). The most parsimonious model for the opportunist guild included host height and host canopy cover as covariates (Table 3D). The opportunists visited *In-situ* mistletoes significantly more than they visited *Same Species* or *Different Species* mistletoes and were significantly influenced by the height and canopy cover of the host tree (Table 3D; Appendix 2, Figure 21C).

3.4 Discussion

In this study, I sought to understand how frugivores find fruiting mistletoes and how their relative dependence on mistletoe fruits influences their foraging strategies. I moved fruiting

mistletoes to different locations – host and non-host trees – representing surroundings increasingly foreign to the original mistletoe location. I made a number of predictions about bird visitation to each of these manipulated mistletoes. First, I expected that the birds would already know where fruitful mistletoes were located in the habitat and that they would use spatial memory to revisit these known mistletoes. This search strategy would be supported if mistletoes that were cut and reattached *in-situ* received more visits than mistletoes that I moved to different trees. Indeed, I found that *In-situ* mistletoes received significantly more visits than the other treatment mistletoes. Second, if the visiting birds used a visual association between the common host (Yarran) and the common mistletoe (Grey Mistletoe) to help them search for fruiting mistletoes, I would expect a preference for *Same Species over Different Species* relocated mistletoes. This expectation was not supported by the findings, which showed no difference in visitation between these two tree species. Third, because of their differing reliance on mistletoe fruits, I expected birds of the different dietary guilds to vary in their preference for a given manipulated mistletoe treatment. This expectation was supported by the findings. Finally, based on the differences in food consumption among the dietary guilds e.g. the reliance on fruits *versus* invertebrates and where these food sources may be found, I expected different vegetation characteristics to influence the dietary guilds differently. Again this expectation was supported by the results, which showed that the mistletoe specialist, generalist frugivores and opportunists were each influenced by different characteristics. Below I discuss these claims in detail and outline some of the implications of these findings.

3.4.1 Foraging strategies

When a food source is hard to find it may be worth remembering where it is located to reduce searching time in future foraging bouts; this learning behaviour is seen in many species (Brodin 2010). In the current study, there were significantly more visits to *In-situ* mistletoes than to mistletoes moved to novel locations. Interestingly, while the number of visits differed among the treatment mistletoes, the number of mistletoes visited, irrespective of how many times each was visited, did not differ. One explanation for the higher number of visits to *In-situ* mistletoes is that birds repeatedly visited ‘known’ mistletoes. This significant preference for *In-situ* mistletoes may be evidence of that the birds already knew where this fruit source was and re-visited it using spatial memory to guide their search (search strategy a).

The *Same Species* treatment was designed to test for a general association by the forager between a fruiting mistletoe species and a particular species of tree that hosts that mistletoe species rather than the exact location of a known food source in a particular tree (search

strategy b). If birds formed this kind of association for a particular host species hosting a certain species of mistletoe (in this case, Yarran hosting Grey Mistletoe) I would expect to see a higher visitation rate to mistletoes relocated to new Yarran trees than to those placed in non-hosting species (White Cypress Pine). Of the mistletoes moved to new trees, birds did not preferentially visit those in new Yarran trees over those in White Cypress Pine. Therefore, the visiting frugivores did not appear to form a general association between fruiting mistletoes and their common host species at this scale, at least not at this local patch scale, where the preference for mistletoes in a known host location was apparently stronger. However, the association between common host species and fruiting mistletoes may be more relevant at a landscape level; for example, to detect patches of mistletoes.

3.4.2 Foraging strategies influenced by dietary guild

The dietary guilds in this study differed significantly in the number of visits to the three treatments. Generalists differed significantly from the specialists and opportunists, in visiting the *In-situ* mistletoes more than the *Same* or *Different Species* (Table 3A). This discrepancy in visitation preference supports the idea that bird's dietary dependence on fruits influences their search patterns. Surprisingly, it was not the case that specialists showed a preference for *In-situ* mistletoes. Although inconclusive, the specialists were not strongly influenced by the overall appearance of the mistletoes (section 2.3.1). Coupled with their apparent lack of visitation preference for the common host species (Yarran), it seems that these mistletoe specialists seek out mistletoes wherever they may be in a known patch irrespective of visual mistletoe health or location in a given tree. The generalists and opportunists preferred to visit *In-situ* mistletoes, even though the opportunists — generally not fruit consumers — were expected to visit opportunistically, by random encounter (search strategy d). Generalist frugivores, who by their broader diet, are believed to have more generalised foraging strategies for fruit-finding and therefore more generalised seed dispersal patterns (Reid 1990), demonstrated the strongest visitation pattern. The generalists were influenced by the number of mistletoes on the host trees; hence this vegetation characteristic being included in the best model for generalist visitation (Table 3C). *In-situ* treatment host trees, hosting a higher number of mistletoes than *Same Species* host trees may have appeared more attractive to the visiting birds, prompting more visits to the manipulated mistletoes. This raises the question of whether generalists have a range of specialised foraging strategies that they use for their various preferred food resources. For example, Spiny-cheeked Honeyeaters feed on invertebrates, nectar and fruits (Pizzey 1997). Mistletoe is only a primary part of their diet when it is seasonally abundant and even then sudden abundance of invertebrates may divert

their foraging efforts from fruits to hawking for insects after rain (Reid 1990). Therefore, the attraction of mistletoe, while being based primarily on the fruits and flowers, may also lie in the abundance of invertebrates in the foliage surrounding or leaf litter beneath the mistletoe (Burns *et al.* 2011).

3.4.3 *Vegetation characteristics influencing foraging strategies*

Here I investigated habitat characteristics on the basis of potential attractiveness to the foraging birds and found that their explanatory power varied among different bird guild groupings. The number of fruits on the manipulated mistletoes positively influenced the overall visitation, of the specialists in particular, as may be expected by their reliance on the mistletoe fruits as a large part of their diet (Watson and Rawsthorne 2013). As the number of fruits was consistent across treatments, and the Mistletoebird did not show a significant visitation pattern, this specialist may have been using the number of fruits as a foraging cue, directing their visits to mistletoes with more fruit, as other frugivores do (Foster 1990, Blendinger *et al.* 2008, Blendinger and Villegas 2011, Albrecht *et al.* 2012).

The bias of the generalists drove the trend for the pattern of visitation to different mistletoe relocation treatments in this experiment. Along with treatment, generalists were influenced by the number of un-manipulated mistletoes on the host and the host canopy cover, preferring more mistletoes and less dense canopy cover. These influences suggest that the visual abundance of mistletoes and their context in the host canopy may provide fine-tuned cues to these frugivorous birds, potentially using spatial memory in combination with the visual cues to find fruitful mistletoes (2.3.1) (Barkley and Jacobs 1998). Mistletoe-consuming birds often show a preference for trees that already host mistletoes, not only preferring to forage in those mistletoes, but also perch and deposit seeds in the host tree (Aukema and Martínez del Rio 2002b).

In a continuous forest habitat with a range of canopy trees, the open canopy of the Yarran trees may present less of a visual barrier for the foraging birds than the comparatively dense canopy of the White Cypress Pine trees. Indeed, the percentage of host canopy cover influenced the number of visits to the manipulated mistletoes, by the generalists and opportunists in particular. Both guilds preferred to visit the *In-situ* manipulated mistletoes in the Yarran species with less dense canopy cover than White Cypress Pine. The higher visitation to Yarran could be reflective of the shape of the canopy, which is open and spreading in Yarran, closed and vertical in White Cypress Pine. Alternatively, it also may reflect the variety of resources to be found in the respective canopies, as both the opportunists and generalists

include invertebrates in their diet. I expected the opportunists to favour a random search strategy when foraging for/in mistletoe clumps as the fruits of the mistletoe are unlikely to be the target of their foraging, but rather, the invertebrates associated with the mistletoes and host canopy (Burns *et al.* 2011, 2015). Opportunistic foragers may feed on a wide variety of grains, fruits, nectar and invertebrates, year round or seasonally when there is either a glut or their preferred foods are unavailable (for example, seasonal specialisation: Vorel *et al.* 2015 and resource waves: Armstrong *et al.* 2016). Therefore, they may use different cues or strategies from the specialists to recognise high quality patches and food resources (Berger-Tal *et al.* 2014). Only mistletoe fruits were investigated in this study, but additional resources should form part of any future study investigating mistletoe use or fruiting plant use by different foraging guilds, as they may act as incidental dispersers (Barea 2008, Watson 2011b), resource defenders (Male and Roberts 2002) or attractants (see anti-pollinator hypothesis Gentry 1978).

3.4.4 *Implications for the seed dispersal of mistletoe*

In a changing environment, where humans influence, disrupt and destroy habitat, investigating interactions among species and how they are created or maintained is important in helping us to not only understand, but also predict how these interactions will change over time. Given the key role of seed dispersers in maintaining vegetation populations in increasingly fragmented habitats, understanding the interaction between fruits and frugivores is particularly important. My findings of an overall preference by mistletoe-eating birds for unmoved mistletoes over those in novel locations helps to further explain observed patterns of aggregated seed dispersal and associated distribution of mistletoe (Ward and Paton 2007, Rawsthorne *et al.* 2011b). It suggests that the birds return to mistletoes where they found abundant or good quality fruits and therefore create an aggregated seed dispersal pattern centred around those known, revisited mistletoes. The use of visual cues such as the number of mistletoes on a host or the number of fruits on an individual mistletoe plant also correlates with the aggregated seed dispersal patterns for both mistletoes and other frugivore dispersed fruiting trees (Rodriguez-Perez *et al.* 2014, Chatterjee and Basu 2015, Viswanathan *et al.* 2015). Dispersal beyond infected hosts may occur via incidental perching in suitable, susceptible trees while searching or travelling between mistletoe patches (Reid 1984, Sasal and Morales 2013). How birds find patches of mistletoe at the landscape scale and create their spatial memories of individual mistletoes, is yet unknown.

Investigating the use of spatial memory in frugivores, especially the conditions under which it is formed and how long it lasts may be important in helping to predict how the interaction may change, not only for mistletoe-eating birds but also for other frugivores. The search strategies explored in this chapter suggest that mistletoe specialist and generalist frugivores use different strategies to find fruiting mistletoes in a known patch of continuous forest. The next chapter explores the potential of these strategies to differ when the mistletoe patch is in a fragmented habitat, with different environmental conditions.

**Chapter 4: Habitat comparison: Continuous forest *versus* roadside
vegetation**



Willie Wagtail (*Rhipidura leucophrys*) perched amongst the Boree (*Acacia pendula*).

4.1 Introduction

Continuous forest or patches of remnant forest are used to investigate the 'natural' processes and interactions of species (for example, Major *et al.* 2001, Seddon *et al.* 2003, Vesik *et al.* 2008). As undisturbed habitats, the behaviour of organisms observed there can be used as a benchmark against which to compare behaviour in fragmented and/or disturbed habitats and guide restoration efforts (Major *et al.* 2001, Seddon *et al.* 2003, Algar *et al.* 2005, Cunningham *et al.* 2008). These behaviours may also be used to judge the effectiveness of fragmented or lesser quality patches in provision of habitat (Major *et al.* 2001). In our rapidly changing environment, habitats are being destroyed, changed and created, with organisms adapting or declining in response. Around the world the need to transport goods and services has driven the increase in roads, creating a lacework of habitat patches, while broad scale agriculture has further reduced once continuous undisturbed habitat (van der Ree *et al.* 2015a). The construction, use and maintenance of roads can have mixed impacts, such as birds and reptiles using warm roads as sources for efficient thermoregulation, offset by the increased risk of wildlife-vehicle collisions (Camacho 2013, Kovar *et al.* 2014). Roads can have negative impacts such as reducing avian community species richness with increasing proximity to road edges (Kociolek *et al.* 2011 and references within), mortality via vehicle-wildlife collisions (Jack *et al.* 2015) and reductions in effective song communication due to high traffic noise affecting both species in residence and transient, breeding populations (Reijnen and Foppen 2006, Parris and Schneider 2009, Summers *et al.* 2011). Roadside habitat is often associated with increased water and nutrients from runoff, which can support vegetative growth and corridors of dispersal, especially for early succession plants or weedy species (Vakhlamova *et al.* 2016). Importantly, however, patches of remnant vegetation left alongside roads, particularly in agricultural areas can provide a sanctuary or a corridor of much needed habitat (Huijser and Clevenger 2006, Reijen and Foppen 2006, Kociolek *et al.* 2011, Morelli *et al.* 2015). These benefits are especially critical in largely agricultural or urban areas, where roadside vegetation patches can sometimes make up a large proportion of the habitat available (van der Ree 2002, van der Ree *et al.* 2015a).

There is a growing body of work investigating the effects of habitat fragmentation and edge effects on plant and animal species, but fewer studies relate to community level responses. The dynamics of seed dispersal by wind, water or animal (Wilkinson 1997), access of resources such as food e.g. carcasses (Olson *et al.* 2016), perches (Polak 2014), nest sites (Bergin *et al.* 2000, Reijnen and Foppen 2006), population dynamics and genetic flow (Garrido-Garduño *et al.* 2016), animal dispersal (van der Ree *et al.* 2010), potential of habitat corridors (Hall *et al.*

2016), patch linkages (Damschen *et al.* 2008) and species adaptations (Bowman *et al.* 2008, Willi and Hoffmann 2012, Cerame *et al.* 2014) are all under investigation. However, while many studies focus on just one aspect of habitat fragmentation or the edge effects on species, seldom does research consider the interactions among species and the flow on effects of those interactions in changing or altered habitats (but see Tewksbury *et al.* 2002; Damschen *et al.* 2014).

Many bird species in roadside habitats, linear patches or disturbed fragments present altered behaviours to those in undisturbed or continuous habitat patches. Forest edges, such as the verge to cropland, have been documented to have different bird community assemblages, influenced by the open canopy and neighbouring land-use (Montague-Drake *et al.* 2009). For example, Noisy miners (*Manorina melanocephala*) are known to dominate forest edges and can be particularly aggressive towards small passerines that cross through those edges (Grey *et al.* 1998, Montague-Drake *et al.* 2011). As forest edges are increased through fragmentation the assemblage of small passerines in those forests may be concurrently reduced as they are chased out by Noisy miners (Major *et al.* 2001, Montague-Drake *et al.* 2011). One avenue of research receiving scant attention is the foraging behaviour of birds in linear roadside patches compared to continuous forest and their possible influence on seed dispersal. Due to their high mobility, certain birds may be regular users of corridor patches and act as plant species dispersers for plants between patches (Levey *et al.* 2005, Damschen *et al.* 2008). The focus of the current work is to compare the behaviour of frugivorous birds in continuous versus roadside patches as they search for the fruits of mistletoe plants.

Hemiparasitic mistletoes are frequently seen in high abundance along roadsides in Australia (Lamont and Southall 1982, Norton and Stafford Smith 1999, Downey 2004). These plants are considered keystone resources in woodland habitats due to the extensive nutrient cycling benefits and secondary interactions with birds (Watson 2001, 2015; Burns *et al.* 2011, Watson and Herring 2012). The presence of mistletoe in roadside patches of vegetation may be an indicator of the quality of the habitat because this presence is only possible if seed dispersers have visited those trees (Watson 2011b). Suggested explanations for the abundance of mistletoes in roadside vegetation have included increased access to water and the accumulation of nutrients from road runoff, availability of light, lack of competing herbivores or seed predators and a general lack of pathogens due to patch isolation (Norton and Stafford Smith 1999). These suggestions concur with findings that mistletoes prefer hosts that have adequate access to soil moisture, light and soil nutrients (Ehleringer *et al.* 1985, Norton and Stafford Smith 1999). However, mistletoe distribution is constrained not only by the

requirement of a suitable host but also by the need to be dispersed to that suitable host. For example, the interacting roles of seed disperser and host have been examined at three levels of habitat disturbance for the South American mistletoe Quintral (*Tristerix corymbosus*). Movement limitations of the key seed disperser of Quintral (Rodríguez-Cabal *et al.* 2007) combined with the preferred growing conditions of the host species (Fontúrbel *et al.* 2017) create different aggregated distributions of the mistletoe across undisturbed forest, transformed habitat and fragmented forest patches (Rodríguez-Cabal *et al.* 2007, Fontúrbel *et al.* 2015, 2017). The interactions between mistletoe, seed disperser, hosts and habitat types are complex and require careful study to discern underlying drivers of change and adaptation. The abundance of mistletoes in roadside habitats may be the result of an interaction between suitable host habitat and seed dispersers creating an aggregated mistletoe distribution. However, this interaction has not yet been investigated.

There are still many questions to be answered about the distribution of mistletoes in roadside vegetation and influences of seed dispersal on that distribution. Despite a few studies mentioning higher abundance of mistletoe on roadsides (Lamont and Southall 1982, Norton and Stafford Smith 1999), there have been no comprehensive surveys to confirm how widespread and consistent this pattern may be or what mechanisms underlie it. Norton and Stafford Smith (1999) suggest that growing conditions (e.g. water availability and ample sunlight) are more favourable in roadside habitats. However, we do not know if this translates into a better rate of reproductive success with a higher production of flowers to attract pollinators, or higher fruit set attracting more dispersers. Nor do we know if these factors translate to greater seed dispersal along roadsides. Likewise, there have been no studies to date that investigate the presence and abundance of birds in these mistletoe-rich roadside patches or their seed dispersal patterns. Seed dispersal by frugivorous birds is one of two main limiters on the distribution of mistletoe. We do not yet know if seed dispersal is higher in roadside habitats or if the chances of a dispersed seed germinating and surviving to maturity are higher in those roadside habitats. Answering the questions above can help us to predict how mistletoe-bird interactions may alter in response to habitat fragmentation, at what scale they respond and can suggest possible avenues to reduce the negative effects of habitat fragmentation by improving connectivity. Comparing visitation and vegetation characteristics across habitat types (roadside and continuous forest) is the first step in elucidating some of the potential influences on bird visitors and reasons underlying the increased abundance of mistletoes along roadsides, including the role of those birds as potential seed dispersers. In this chapter, I compare the abundances of birds visiting fruiting mistletoe in a continuous

patch of forest with that in remnant roadside patches of vegetation. Using methods and data modified from Chapter 3, this study was designed to compare bird visitation not only at the treatment level, but also between habitat types. I investigated whether or not there is a higher abundance of Grey Mistletoe (*Amyema quandang*) hosted by Boree (*Acacia pendula*) in roadside remnant vegetation compared to Grey Mistletoe hosted by Yarran (*Acacia homalophylla*) in a continuous patch of forest (Binya State Forest). If there was a higher abundance of Grey Mistletoe in the roadside vegetation I would expect a higher abundance of visiting frugivorous birds (Sargent 1990). Based on the spatial memory searching behaviour indicated in Chapter 3, do birds visiting the roadside vegetation utilise the same strategy as they do in continuous forest? That is, will the birds visit more *In-situ* mistletoes than moved *Same Species* mistletoes? Additionally, what variables within the habitat influence the searching behaviours of mistletoe visiting birds in roadside vegetation as compared to continuous forest?

4.2 Methods

4.2.1 Site and species description

In the Riverina area of NSW, Grey Mistletoe (*Amyema quandang*, Loranthaceae) parasitises a limited number of hosts (see 2.2.1). Yarran (*Acacia homalophylla*, Mimosaceae) and Boree (*A. pendula*, Mimosaceae) are the dominant hosts in this area. The natural vegetation of the region is open grassy woodland, where various *Eucalyptus* species exist alongside *Callitris* and *Acacia* species, with Yarran and Boree being relatively common over-storey components. Pollination and seed dispersal services are provided predominantly by mistletoe specialists and generalist frugivores (see 2.2.1). Two habitat types were compared: continuous woodland (the study site for Chapters 2 and 3) and relictual roadside stands of host trees (Figure 9).

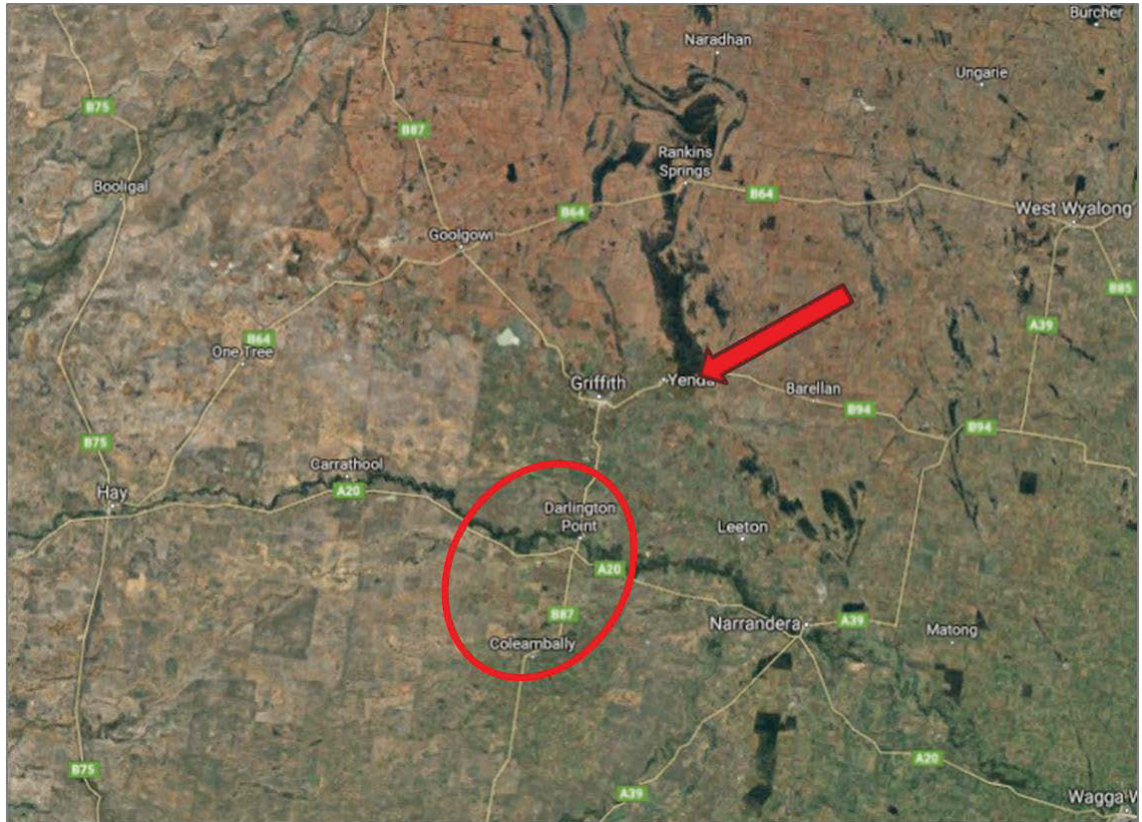


Figure 9. Aerial photo of the Riverina area with Binya State forest indicated by an arrow and the roadside site indicated by a circle. Note the lack of large connected patches of native vegetation (Google maps 2016).

Continuous woodland

The continuous woodland is represented by Binya State Forest, 20 km east of Griffith, 34°13'S, 140°16'E (Figure 10), where Yarran hosts Grey Mistletoe (Figure 1, 11). Continuous woodland forest in Binya State Forest (see Chapter 2 for a full site description) had four species of mistletoe including Grey Mistletoe, Box mistletoe (*Amyema miquelii*, Loranthaceae), Buloke Mistletoes (*Amyema linophylla*, Loranthaceae) and Harlequin Mistletoe (*Lysiana exocarpi*, Loranthaceae). Box, Buloke and Harlequin mistletoes were limited to a just a few individuals on a few host trees scattered throughout Binya State Forest, none were in fruit at the same time as Grey Mistletoe, which was the most common. Data for the continuous woodland were those described in Chapter 3, collected from November 2014 – February 2015. During that period, the Griffith region received 193.4 mm of rain and temperatures ranged between 17.3 – 32.4 °C (min – max) (Bureau of Meteorology 2016b, c, e, f). Mistletoes used in this experiment were located on hosts that were a minimum of 50 m from the main roads bordering Binya State Forest (Burley Griffin Way B94 and Whitton Stock Route Road). Host

trees were commonly found near interior unsealed 4WD roads and small clearings (Figure 11). No vehicles passed the experimental trees during the observations in the 37 day sampling period.



Figure 10. Map of Binya State Forest, with a circle indicating the southern half of the state forest where Yarran (*Acacia homalophylla*) hosts Grey Mistletoe (*Amyema quandang*) (Google maps, 2016).

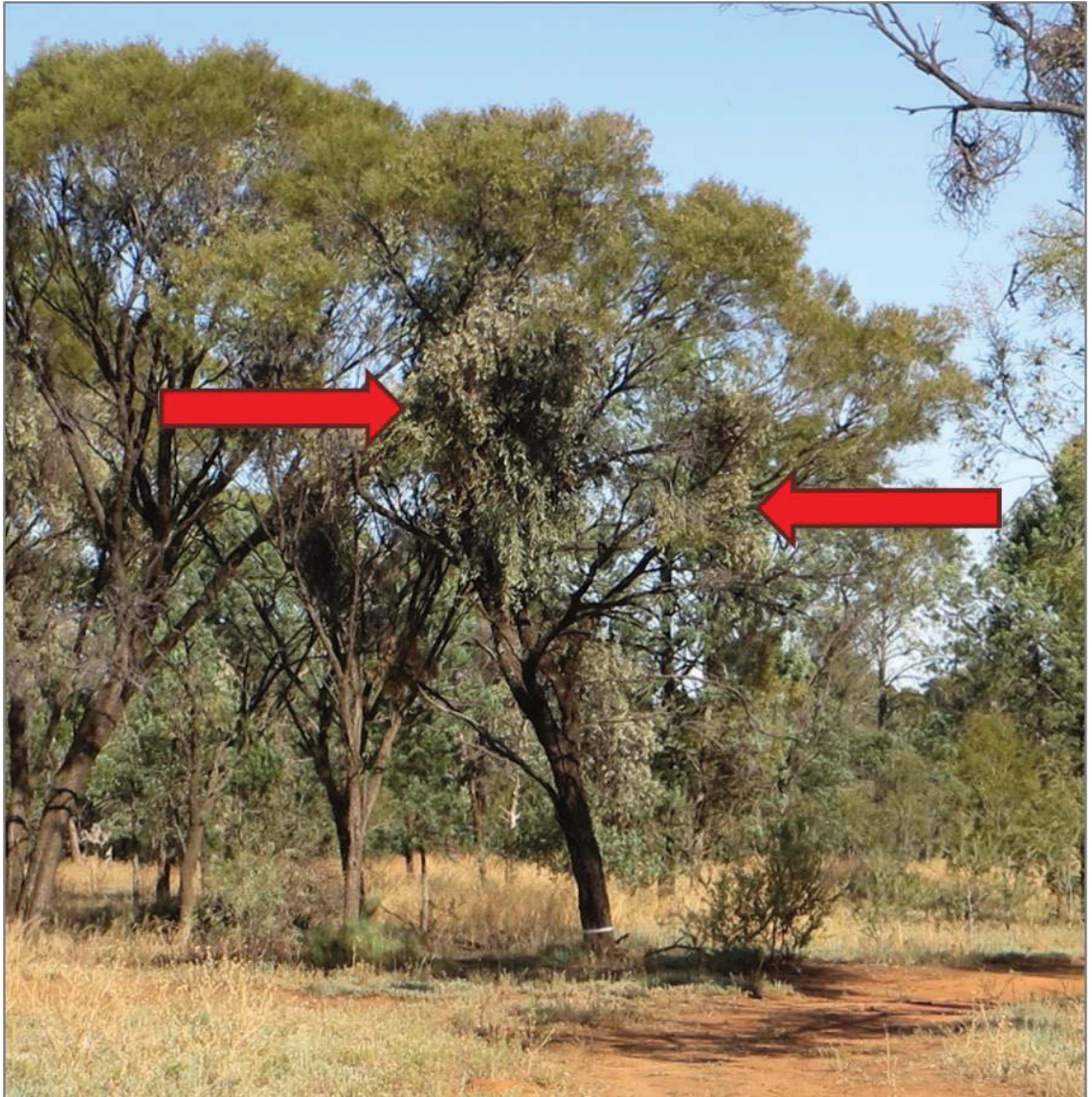


Figure 11. Yarran (*Acacia homalophylla*) hosting Grey Mistletoe (*Amyema quandang*) in Binya State Forest (mistletoes indicated by arrows). A typical narrow access track is visible running through the bottom right corner of the photo.

Roadside patches

The verges of four roads in the Riverina area were identified as having remnants of Boree woodland hosting fruiting Grey Mistletoe (Figure 12). The dominant mistletoe species in these roadside patches was Grey Mistletoe, with the occasional Fleshy Mistletoe (*Amyema mirabilosa*). Grey Mistletoe was hosted by Boree (*Acacia pendula*), which was the dominant tree in the roadside making up most of the canopy. The four roads were: Murrumbidgee River Road, Kook Road, Erclidoune Road and Four Corners/Southern Boundary Road, south of Griffith. Patches of roadside vegetation along each of the four roads were selected for this

experiment if there was fruiting Grey Mistletoe present. Twenty replicate mistletoes were used for each of the two treatments (section 4.2.2) spread across the four roadside patches. Replicate mistletoes were chosen if they were ten or more meters from another replicate and there was sufficient tree cover for the observers to be several meters from the mistletoe without being conspicuous in the habitat. In total, 24 experimental mistletoes were located along Four Corners Road/ South Boundary Road, four along Kook road, and six each along Erclidoune Road and Murrumbidgee River road (Figure 13). Data for the roadside site sites were collected during January 2016. During that summer of roadside sampling, Griffith received 116.2 mm of rain and during January temperatures ranged 18.8 – 32.5 °C (Bureau of Meteorology 2016d, e, f).



Figure 12. Boree (*Acacia pendula*) hosting Grey mistletoe (*Amyema quandang*), mistletoes indicated by arrows.

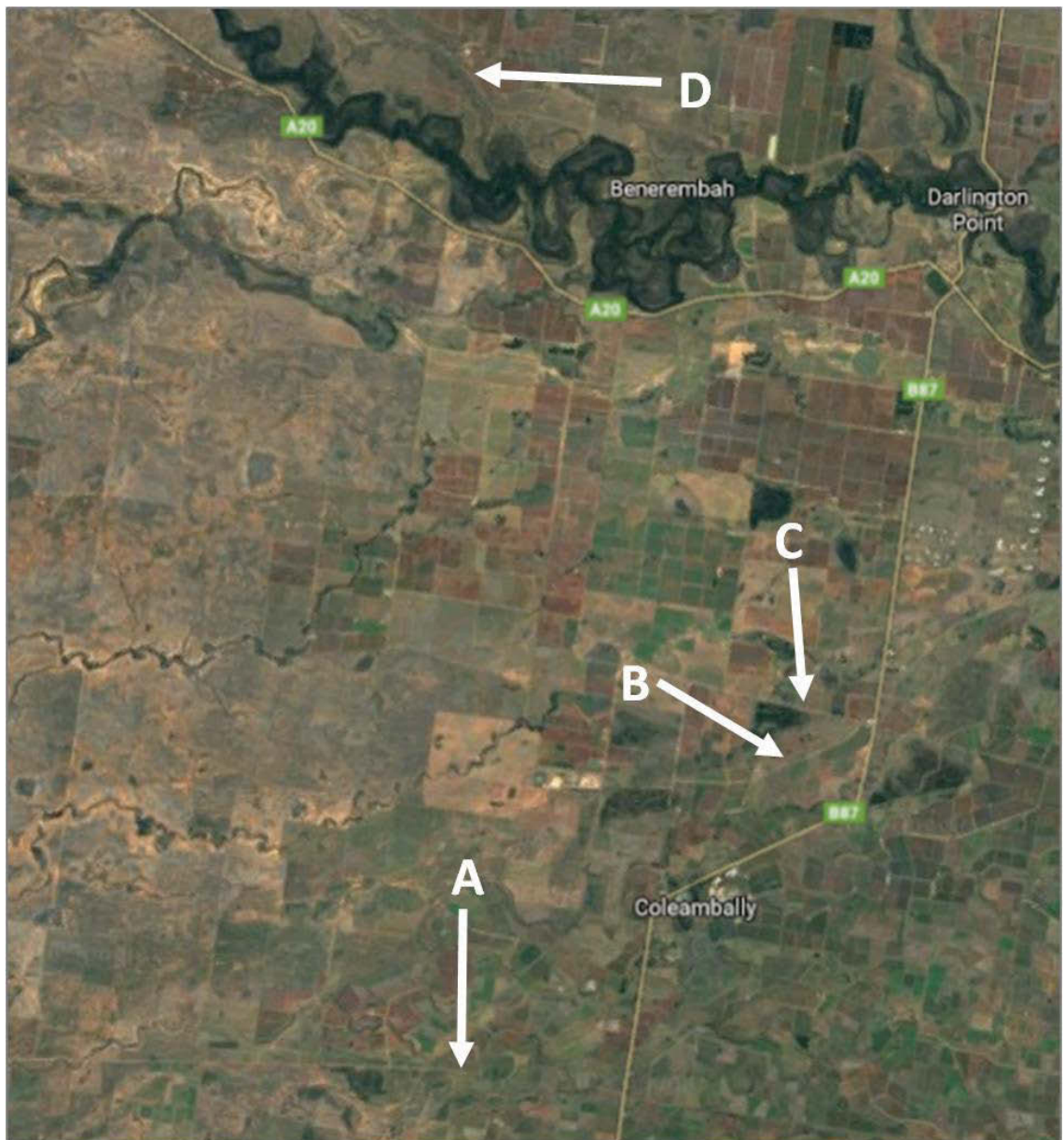


Figure 13. Map of roadside sub-sites in the Riverina area south of Griffith, NSW. (A) Four Corners Road, (B) Kook Road, (C) Erclidoune Road and (D) Murrumbidgee River Road (Google maps, 2016).

4.2.2 *Experimental procedure*

To determine the extent to which foraging patterns varied between continuous forest *versus* roadside habitats, I conducted a relocation experiment in the roadside habitat using methods modified from Chapter 3. I then standardized the data from the continuous forest (section 3.3) and compared these with the data collected from the roadside vegetation. Visits to experimental mistletoes were compared across treatments within each habitat type and across habitat types. In the absence of non-host trees, only two treatments were observed at

roadside sites, while corresponding data (visitation data to *In-situ* and *Same Species* manipulated mistletoes) were used from Chapter 3.

Following section 3.2.2 the *In-situ* and *Same Species* treatments were aimed at uncoupling the influence of host identity and mistletoe location on bird visitation and hence the likelihood of fruit removal and subsequent seed dispersal. Visits to *In-situ* mistletoes may indicate the use of spatial memory by the visiting birds as the mistletoe has simply been cut and replaced in its original location (note that cutting and replacing controls for the effect of cutting). Visits to *Same Species* mistletoes may indicate that visiting birds have an association between the host foliage and fruiting mistletoe. In most cases, the Yarran hosts used for treatment were not heavily infested. Mistletoes were cut and moved as per the *In-situ* and *Same Species* treatments detailed in Chapter 3 (3.2.2). Mistletoes were either cut from their original host tree and reattached using black cable ties (*In-situ* treatment, 20 replicates) or cut from their original host tree, moved and attached to another potential host tree (*Same Species* treatment, 20 replicates). Roadside mistletoes were cut and relocated pre-dawn with all bird observations beginning by 7:10 am and ending by 12:15 pm. Roadside observations lasted an average of five hours in the morning, with no afternoon period of observation as the bird activity was limited and did not pick up until dusk when the air temperature had dropped considerably from the afternoon peak. In this respect, roadside observations contrasted continuous forest observations, which were longer due to a late afternoon period of activity.

Because observations recorded in the continuous forest were longer, visits were standardised by using a fixed period of observation time. Accordingly, only visits recorded between the hours of 7 am and 12 pm were included in the analysis. There was some minor variability in the length of observations, due mainly to two observation periods being prematurely ended by rain. The length of observations was not significantly different between habitats or treatments (ANOVA: habitat (continuous forest/roadside) $F_{(1, 72)} = 2.041, P = 0.157$; treatment (*In-situ*, *Same Species*) $F_{(1, 72)} = 0.122, P = 0.728$); or habitat x treatment $F_{(1, 72)} = 2.751, P = 0.102$). In addition to the observations recorded for the experimentally manipulated mistletoes for each treatment, and to control for the effects of human presence during manipulation, observations were concurrently taken for the host tree and un-manipulated host mistletoes as well as experimentally un-manipulated trees and mistletoes hosted by those trees (see 3.2.2.2 for a detailed explanation, Figure 8).

Observations were made following the same procedure detailed in sections 2.2.2 and 3.2.2.2. Briefly, all visits where a bird landed in the manipulated mistletoe were considered potential

foraging episodes. Species that visited the manipulated mistletoes were divided into three diet-based functional groups: mistletoe specialist, generalist frugivore and opportunist. Bird species assemblage and richness were determined for each manipulated mistletoe replicate and compared across habitat.

Following the variable selection in 3.2.2 three vegetation characteristics were chosen to be included in analyses comparing the number of visits to manipulated mistletoes across treatments and habitat types. These variables were chosen for their potential to influence the perceived 'attractiveness' of the mistletoe to potential foragers. The characteristics were: the percentage of host canopy cover, the number of (un-manipulated) mistletoes pre-existing on the host tree and the number of fruits on the manipulated mistletoe. The composition of canopy trees was also determined for each habitat type (continuous forest/roadside). The tree closest in distance to the host tree was identified and the percentage of each 'closest' tree species calculated as a proportion of the total number of canopy trees to obtain an estimate of canopy species diversity for each habitat type.

4.2.3 Statistical analysis

Generalised linear models (GzLMs) were used to compare the effect of habitat type on the pattern of visitation to various trees and manipulated mistletoes, using SPSS (IBM SPSS Statistics v22, 2013). Similar to data for Chapter 3, these data were zero inflated, so models using Poisson *versus* negative binomial error distributions were compared, the latter providing a better fit to the data (based on Pearson's Chi-squared values approaching one and lowest scores for Akaike's Information Criterion, AIC), unless specified. Parameter estimates obtained through the GzLMs were used to suggest direction and strength of the main effects and interactions. Bird species richness was compared across habitats for all visits to manipulated mistletoes. An MDS plot was constructed to graphically illustrate the differences in community assemblage (i.e. the number of visits made by each species to manipulated mistletoes) between the two habitat types. Following section 3.2.3, to determine if the number of mistletoes on the treatment host tree was responsible for any differences in visitation to *In-situ versus Same Species* manipulated mistletoes, the number of visits to un-manipulated mistletoes on the host and nearest-host trees of these two treatments were compared in the roadside habitat (as for continuous forest, see 3.3.3). In this model, treatment (*In-situ/Same Species*) and un-manipulated mistletoes (host/nearest-host) were predictors and the number of visits to those mistletoes was the response.

To explore the influence of treatment and habitat type on the number of visits to manipulated mistletoes I ran a series of models. Specifically, these aimed to determine how visits to manipulated mistletoes were influenced by A) bird visits to un-manipulated mistletoes, B) treatment and habitat, C) vegetation characteristics, D) dietary guild and vegetation characteristics within each guild: E) mistletoe specialist, F) generalist frugivore and G) opportunist). Within each discrete category (B-G above), models were compared using AIC values and Pearson's Chi-square, following 3.3.4. The most parsimonious model (lowest AIC value) was then selected as per the information theoretic approach, as being the best model explaining the data (Richards 2005, Symonds and Moussalli 2011). The Omnibus test was used to determine the validity of the selected models with significance of <0.05 indicating a valid model.

The model to determine the influence of bird visits to un-manipulated mistletoes on the number of visits to manipulated mistletoes included the number of visits to un-manipulated host and un-manipulated nearest-host mistletoes as covariates. Habitat type (continuous forest/roadside) and treatment (*In-situ/Same Species*) were included as predictors and the response variable was the number of visits to manipulated mistletoes. If the AIC values were lower in models that included the un-manipulated mistletoe covariates, it would signal the need to include un-manipulated mistletoe visits in future models. Based on the AIC value of this model these covariates were not included in any further model.

Unless otherwise specified, all models hereafter B-G (as above), included habitat type (continuous forest/roadside), treatment (*In-situ/Same Species*) and an interaction between habitat x treatment. No interactions between covariates or covariates and predictors were included in the models. The overall guild model (D, above) included visits to manipulated mistletoes by the three dietary guilds as the response variable and guild designation (specialist/generalist/opportunist), habitat type (continuous forest/roadside) and treatment (*In-situ/Same Species*) as predictors. First level interactions were included in the model (diet x habitat, diet x treatment, habitat x treatment). Vegetation characteristics were added as covariates in the models and included the canopy cover of the host tree, the number of un-manipulated mistletoes on the host tree (not including the mistletoe manipulated for *In-situ* or *Same Species* treatments) and the number of fruits on the manipulated mistletoes after re-attachment. To investigate the influences of vegetation characteristics on visitation to habitat and treatment, seven versions of models C and E-G (above) were created. These seven versions were the seven possible combinations of vegetation characteristics. For the individual guild models (models E-G), the response variable was the number of visits by guild to

manipulated mistletoes; the predictors were habitat type, treatment and habitat x treatment and the vegetation characteristics were covariates.

4.3 Results

4.3.1 Bird visitation

A total of 348.92 hours of observations over 64 days were recorded across two summers for this study. Using the standardised fixed period of observation (observations recorded between 7 am and 12 pm), observations in the continuous forest totalled 174.84 hours, while the roadside observations totalled 172.55 hours. Across the two habitat types 191 visits were made to un-manipulated mistletoes on the host trees (hosting the experimentally manipulated mistletoes). Continuous forest habitat un-manipulated host mistletoes received 83 visits, while roadside habitat received 108 visits to un-manipulated host mistletoes. Nearest-host mistletoes received 131 visits: 62 visits in the continuous forest and 69 in the roadside habitat.

Across the two habitat types 57 visits (Figure 16) were made by birds to 23 of the experimentally manipulated mistletoes. In the continuous forest habitat 41 bird visits were recorded across 14 mistletoes, while in the roadside habitat 16 visits were recorded across nine mistletoes. Birds that visited manipulated mistletoes were from 12 species across the two habitat types. The continuous forest observations recorded visits from 11 species, while the roadside habitat recorded six species and this difference was significant ($\chi^2 = 3.988$, $df = 1$, $P = 0.046$). An MDS plot was created to visualise the differences in species assemblage; while there was overlap between the suites of species found in the roadside habitat, the continuous forest had a greater range of species than the roadside habitat (Figure 14).

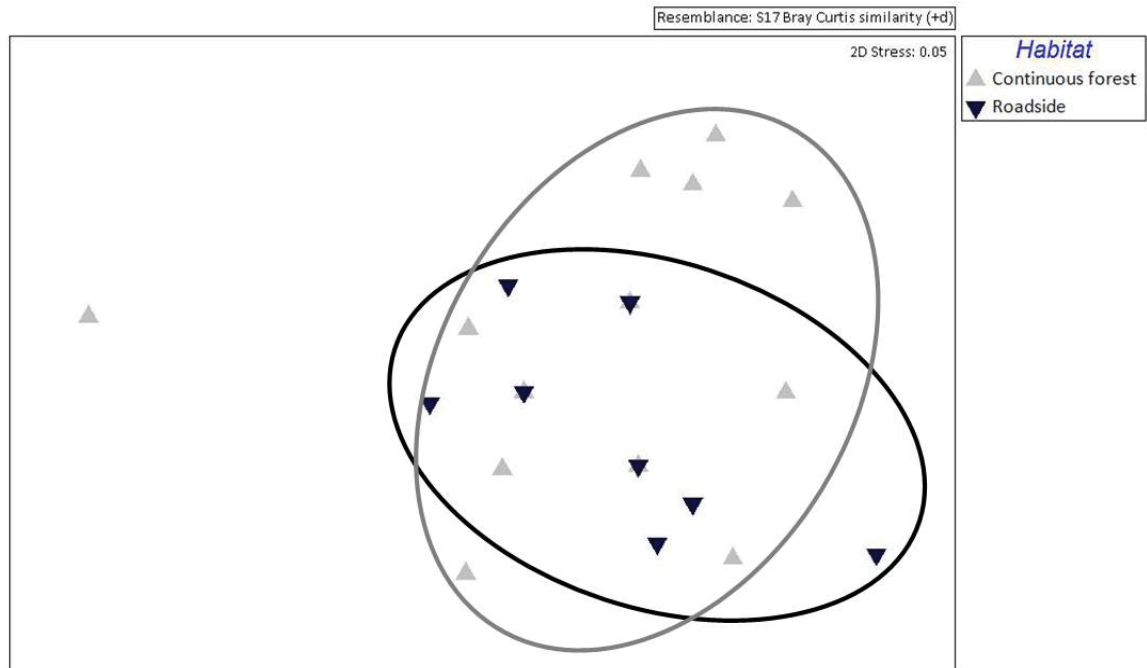


Figure 14. MDS showing the spread of species assemblage of birds visiting manipulated mistletoes across habitat type (continuous forest/roadside).

In both locations, there was one mistletoe specialist bird species (Mistletoe bird) recorded as visiting manipulated mistletoes. Of the visiting roadside species there were two generalist frugivores (Spiny-cheeked Honeyeater and Singing Honeyeater) and four opportunist species (Chestnut-rumped Thornbill, Noisy Miner, Yellow Thornbill and thornbill *sp.*). Of the species visiting continuous forest manipulated mistletoes there were four generalists (Spiny-Cheeked Honeyeater, Singing Honeyeater, Striped Honeyeater and Silvereye) and eight opportunist species (Double-barred Finch, Inland Thornbill, Noisy Miner, Red-capped Robin, Rufous Whistler, Splendid Fairy Wren, Yellow Thornbill and unknown *sp.*) (see Appendix 3, Figures 22, 23 for visit durations and visits over time and Appendix 4, Table 16 for species names).

4.3.2 Effects of human presence during experimental manipulation

In this study, observations of birds visiting un-manipulated mistletoes were recorded to test for the effects of pre-dawn human presence in setting up experimental manipulation. The number of visits to un-manipulated mistletoes on the host tree did not differ significantly from the number of visits to mistletoes on the nearest-host tree (GzLM: $\chi^2 = 0.089$, $df = 1$, $P = 0.765$) but did differ significantly between locations (GzLM: $\chi^2 = 6.934$, $df = 1$, $P = 0.008$, Table 4) (see 3.2.2.2, Figure 8 for explanation of terms).

Table 4. Number of visits to un-manipulated host mistletoes and nearest-host mistletoes, by treatment (*In-situ*/IS and *Same Species*/SS) in continuous forest and roadside habitats. Average number of visits in brackets.

Treatment	Continuous forest	Roadside
Host mistletoe IS	51 (2.6)	72 (3.6)
Host mistletoe SS	32 (1.6)	36 (1.8)
Nearest-host mistletoe IS	32 (1.6)	46 (2.3)
Nearest-host mistletoe SS	30 (1.5)	23 (1.2)

4.3.3 Vegetation characteristics

The number of fruits on the continuous forest manipulated mistletoes was significantly higher (mean: 40.6 fruits \pm 5.72 SE) than the roadside manipulated mistletoes (24.0 \pm 3.62, mean \pm SE) (GzLM: $\chi^2 = 5.174$, $df = 1$, $P = 0.023$) (Figure 15A). The percentage canopy cover of roadside host trees was 23 \pm 3.57 % (mean \pm SE), significantly lower than the 47 \pm 2.69 % (mean \pm SE) in continuous woodland (GzLM: $\chi^2 = 10.141$, $df = 1$, $P = 0.001$) (Figure 15B). The number of un-manipulated mistletoes per treatment host tree in the roadside stands was 7.1 \pm 1.67 (mean \pm SE) compared to 5.5 \pm 0.99 (mean \pm SE) for continuous woodland (Figure 15C). The number of un-manipulated mistletoes on the *In-situ* treatment host tree was significantly higher than on the *Same Species* treatment host tree and habitat type had no effect on the significance (GzLM: $\chi^2 = 15.993$, $df = 1$, $P < 0.001$). In the continuous forest, Yarran made up 56.4% of the canopy, with White Cypress Pine (28.21%), Belah (5.13%) and Poplar Box (2.56%), *Hakea sp.* (2.56%), *Exocarpus sp.* (2.56%) and *Eucalyptus sp.* (2.56%) making up the remaining 43.59%. In the roadside, Boree made up 92.5% of the canopy, with Wilga (*Geijera parviflora*) (2.5%) and other *Acacia sp.* (5%) making up the remaining 7.5%.

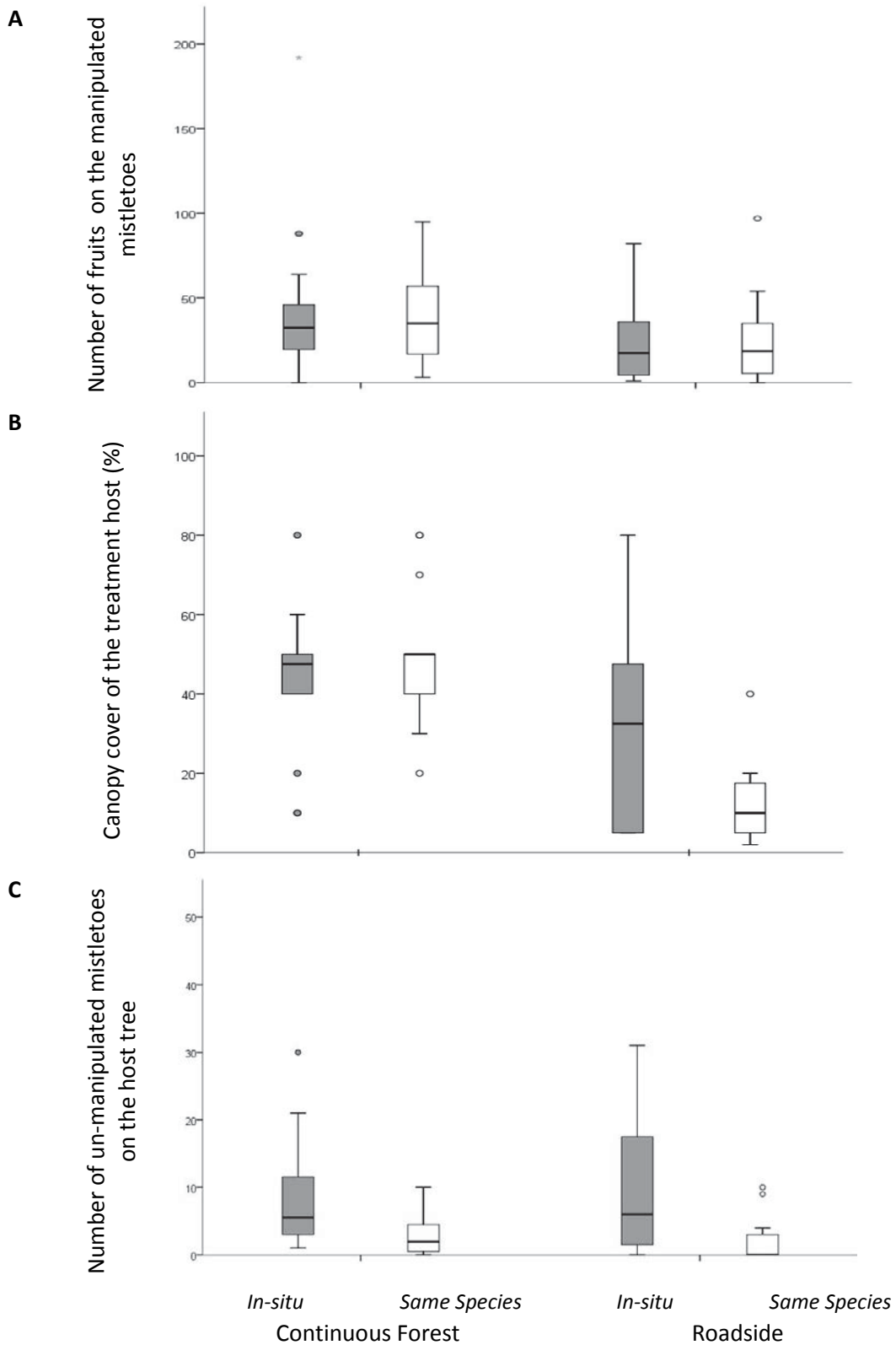


Figure 15. Vegetation characteristics used to find the most parsimonious model compared by habitat (continuous forest/roadside) and treatment (*In-situ*/*Same Species*). Dark grey plots are *In-situ* and white plots are *Same Species*, circles are outliers. (A) Number of fruits on the manipulated mistletoes, (B) percentage canopy cover of the treatment host, (C) number of un-manipulated mistletoes on the treatment host trees.

4.3.4 Effects of habitat type and treatment

To account for the influence of mistletoe infestation on *In-situ versus Same Species* host trees, the number of visits to host and nearest-host un-manipulated mistletoes was compared between the *In-situ* and *Same Species* treatments. In the continuous forest there was no significant difference in the number of visits to the un-manipulated mistletoes on the host and nearest-host trees (section 3.3.3). In the roadside habitat, the number of visits to un-manipulated host and nearest-host mistletoes was significantly higher for the *In-situ* than the *Same Species* treatment ($\chi^2 = 6.299$, $df = 1$, $P = 0.012$), but did not differ between host and nearest-host trees ($\chi^2 = 2.652$, $df = 1$, $P = 0.103$). Further, the number of visits to un-manipulated mistletoes did not significantly influence the number of visits to manipulated mistletoes; habitat type and treatment were also non-significant (Table 5A). The interaction between habitat type and treatment was significant. However, because the ΔAIC value was > 2 higher than the model excluding visits to un-manipulated mistletoes, these covariates were excluded from further models.

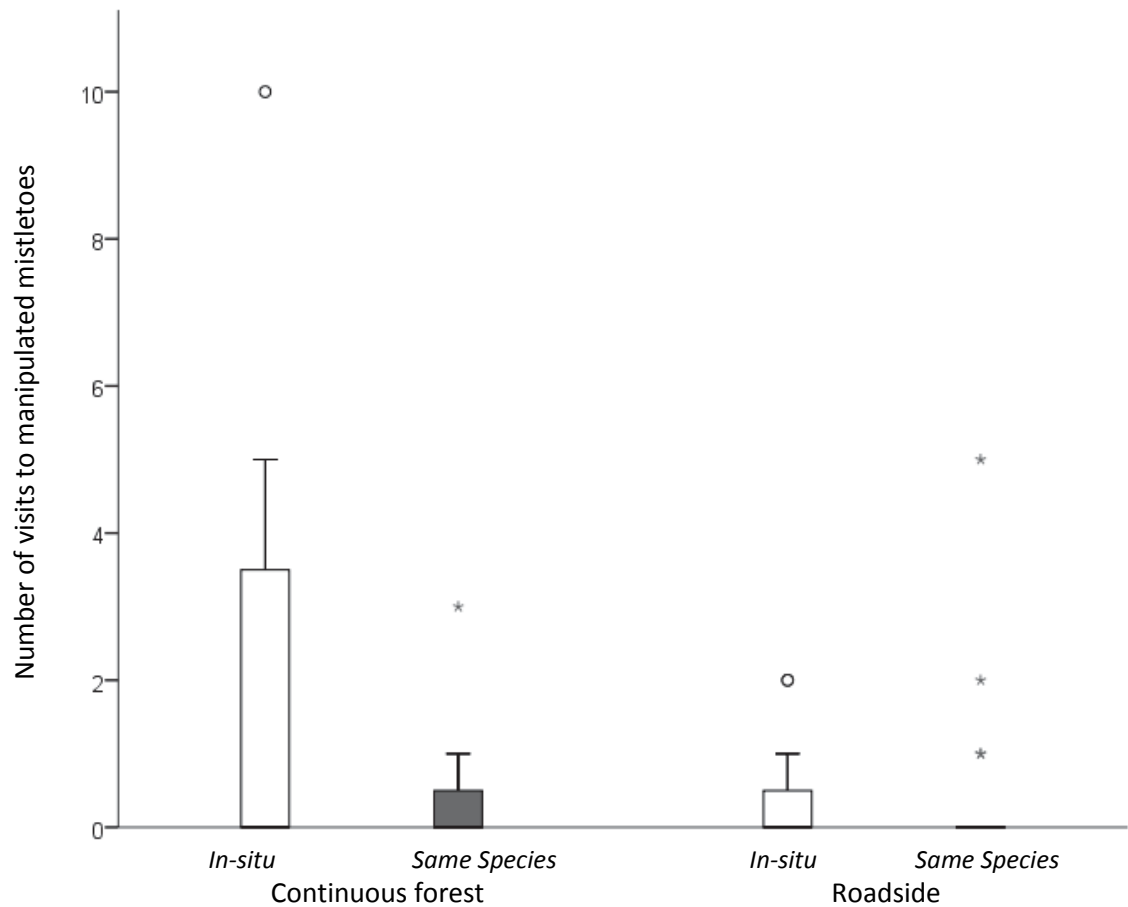


Figure 16. Number of visits to manipulated mistletoes by habitat type and treatment. Grey bars are *In-situ* mistletoes and white bars are *Same Species* mistletoes. Circles are outliers.

The number of visits to manipulated mistletoes was significantly influenced by the interaction between habitat type and treatment such that *In-situ* mistletoes in the continuous forest habitat received significantly more visits than any other treatment-habitat combination (Table 5B, Figure 16). To determine the influence of habitat characteristics on the visitation patterns of frugivores visiting the manipulated mistletoes, the most parsimonious model included only the number of fruits on the manipulated mistletoes (Table 5C). The interaction between of habitat type and treatment remained significant (Table 5C).

Table 5. Generalised linear models investigating the influences of visits to un-manipulated mistletoes, habitat type, treatment and vegetation characteristics on the number of visits to manipulated mistletoes. Model (A) the influence of visits to un-manipulated host mistletoes, as well as habitat type and treatment (AIC = 178.462); (B) the effects of habitat type and treatment (AIC = 176.919); and (C) the influence of the number of fruits on manipulated mistletoes (AIC = 176.814, see Appendix 3, Table 11 for selection of most parsimonious model). Habitat types were roadside and continuous forest habitat. Treatments: *In-situ*: manipulated mistletoes (n = 20) were cut and replaced *in situ* in the original site in the host tree (IS) or *Same Species*: manipulated mistletoes (n = 20) were cut and placed in a different host tree of the same species (SS). Significance is shown in bold.

Source of variation	Wald chi-square value	Degrees of freedom	Main effects (P - value)	Interaction (P - value)	Direction of relationship
A. Effect of habitat and treatment (predictors) on the number of visits to manipulated mistletoes (response) including visits to un-manipulated mistletoes (covariates)					
Habitat	3.729	1	0.053	-	-
Treatment	2.243	1	0.134	-	-
Habitat x Treatment	5.756	1	-	0.016	Continuous forest IS > all other manipulated mistletoes
Host mistletoes	2.464	1	0.116	-	-
Nearest-host mistletoes	0.000	1	0.984	-	-
B. Effect of habitat and treatment (predictors) on the number of visits to manipulated mistletoes (response)					
Habitat	2.821	1	0.093	-	-
Treatment	2.821	1	0.093	-	-
Habitat x Treatment	5.358	1	-	0.021	Continuous forest IS > all other manipulated mistletoes
C. Effect of habitat and treatment (predictors) on the number of visits to manipulated mistletoes (response) including the number of fruits on manipulated mistletoes (covariate)					
Habitat	3.044	1	0.081	-	Continuous forest > roadside
Treatment	2.074	1	0.150	-	-
Habitat x Treatment	4.312	1	-	0.038	Continuous forest IS > all other manipulated mistletoes
Number of fruits	0.172	1	0.678	-	-

4.3.5 Dietary Guilds

When dietary guild was included on the model, there was no significant difference in the number of visits made to manipulated mistletoes by birds of the different dietary guilds (specialist, generalist and opportunist) (Table 6A). However, habitat type and the interaction between habitat type and treatment were both significant (Table 6A). In the continuous forest, *In-situ* mistletoes in particular received significantly more visits than the manipulated mistletoes in the roadside habitat (Table 6A). When the number of fruits on manipulated mistletoes was included in the model of best fit for the specialist guild and there were significantly more visits to manipulated mistletoes in the continuous forest than the roadside habitat (Table 6B). No interactions between predictors were included in the model of best fit for the specialist guild. The model of best fit for the generalists did not include any covariates. The *In-situ* treatment and in particular the continuous forest *In-situ* manipulated mistletoes received significantly more generalist visits than the *Same Species*, or roadside manipulated mistletoes (Table 6C). No model for the opportunist guild is presented as models created were invalid (Omnibus test $P > 0.05$).

Table 6. Results of the Generalised Linear Models investigating the visitation patterns of the dietary guilds both together (A), and individually: (B) mistletoe specialist (no interactions) and (C) generalist frugivore. Visits by the dietary guilds were added as the response variable; habitat type and treatment as predictor variables and vegetation characteristics as covariates (see Appendix 3, Tables 12 and 13 for selection of most parsimonious models). Habitat types were roadside and continuous forest habitat. Habitat types were roadside and continuous forest habitat. Treatments: *In-situ*: manipulated mistletoes (n = 20) were cut and replaced in situ in the original site in the host tree (IS) or *Same Species*: manipulated mistletoes (n = 20) were cut and placed in a different host tree of the same species (SS). Significance is shown in bold.

Source of variation	Wald chi-square value	Degrees of freedom	Main effects (P - value)	Interaction (P - value)	Direction of relationship
A. Effect of dietary guild (predictor) on visits to manipulated mistletoes (response) including interactions with habitat and treatment (predictors)					
Dietary guild	3.923	2	0.141	-	-
Habitat	4.913	1	0.027	-	Continuous forest > roadside
Treatment	1.507	1	0.220	-	-
Dietary guild x habitat	3.311	2	-	0.191	-
Dietary guild x treatment	2.598	2	-	0.273	-

Habitat x treatment	7.546	1	-	0.006	Continuous forest IS > all other manipulated mistletoes
B. Effects of the number of fruits (covariate), habitat and treatment on visits to manipulated mistletoes by the specialist guild (response)					
Habitat	4.055	1	0.044	-	Continuous forest > roadside
Treatment	0.109	1	0.742	-	-
Number of fruits	1.013	1	0.314	-	-
C. Effect of habitat and treatment (predictors) on the number of visits to manipulated mistletoes by the generalist frugivore guild (response)					
Habitat	0.002	1	0.961	-	-
Treatment	4.151	1	0.042	-	IS > SS
Habitat x treatment	4.151	1	-	0.042	Continuous forest IS > all other manipulated mistletoes

4.4 Discussion

Here I set out to determine the effects of different habitat type on bird visitation to unmoved (*In-situ*) versus relocated (*Same Species*) mistletoes. I also sought to determine whether birds from different dietary guilds would display different visitation patterns in each habitat. Using methods and data modified from Chapter 3, I compared the number of visits to each manipulated mistletoe treatment in a continuous forest to those in a roadside habitat. I expected the roadside habitat to host a greater abundance of mistletoe than the continuous forest. As a result of this greater abundance I also expected the roadside habitat to attract more bird visits. By contrast I found the roadside habitat in this study did not follow the pattern described by Norton and Stafford Smith (1999) in terms of mistletoe abundance or expected bird visitation. As was the case in continuous forest (see Chapter 3), I expected that in the roadside habitat, *In-situ* mistletoes, cut and reattached in their original host tree, would be visited more than *Same Species* mistletoes attached to another tree of the same species. In the simplest model investigating visitation to manipulated mistletoes, there was no effect of either habitat type or treatment (Table 5B). However, there was a significant interaction between the habitat type and treatment. The continuous forest *In-situ* mistletoes received significantly more visits than continuous forest *Same Species* or roadside manipulated mistletoes (Table 5B).

Several studies have noted that a high abundance of mistletoe in a habitat corresponds to the presence of a high number of bird species (Ikin *et al.* 2014, Napier *et al.* 2014), especially mistletoe specialists (Bowen *et al.* 2009). In the current study, the number of fruits on the manipulated mistletoes was significantly different across habitats (Figure 15A), and influenced positively the number of visits to treatment mistletoes (Table 5C). The three dietary guilds did not significantly vary from each other when visiting manipulated mistletoes across habitats (Table 6A). However, dietary preference did appear to influence the pattern of visitation to the habitat types, with the continuous forest still receiving significantly more visits than the roadside habitat (Table 6A). In the sections below I explore the relationships and possible influences of habitat type, treatment, dietary guild, and vegetation characteristics on the searching strategies of visiting birds.

4.4.1 *Effects of habitat context on foraging patterns*

Continuous and remnant forests provide habitat for a range of species with differing habitat requirements through vegetation complexity and maturity compared to revegetating or isolated roadside patches (Seddon *et al.* 2003, Vesk *et al.* 2008). In the current study, I found that the number of species to visit the continuous forest manipulated mistletoes was nearly double that of the roadside manipulated mistletoes. Such differences in bird species richness may be linked to the more complex canopy composition and connectivity or size of the respective habitats (Meunier *et al.* 1991, Collard *et al.* 2009, Hall *et al.* 2016).

Roadside stands containing mistletoe are thought to be used as thoroughfares or corridors connecting patches of better quality habitat (Lamont and Southall 1982). Consistent with this hypothesis, in the current study, I found that the birds in roadsides did not demonstrate a preference for unmoved over moved mistletoes. As these treatments were designed to test for two different searching strategies, (*In-situ*: spatial memory and *Same Species*: host-mistletoe association) the lack of a preference suggests that the birds in these environments do not use those strategies when searching for fruiting mistletoe. If roadside patches of mistletoes only act as infrequent corridors, rather than primary habitat through the fruiting season, there would be no reason to expect the frugivores to remember the location of individual hosts, let alone individual mistletoes on those hosts (Norton *et al.* 1995). Rather, we might expect the frugivores to remember the route they travel between patches and the fruitful patches they use as stopovers. This expectation implies that the frugivores would forage opportunistically along the patch. For example, Singing Honeyeaters eat mistletoe fruits, but during the field study, also frequently consumed the bright red fruits of the Ruby Saltbush and probed the

curled up leaves of the Boree for arthropods and invertebrate larvae (Pers. Obs., 2016). The possibility also exists that the different host species influenced the observed searching behaviours. Boree, the dominant roadside host, had long drooping branches with leaves that were a pale green-grey, similar to those of Grey Mistletoe (Figure 12). From a human's eye perspective, these mistletoes are more difficult to detect in the pendulous foliage of the Boree compared to the more open canopy of Yarran (Figure 11). This visual similarity may override the potential formation of host-mistletoe associations in the minds of foraging birds and more field observations are needed to confirm this hypothesis. Although this aspect of visual similarity was not tested during this study, it would be interesting to address whether or not the foraging frugivores can detect visual similarities or differences when searching for Grey Mistletoe in Boree compared to Yarran. Do their visual foraging patterns change in habitats of differing visual complexity?

4.4.2 Influences on birds' foraging preference

Habitat fragmentation can reduce the quality of the habitat, especially for forest specialists, by increasing edge effects, such as a changed vegetation gradient, water hydrology and resident species composition (for example, van Etten 2014). Indeed, the presence of aggressive, highly territorial edge species such as Noisy Miners (*Manorina melanocephala*) has been cited as a significant deterrent for small insectivorous or nectivorous birds that prefer forest habitats (Montague-Drake *et al.* 2011, Hall *et al.* 2016). The presence of dense canopy and shrubby understorey layers discourages the Noisy Miners (Hastings and Beattie 2006), while encouraging other species. In this study, I found that canopy cover differed between habitats overall, being significantly greater in the continuous forest. The complexity of the canopy in the continuous forest was greater than the roadsides. The number of potential hosts however, was higher in the roadside habitat (92.5% Boree) compared to the more diverse continuous forest (56.4% Yarran). Vegetation complexity is generally used as a good indicator of avifauna assemblages (Major *et al.* 2001, Seddon *et al.* 2003). Interestingly, however, factors such as canopy cover (Oliver *et al.* 2003, Barea 2008) and habitat fragmentation (Crampton *et al.* 2011) are thought to play a lesser role than the local abundance of fruiting plants, in influencing the attractiveness of individual fruiting plants to foraging birds (Crampton *et al.* 2011). In the current study, the abundance of mistletoes did not significantly differ between the habitats; therefore, other characteristics may have influenced the birds' visitation preferences. For example, a number of visual characteristics have been found to increase the likelihood of attracting frugivores to fruiting plants, for example, crop size (Oliver *et al.* 2003, Crampton *et al.* 2011) and the quality of the fruits on offer (Blendinger *et al.* 2015). Indeed, I found that the

number of fruits on manipulated mistletoes was significantly greater in continuous habitat relative to roadsides. Importantly, however, birds of differing diets, life histories and movements respond differently to the same influences and cues, which is why it is important to understand the different groups in any avian community under study.

If mistletoes were a primary food source for a particular bird species, one might expect that the presence of mistletoe in any given area would increase attractiveness of that area and therefore overall visitation by that species. In studies investigating frugivore-mistletoe interactions, the numbers of mistletoes per host strongly influence the likelihood of frugivorous birds visiting and consuming the mistletoe fruits (Oliver *et al.* 2003, Barea 2008). In the current study, the number of mistletoes per host was not significantly different across the two habitats and was not included in the parsimonious models explaining visitation patterns to manipulated mistletoes. In Chapter 3, the generalist frugivores in the continuous forest were significantly influenced by the number of mistletoes on the host tree, but this pattern was not repeated in the roadside habitat. The fact that host mistletoe abundance only influenced visitation in the continuous forest suggests that foraging behaviour by generalists is influenced by different cues in different habitats. Neither the specialist nor opportunist guilds were significantly influenced by the number of mistletoes on the host trees in either habitat, suggesting other cues influence their foraging decisions.

Although the number of fruits did not influence bird visitation to different habitats overall in the current study, when looking within dietary guild, a pattern did emerge. The specialists were more likely to visit manipulated mistletoes with more fruits, but this was not the case for generalists. It is possible that the low overall number of visits by generalists to the manipulated mistletoes precluded the ability to discern influential factors. However, as explored in Chapter 3, the generalists in the continuous forest were influenced by the percentage of host canopy cover and the number of mistletoes on the host, while using spatial memory to find the known fruitful mistletoes. Therefore, I suggest that while moving through roadside patches, generalists forage opportunistically, on a range of resources.

4.4.3 Fragmentation and surrounding landscape use

Aside from the features of the habitat itself, attractiveness of a given habitat patch also can be influenced by the adjoining landscape. In particular, surrounding land-use plays a part in the quality of the roadside patch for birds (Watson *et al.* 2000, 2005, Collard *et al.* 2009, Lindemayer *et al.* 2010, de Torre *et al.* 2015). As patches of remnant or regenerating habitat that are often long, narrow and discontinuous, roadside patches can play a substantial role in

connecting remnant and continuous habitat patches (Huijser and Cleverger 2006, Reijen and Foppen 2006, Kociolek *et al.* 2011), especially in fragmented agricultural landscapes (Fortin and Arnold 1997, Hall *et al.* 2016). Windbreaks between paddocks or crop fields have the potential to play the same connective role, effectively increasing the home ranges of birds in isolated remnant patches (Kinross 2004). On the other hand, in areas that are historically agricultural, these roadside patches can often be the only patches of remnant or regenerating habitat (Norton *et al.* 1995), much like the patches of Boree used in this study. Thus, they may provide refuge and habitat services usually assigned only to continuous or undisturbed habitats (Arnold and Weeldonburg 1990, Carthew *et al.* 2013).

Isolated patches may act as linkages between larger, better quality patches for pollinators and seed dispersers (mammal, invertebrate or bird) (Levey *et al.* 2005, Damschen *et al.* 2008, Elliott *et al.* 2012, Herrmann *et al.* 2016). Thus, these animals they can either link patches, ensuring genetically viable plant populations (including spreading exotic species) or break the link (through not being able to cross the distances, reduced seed disperser populations etc), reducing the chances of the patches surviving indefinitely (Sekercioglu 2006). Mistletoe-frugivore interactions provide unique insight into the effects of habitat fragmentation. As hemi-parasites, mistletoes must be attached to a suitable/susceptible host, drawing energy from their hosts xylem and phloem in addition to their own photosynthetic products (Calder and Bernhardt 1983, Ehleringer *et al.* 1985, Watson 2011b). They must also attract suitable pollinators and seed dispersers to ensure the continuation of their genes. Mistletoes have been noted in great abundance along roadsides, with greater access to water and nutrient runoff from the road cited as the main reasons for the aggregations, followed by increased light availability and the use of roadside trees as a thoroughfare with perching and foraging opportunities (Norton *et al.* 1995).

Like road houses offering an abundance of pies, sausage rolls and energy drinks, aggregated mistletoes may draw in the travelling frugivores. However, the physical connectivity (distances between patches) of these roadside mistletoe patches has scarcely been investigated. By influencing the foraging decisions of seed dispersing frugivores, the usage of the surrounding landscape and the distance to remnant or continuous forest may play an influential role in the distribution of these mistletoe-rich patches. Therefore, notwithstanding the idea that many roadsides contain more abundant patches of mistletoes (Norton and Stafford Smith 1999) and should thus be very attractive to frugivorous birds (Sargent 1990), the surrounding land use (and potential lack of connectivity) means that these mistletoes may be under-utilised in roadside patches. Mistletoes, while potentially enhancing the quality of the patches, may not

be enough to attract equivalent numbers of birds or visits as the mistletoes in the continuous forest, unless the patches are well connected or the surrounding land use provides suitable habitat for the frugivores (Collard *et al.* 2009). The increased access to water (Norton and Stafford Smith 1999, Homyack *et al.* 2016, Staniaszek-Kik *et al.* 2016) and other potentially aggregated vegetation resources such as exotic grasses or flowering 'weeds' (Carthew *et al.* 2013, Hanley and Wilkins 2015) means that these roadside habitats may potentially function as seasonal storehouses or refugia in times of drought or resource scarcity, similar to the function of riparian zones in continuous forest habitats (Bennett 2003, Palmer and Bennett 2006). For these roadside patches to maintain viable populations, however, they must cover enough area to be effective habitat for the selected species (Bennett 2003), or be closely connected to other patches (Travis and Dytham 1999, Villard and Metzger 2014).

Current research into the effects of habitat loss and fragmentation on species declines asks several questions. Research into what constitutes good quality patches explores the types of habitat, characteristics and assemblages of species in patches (Villard and Metzger 2014, Avon and Bergès 2016, Pirnat and Hladnik 2016) while the effectiveness of corridors for connecting remnants explores the scale and types of connectivity (Herrmann *et al.* 2016, Perez-Hernandez *et al.* 2015, Rayfield *et al.* 2016). These areas of research consider not only individual species responses (Arroyo-Rodríguez *et al.* 2016, Jackson *et al.* 2016, Rayfield *et al.* 2016, Schlinkert *et al.* 2016) or community level responses (Schultz *et al.* 2014, Buse *et al.* 2016, Hall *et al.* 2016, Hooftman *et al.* 2016) but also the roles and interactions among the species that make up those communities (Coulsen *et al.* 2014, de Torre *et al.* 2015, Perez-Hernandez *et al.* 2015, Herrmann *et al.* 2016). One area of interest concerns the revegetation of roadsides and the role that seed dispersers play in maintaining viable vegetation communities (deTorre *et al.* 2015, Herrmann *et al.* 2016, McConkey and O'Farrill 2016). My research has shown that seed dispersing frugivores seek out known mistletoes that are abundantly fruitful and visually healthy. Mistletoes may therefore represent a way to help ameliorate the declines of woodland birds in fragmented landscapes by 'seeding' roadside vegetation and connecting patches.

Chapter 5: Synthesis



Two pairs of Superb Parrots (*Polytelis swainsonii*) feeding in Yarran (*Acacia homalophylla*) canopy, Binya State Forest, NSW.

5.1 Preamble

Exploiting patchy resources can require specialised foraging strategies. A key strategy for reliably locating patchy or visually cryptic resources is the use of a search image (Lawrence and Allen 1983). A search image focuses search effort and directs foraging using specific visual cues (Reid 1991). Strategies to locate resources that are patchy in time often involve using spatial memory, such as traplining to exploit reducible nectar resources (González-Gómez *et al.* 2011) or the use of spatial cues to remember, store and relocate resources (Vander-Wall 2001). Each of these strategies first requires some form of learning (Shettleworth 1985): learning when resources are exploitable, nutritious or predictable at some seasonal or annual scale (Wilhelmson 1999); learning which strategy works best for optimal food rewards for effort expended (Pyke 1984); learning to recognise specific resource-related cues to aid the visual or spatial search (Herborn *et al.* 2011, Marshall *et al.* 2012); and potentially social learning, from parents, conspecifics and other species about where and how to exploit the resource (Floyd and Woodland 1981).

Hemi-parasitic mistletoes, reliant on their host plant for survival, are easily manipulated and so are ideal for experimental investigations. Some species of mistletoe, especially in temperate to arid zones, have close interactions with a limited number of seed-dispersers (for example, Mesquite Mistletoe (*Phoradendron californicum*) and Phainopepla (*Phainopepla nitens*) (Aukema and Martínez del Rio 2002b); Quintral Mistletoe (*Tristerix corymbosus*) and Monito del Monte (*Dromiciops gliroides*) (Amico *et al.* 2009) and Grey Mistletoe and Mistletoebird (Rawsthorne 2011b). In these relationships, the seed dispersers often rely heavily on the fruits provided by the mistletoes and so offer a unique insight into specialised foraging behaviour in fruit-frugivore systems. Here in Australia, the dependence of mistletoes on just a few effective seed dispersers creates a system that can be manipulated to ask probing questions relating to dispersers' dietary dependence, searching and wider movement patterns. The answers may be used to help explain the aggregated patterns of mistletoe seed dispersal and the implications for the use of mistletoes as a tool for conservation.

The complexity of interactions between pollinators and seed dispersers means that mistletoes provide an excellent platform from which to study fruit-frugivore relationships. The small number of manipulative experiments exploring frugivorous bird foraging behaviour in the field typically involve removing or covering fruits to ascertain frugivore foraging patterns (Aukema and Martínez del Rio 2002b, Amsberry and Steffen 2008). These studies are generally observational, focussed on determining seed deposition rates (García *et al.* 2009, Bonilla and

Pringle 2015), seed dispersal kernels (Chavez-Ramirez and Slack 1994), seasonal fruit tracking (Rey 1995, Saracco *et al.* 2004, Blendinger *et al.* 2012) and the functional role of the frugivore (Côrtes and Uriarte 2013). Very few studies have manipulated or moved the entire plant (but see Aukema and Martínez del Rio 2002b) as most fruiting plants are large or rooted in the soil making transplanting difficult. Using experimentally manipulated mistletoes, I provide evidence for the use of certain search strategies by frugivorous birds to find fruiting mistletoes. I showed that the extent to which birds relied on mistletoe as part of their diet influenced their foraging strategies. The mistletoe specialist, generalist frugivores and opportunistic foragers each demonstrated different patterns of visitation to the experimental mistletoes, indicating differences in search strategies. Characteristics of both the host plant and experimental mistletoes influenced these three guilds differently too, as did the overall habitat location. In this chapter, I explore some of the implications of my findings in the wider context of fruit-frugivore systems. I also consider ways that the findings of my research may be extended with focused research approaches to understand the use and formation of search images in finding patchy resources, the scale at which foraging strategies may change and how mistletoes could be used to enhance degraded habitat.

5.2 Visual influences on foraging behaviour: search images and other visual cues

In Chapter 2, I detailed a defoliation experiment designed to elucidate the role of mistletoe leaves in attracting or influencing foraging frugivores. This was motivated by a hypothesis suggesting that foliage may be used as a visual cue or search image to aid frugivores when foraging for mistletoe, especially if the mistletoe foliage mimics that of the host (Calder 1983). The idea that foliage may act as a visual cue was tentatively supported by my findings as there appeared to be a visitation preference for mistletoes with leaves, especially for the generalists. In contrast, there was no evidence that the specialist Mistletoebird showed a preference for either foliated or defoliated mistletoes, although further research should be undertaken to confirm this finding. In the mistletoe relocation experiment (Chapter 3), Mistletoebird visitation was positively influenced by the number of fruits on manipulated mistletoes. Further investigation may reveal the role that leaves, or visual appearance altogether, plays in influencing the foraging strategies of these specialist frugivores compared with generalist foragers. This investigation should include more replicates to a) verify my findings and b) elucidate statistically and, importantly, biologically relevant patterns. For example, a foraging

preference study under controlled conditions might present Mistletoebirds and Spiny-cheeked Honeyeaters in an aviary with a series of repeated, visually manipulated clumps of mistletoe. Visual manipulations could include augmenting the number of fruits and augmenting or removing leaves. Individual birds would be allowed to forage in the mistletoe clumps with foraging behaviour and effort recorded both by observer and video camera. Measurements of time before first approach to the mistletoe, time before first peck or probe and time spent foraging in the mistletoe could be analysed to ascertain search rate and exploratory behaviour (Courant and Giraldeau 2008, Sol *et al.* 2011, 2012). Differences between approach and foraging times and the relationship between timing and eye and head movements before first approach and first peck would allow the separation of the use of increased search rate from search image (Lawrence 1988, Dawkins 2002), thus providing evidence for or against the use of a search image as defined by Lawrence and Allen (1983).

Certain visual cues used by foragers are not apparent to humans; for example UV nectar guides on flowers (Chittka and Menzel 1992). To examine if birds use extra visual cues as part of a search image, the range of visual contrast, in relation to the birds own visual range, could be explored via spectroscopy of the foliage, fruits and flowers. To further investigate potential visual cues used by birds searching for mistletoe fruits, another treatment could involve mistletoe with fruits painted with UV paint, to enhance the visibility of the fruits within the foliage. Spectroscopy could be used to ascertain the relative difference in visibility of the foliage and unpainted fruits *versus* the foliage and UV-enhanced painted fruits, providing evidence for previously overlooked visual foraging cues *sensu* Siitari *et al.* (1999). Outcomes would help to illuminate whether or not the relative UV visibility of the fruits is used as a foraging cue and if so, whether this differs among specialists and generalists.

Differences in the foraging strategies by birds in different dietary guilds were observed in my study. The differences between specialist and generalist foragers, however, contrasted my expectations. I expected the specialists to use a search image derived from mistletoe-scale cues (e.g. visual appearance of the mistletoe) to increase the efficiency of their search for mistletoe fruits. While they were influenced by the number of fruits on the mistletoe, they did not appear to be influenced by either the presence of mistletoe leaves (section 2.3.1) or the host in which the mistletoe was located (section 3.3.4). This was unexpected considering the dietary specialisation of the Mistletoebird compared to the generalists, but offers insight into alternate foraging techniques. While not influenced by cues at the whole-tree scale, such as canopy cover or height or even host species, Mistletoebirds may use a combination of landscape-scale cues, augmented by visual cues concerning individual mistletoes such as the

number of fruits, to form a memory of the spatial location of abundantly fruitful mistletoes (section 4.3.5).

The generalist frugivore guild used cues at the scale of both individual mistletoes e.g. the presence of leaves (Chapter 2), and at the whole-tree scale, for example, the canopy cover of the host tree and the number of mistletoes on the host tree (Chapter 3). While I expected to find evidence that generalists form an association between the host-tree and the mistletoe species by using whole-tree scale cues, such as the number of mistletoes present, this was not supported by my findings. The generalists were indeed influenced by the number of mistletoes on the host tree, but I found no evidence that they formed an association between the host and mistletoe species. Instead, they visited un-moved mistletoes significantly more than those moved to the same host species in novel locations (section 3.3.4). This search strategy was observed in both habitat types (section 4.3.5). Therefore, I suggest that the generalists are influenced by host canopy cover and particularly, the abundance of mistletoes in individual trees. I suggest that they use this information to form a memory of the location of specific host trees. Thus, by visiting trees that host many mistletoe plants, the generalists can minimise the effort of locating and visiting multiple different trees, while maximising their chances of finding ripe fruits.

5.3 Interactions between time and space and foraging behaviour

The extent to which spatial memory influences searching behaviour is likely to vary temporally, possibly based on the need to acquire and maintain that memory for different patchy resources. My findings in Chapter 3 provide some evidence for spatial memory as a searching strategy, and that different strategies may be used based on dietary guild, particularly with respect to reliance on fruits as a food source. The use of spatial memory in generalist frugivores is evidenced by a higher number of visits to mistletoes in known locations over those in new locations. Do these differences in spatial memory in fact relate to variation among these groups in seasonal movements? For example, some of the generalist frugivores in the continuous forest e.g. Spiny-cheeked Honeyeaters, may have been resident there during the peak fruiting season (Pizzey 1997), establishing territories and selecting mistletoes to visit and revisit (Reid 1990). My study did not preclude those possibilities, but nor did it have the scope to investigate season-long mistletoe fidelity, trap lining or territorial resource use and defence.

Two important lines of questioning are brought to mind when considering the possibility of spatial memory as a search strategy. Firstly, how does that memory form? How long or how many successful visits are required to create the memory and how long does it last? We know that if a search image is formed it, may be transient (Ishii and Shimada 2010) and that this kind of learning has been explored for spatial memory in caching animals (Smith and Reichman 1984, Kaplan 2015 and references therein), but it has not been addressed in frugivores. Secondly, at what scales – spatial and temporal – is that memory apparent or most effective? At what spatial scale, within-patch or between patches, do birds form spatial memories of mistletoe distribution and location? Do they form a spatial map of the good patches of mistletoe within a patch or do they form a memory of the distribution of mistletoes between patches, across landscapes? At a temporal scale do the memories form over a few days and last a single fruiting season or do they form over many fruiting seasons and update from season to season? Do the seasonal movements of birds, whether they are residents or nomads or seasonally resident, influence their ability to form spatial memory and the scales at which it is formed? I hypothesise that generalist frugivores, e.g. Spiny-cheeked Honeyeater, develop a spatial map or memory during early seasonal mistletoe fruiting, assessing the mistletoes for fruiting potential and revisiting them during peak fruiting. Unlike generalists, I expect that the specialist Mistletoebird develops a spatial map over many seasons, locating fruitful patches and revisiting them. To test these hypotheses, an experiment could be conducted with tagged and radio tracked individuals. Tags and radio tracking devices would be attached early in the fruiting season and motion-sensor cameras deployed in local mistletoe patches to confirm visits and revisits. If individual birds visited and revisited specific mistletoes in a predictable pattern, it would indicate the use of a traplining strategy (Ayers *et al.* 2015). On the other hand, if the birds set up territories and were loyal to specific mistletoes, it would indicate territorial resource defence and exploitation (Reid 1984, Male and Roberts 2002). The experiment would run over at least three fruiting seasons to track the movements of the frugivores across seasons for potential patch re-visitation. This experiment would inform on seed disperser's movements within peak fruiting season and across seasons, as well as enabling us to map the movement patterns of mistletoe seed dispersers and their use of habitat patches.

5.4 Application of mistletoes as habitat enhancement tools

Patches of roadside vegetation, especially in highly fragmented areas, may contain remnant or revegetated habitats that are vital to species survival (Carthew *et al.* 2013, Kasten *et al.* 2016). These roadside patches, while potentially providing refugia or areas of sanctuary for some species may also be poor quality habitat for others (Lindenmayer *et al.* 2012, Knapp *et al.* 2013). Lack of connectivity between patches (Hooftman *et al.* 2016), abundant edges and edge specialist species (Grey *et al.* 1998, Montague-Drake *et al.* 2011) and close proximity to traffic (risk of mortality and disturbing noise levels) (Paris and Schneider 2009, Summers *et al.* 2011, Kovar *et al.* 2014, Chen and Koprowski 2016) may all have negative effects on species inhabiting those patches. As I demonstrated in Chapter 4, roadsides were not a preferred habitat for mistletoe-eating birds compared with continuous forest habitat. As mistletoe infestation was similar across habitats, but the number of bird species was not, I attributed these differences largely to the habitat context and/or surrounding land use. This is especially interesting given observations that mistletoes are more abundant on roadsides than continuous forest due to superior access to water and light in the former (Lamont and Southall 1982, Norton and Stafford Smith 1999). On the other hand, Norton *et al.* (1995), studying patches of Salmon Gum (*Eucalyptus salmonophloia*) hosting Box Mistletoe (*Amyema miquelii*), found that large patches were more likely to host mistletoes than small patches. Moreover, in that study, land use may have affected the presence of mistletoe, with a paucity of mistletoes in grazed land and roadside patches. The authors suggest that the roadside habitats, despite being considered good habitat for mistletoes (Norton and Stafford Smith 1999), may not be good enough for seed dispersing birds to pass through, let alone live in (Norton *et al.* 1995). Thus, forest cover may be of vital importance in maintaining seed-disperser populations, perhaps explaining some of the discrepancy between varying roadside mistletoe abundance. Indeed, MacRaidl *et al.* (2010) found a disproportionately large drop in the incidence of mistletoes when forest cover dropped to 15% or less, which they suggested was the result of the patch no longer being large enough to support the seed-dispersing Mistletoebird. These results appear to suggest that there is a critical limit in the distribution of the Mistletoebird, where patch size and forest cover interact to create suitable habitat. Indeed, while tracking Mistletoebirds in South Australia to investigate the seed shadow for Box Mistletoe (*Amyema miquelii*), Ward and Paton (2007) measured the home range of the birds and found that it was 21 ha with only 0.8 ha of that being classed as the area of core activity. Therefore, it is possible that despite inhabiting an extensive geographic range that covers all the regions of Australia where mistletoe grows (Keast 1958) individual birds may be only locally nomadic and have

smaller home ranges than previously supposed. The factors contributing to the nomadic behaviour or maintenance of home ranges may be directly related to the abundance of resources, mainly mistletoe fruits and nectar but are currently under-investigated (Ward and Paton 2007). In order to determine the critical habitat limit for the Mistletoebird, a series of standardised avifauna surveys (Watson 2004b) could be conducted in a range of habitats. By quantifying the habitat characteristics, surrounding land use, patch size and connectivity (distance to nearest patches), it would be possible determine the minimum patch size, habitat type and connectivity distance required by this species. Further, understanding where Mistletoebirds are found in different patches is necessary for predicting which patches mistletoe infections will be spread or from where they will retreat.

Through their prolific leaf cycling and expansive, complex interactions with avifauna, Loranthaceae and Viscaceae mistletoes present an intriguing case for habitat enhancement (Watson 2009a), especially for areas of conservation or connectivity importance. As root parasites, *Rhinanthus angustifolius* and *R. minor*, have been used to experimentally improve semi-natural grasslands in Belgium (Ameloot *et al.* 2008); mistletoes could also be utilised to improve degraded habitat and increase biodiversity. This idea, however, has never been rigorously pursued. To test this theory, I propose a long-running experiment to inoculate areas of degraded habitat with mistletoe and compare indices of habitat health after time with 1) comparable areas of degraded habitat, and 2) comparable areas of quality habitat that is either revegetated or has never experienced degradation. To be effective, inoculated habitats must be visited by seed dispersing birds. Using the radio tracked movement data from experiments suggested above, habitats for inoculation could be selected based on the dispersers that visit or move through them. Ideally, this experiment would be open-ended in order to build a comprehensive data base of individual and community level responses and interactions, both biotic and abiotic. An experiment of this scale is only possible by through extensive collaboration with private landowners, National Parks and Wildlife Services, State Forests, local government, researchers, rangers and local community groups. If utilised effectively, local community groups e.g. Bushcare, Landcare, Birdlife Australia and the Australian Herpetological Society, could be responsible for regular monitoring under the supervision of a lead researcher. Crowd-funding and rigorously designed citizen science data collection could be used to support such an extensive experiment. Such a database could be used to guide conservation efforts and inform conservation and land management policy by providing information on species presence and absence, the habitat types in which they are found and the level of connectivity that may affect population dynamics. Such a study would

also help to fill gaps in our knowledge about species interactions and responses over time in habitats of differing levels of degradation, including, for example, the tertiary effects of mistletoe removal (or addition) on insectivorous lizards, snakes, amphibians and small mammals.

5.5 Final thoughts

As locally abundant but patchy resources around the world, fruiting plants share complex interactions with their pollinators and seed dispersers. As such, the study of these interactions is equally complex. Hemi-parasitic mistletoes, with their abundant fruits, highly restricted dispersal requirements and limited range of specialist and generalist dispersers present a compelling platform from which to study fruit-frugivore interactions. Using novel experimental methods, my research has revealed that dietary specialists, generalists and opportunists use very different search strategies to locate fruiting mistletoes. Each dietary guild was influenced by various visual characteristics of host and/or mistletoe, prompting ideas for new experiments and testable hypotheses. The findings of my investigations may be applied and tested in a variety of mistletoe and other plant-frugivore systems; for example, similarly specialised animals, such as frugivorous bats. Frugivorous bats play an important role in the dispersal of many fruit-bearing species in the Neotropics (Palmeirim *et al.* 1989, Sarmiento *et al.* 2014). They are also important for dispersing seeds across areas of fragmented habitat (Reid *et al.* 2015), while relying on the remnant forest for roosting (Ripperger *et al.* 2015). Understanding the foraging patterns of frugivorous bats, potential use of spatial memory in combination with echolocation or olfactory cues may be useful in predicting bat population movements. More broadly, such insights would contribute to knowledge of seed dispersal patterns and subsequent plant population dynamics, especially in fragmented or disturbed habitat.

Appendix 1. Extra visitation data for Chapter 2: The role of leaves in foraging strategies

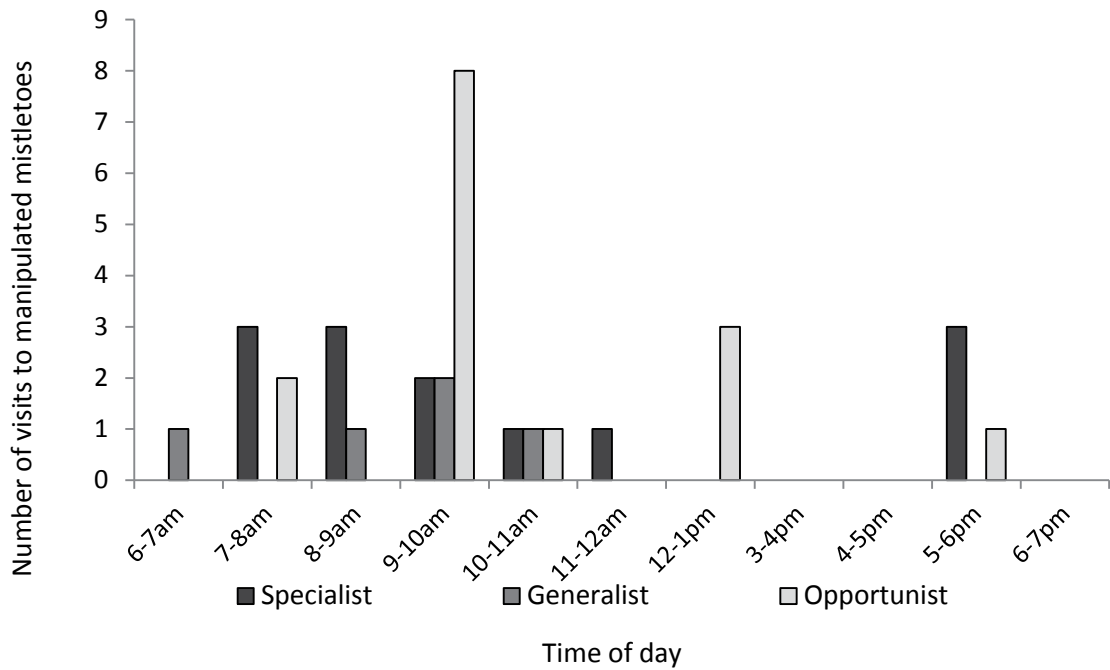


Figure 17. Chapter 2: Number of visits per hour by guilds, pooled across treatments. Treatment: intact (mistletoe leaves left on plant) (n = 20), defoliated (mistletoe with >90% leaves removed) (n = 20).

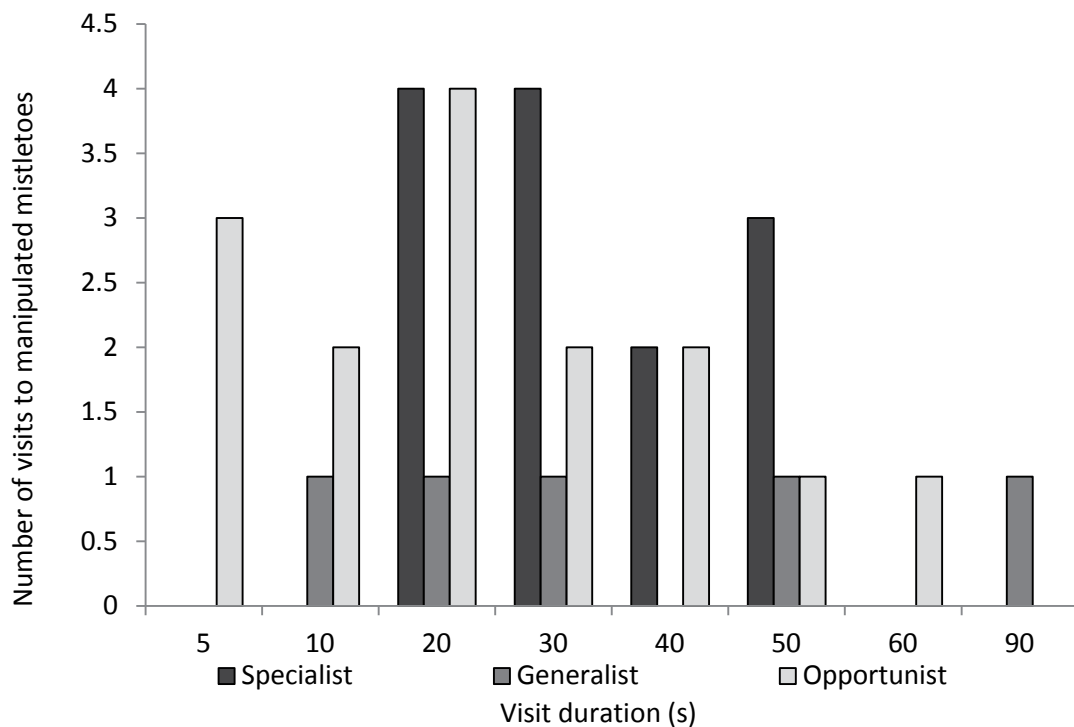


Figure 18. Chapter 2: Binned visit durations by guilds, pooled across treatments. Treatment: intact (mistletoe leaves left on plant) (n = 20), defoliated (mistletoe with >90% leaves removed) (n = 20).

Appendix 2. Extra visitation data for Chapter 3: Cut-and-paste mistletoe relocation

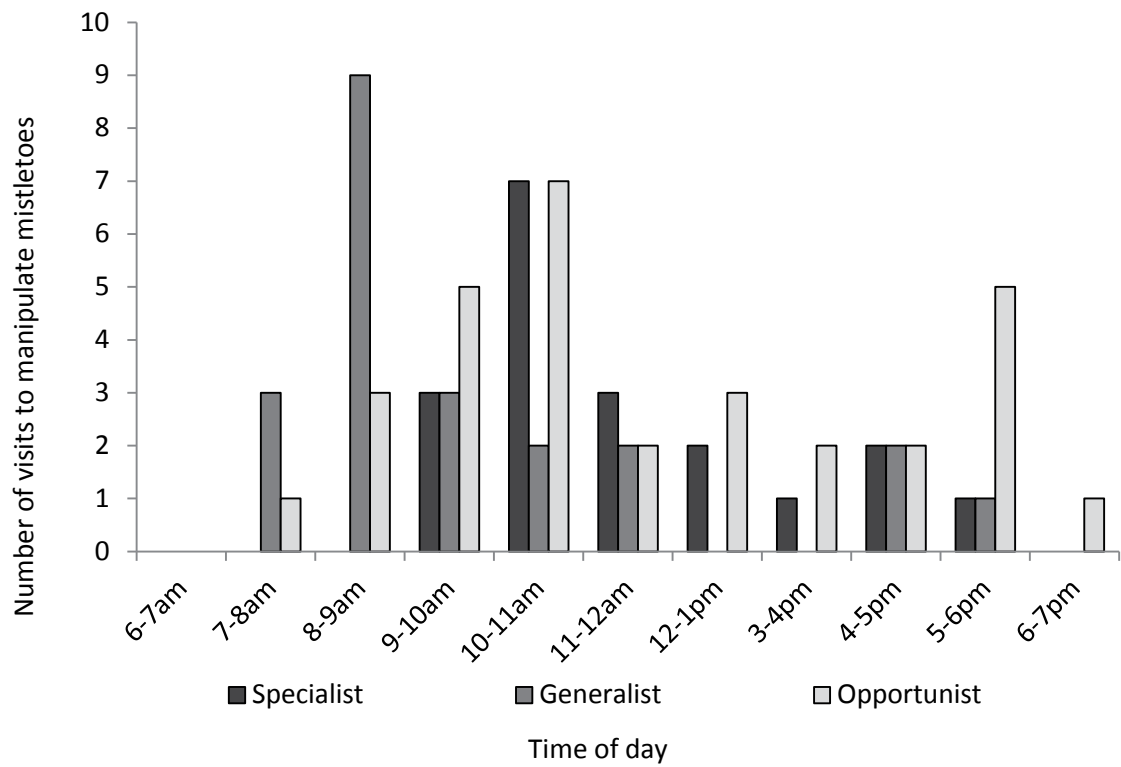


Figure 19. Chapter 3: Number of visits per hour by guilds, pooled across treatments. *In-situ* (IS) cut from the original host tree and reattached exactly where it was, *Same Species* (SS), moved to another tree of the same species as the original host and *Different Species* (DS), moved to a species that never hosts Grey Mistletoe

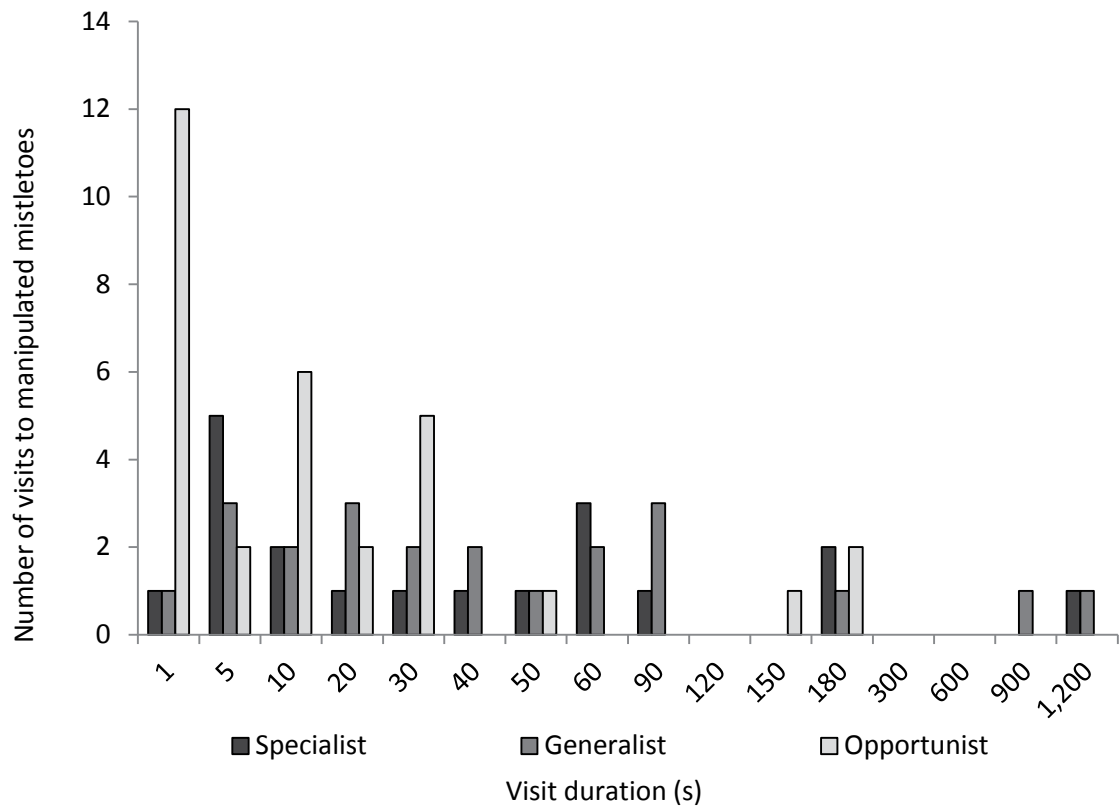


Figure 20. Chapter 3: Binned visit durations by guilds, pooled across treatments. *In-situ* (IS) cut from the original host tree and reattached exactly where it was, *Same Species* (SS), moved to another tree of the same species as the original host and *Different Species* (DS), moved to a species that never hosts Grey Mistletoe

Table 7. Chapter 3: Suite of GzLMs (negative binomial log link) investigating the effects of habitat variables on bird visits to treatments. AIC and Δ AIC values (as compared to the basic model) presented for model of best fit selection. Treatment: *In-situ* (IS) cut from the original host tree and reattached exactly where it was, *Same Species* (SS), moved to another tree of the same species as the original host and *Different Species* (DS), moved to a species that never hosts Grey Mistletoe. Selected model in BOLD.

Covariate	AIC	Δ AIC
None	176.027	
Host height	177.989	-1.962
Host height Host canopy cover	176.604	-0.577
Host height Host canopy cover Number of mistletoes	-	-
Host height Host canopy cover	176.022	0.055

Number of mistletoes Number of fruits		
Host canopy cover Number of mistletoes Number of fruits	175.161	0.866
Number of mistletoes Number of fruits	176.226	-0.199
Number of fruits	175.888	0.139
Host canopy cover Number of fruits	174.155	1.872
Host height Host canopy cover Number of fruits	175.488	0.539
Host height Number of fruits	176.938	-0.911
Number of mistletoes	176.985	-0.958
Host canopy cover Number of mistletoes	175.698	0.329
Host height Number of mistletoes	178.798	-2.771
Host canopy cover	174.907	1.12
Host height Number of fruits Number of mistletoes	177.799	-1.772

AIC (-) this test was not valid

Table 8. Chapter 3: Suite of GzLMs (Poisson, log linear) investigating the effects of habitat variables on specialist bird visits to treatments. AIC and Δ AIC values (as compared to the basic model) presented for model of best fit selection. *In-situ* (IS) cut from the original host tree and reattached exactly where it was, *Same Species* (SS), moved to another tree of the same species as the original host and *Different Species* (DS), moved to a species that never hosts Grey Mistletoe. Selected model in BOLD.

Covariate	AIC	Δ AIC
None	97.518*	
Host height	-	-
Host height Host canopy cover	-	-
Host height Host canopy cover Number of mistletoes	-	-
Host height Host canopy cover Number of mistletoes	93.468	4.05

Number of fruits		
Host canopy cover Number of mistletoes Number of fruits	91.605	5.913
Number of mistletoes Number of fruits	90.537	6.981
Number of fruits	89.411	8.107
Host canopy cover Number of fruits	90.287	7.231
Host height Host canopy cover Number of fruits	92.096	5.422
Host height Number of fruits	91.372	6.146
Number of mistletoes	-	-
Host canopy cover Number of mistletoes	-	-
Host height Number of mistletoes	-	-
Host canopy cover	-	-
Host height Number of fruits Number of mistletoes	92.513	5.005

*This test was not valid Omnibus test ($\chi^2 = 5.298$, $df = 2$, $P = 0.071$)

AIC (-) this test was not valid.

Table 9. Chapter 3: Suite of GzLMs (Poisson, log linear) investigating the effects of habitat variables on generalist bird visits to treatments. AIC and Δ AIC values (as compared to the basic model) presented for model of best fit selection. *In-situ* (IS) cut from the original host tree and reattached exactly where it was, *Same Species* (SS), moved to another tree of the same species as the original host and *Different Species* (DS), moved to a species that never hosts Grey Mistletoe. Selected model in BOLD.

Covariate	AIC	Δ AIC
None	62.397	-
Host height	74.954	101.073
Host height Host canopy cover	76.431	99.596
Host height Host canopy cover Number of mistletoes	64.257	111.77
Host height Host canopy cover	65.221	110.806

Number of mistletoes Number of fruits		
Host canopy cover Number of mistletoes Number of fruits	63.329	112.698
Number of mistletoes Number of fruits	66.465	109.562
Number of fruits	90.332	85.695
Host canopy cover Number of fruits	85.248	90.779
Host height Host canopy cover Number of fruits	77.523	98.504
Host height Number of fruits	75.804	100.223
Number of mistletoes	66.922	109.105
Host canopy cover Number of mistletoes	62.397	113.63
Host height Number of mistletoes	63.976	112.051
Host canopy cover	84.012	92.015
Host height Number of fruits Number of mistletoes	64.257	111.77

Table 10. Chapter 3: Suite of GzLMs (Poisson, log linear) investigating the effects of habitat variables on opportunist bird visits to treatments. AIC and Δ AIC values (as compared to the basic model) presented for model of best fit selection. *In-situ* (IS) cut from the original host tree and reattached exactly where it was, *Same Species* (SS), moved to another tree of the same species as the original host and *Different Species* (DS), moved to a species that never hosts Grey Mistletoe. Selected model in BOLD.

Covariate	AIC	Δ AIC
None	138.876	
Host height	137.876	0.555
Host height Host canopy cover	133.249	5.182
Host height Host canopy cover Number of mistletoes	135.200	3.231
Host height Host canopy cover	134.182	4.249

Number of mistletoes Number of fruits		
Host canopy cover Number of mistletoes Number of fruits	-	-
Number of mistletoes Number of fruits	-	-
Number of fruits	-	-
Host canopy cover Number of fruits	-	-
Host height Host canopy cover Number of fruits	132.193	6.238
Host height Number of fruits	-	-
Number of mistletoes	-	-
Host canopy cover Number of mistletoes	137.624	0.807
Host height Number of mistletoes	-	-
Host canopy cover	135.638	2.793
Host height Number of fruits Number of mistletoes	-	-

AIC (-) this test was not valid.

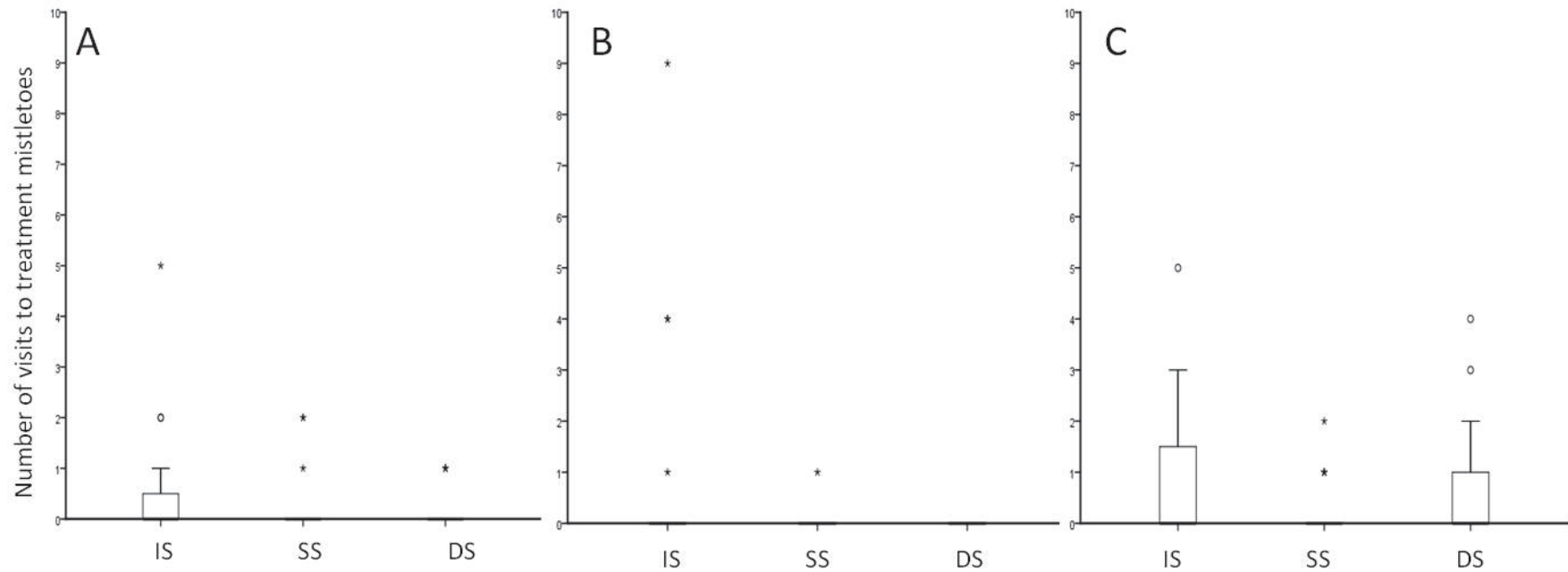


Figure 21. Referred to in Chapter 3. Box plots depicting the number of visits by each individual bird dietary guild to experimentally manipulated mistletoes: (A) mistletoe specialist, (B) generalist frugivores and (C) opportunist. Treatments: *In-situ* (IS) cut from the original host tree and reattached exactly where it was, *Same Species* (SS), moved to another tree of the same species as the original host and *Different Species* (DS), moved to a species that never hosts Grey Mistletoe. Circles are outliers.

Appendix 3. Extra data for Chapter 4: Habitat comparison: continuous forest *versus* roadside vegetation

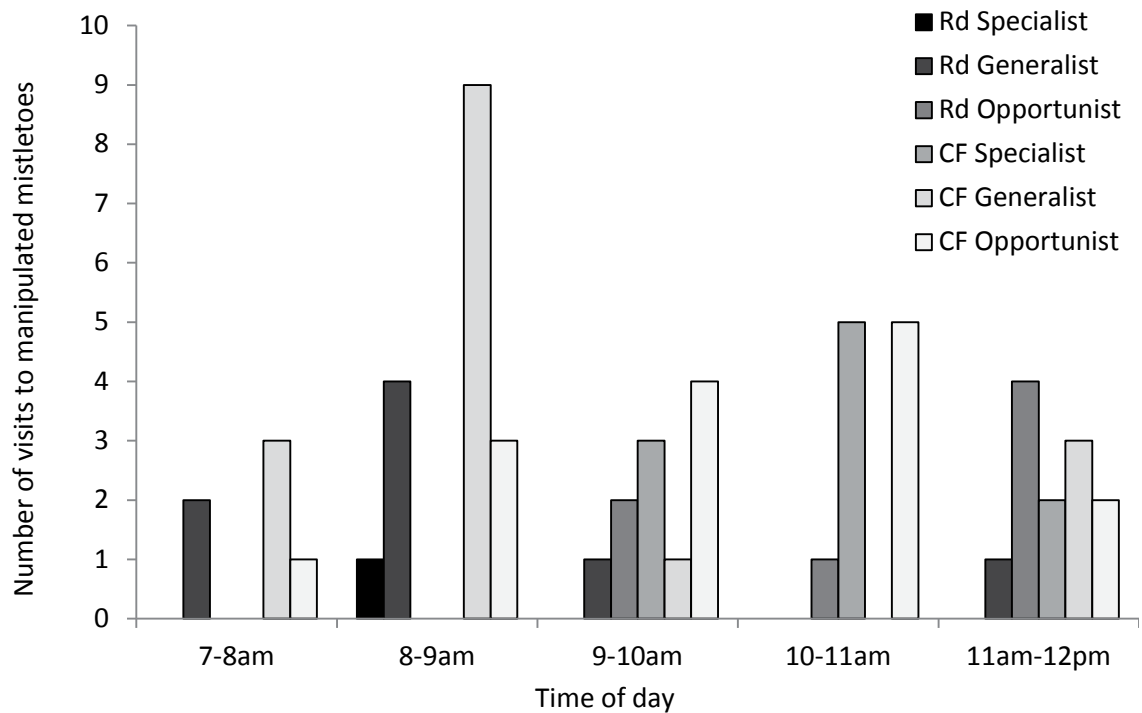


Figure 22. Chapter 4: Number of visits per hour by guilds (mistletoe specialist, generalist frugivore and opportunist), pooled across treatments (*In-situ* (IS) cut from the original host tree and reattached exactly where it was and, *Same Species* (SS), mistletoe cut and moved to another tree of the same species as the original host). Habitat types: roadside (Rd)/continuous forest (CF).

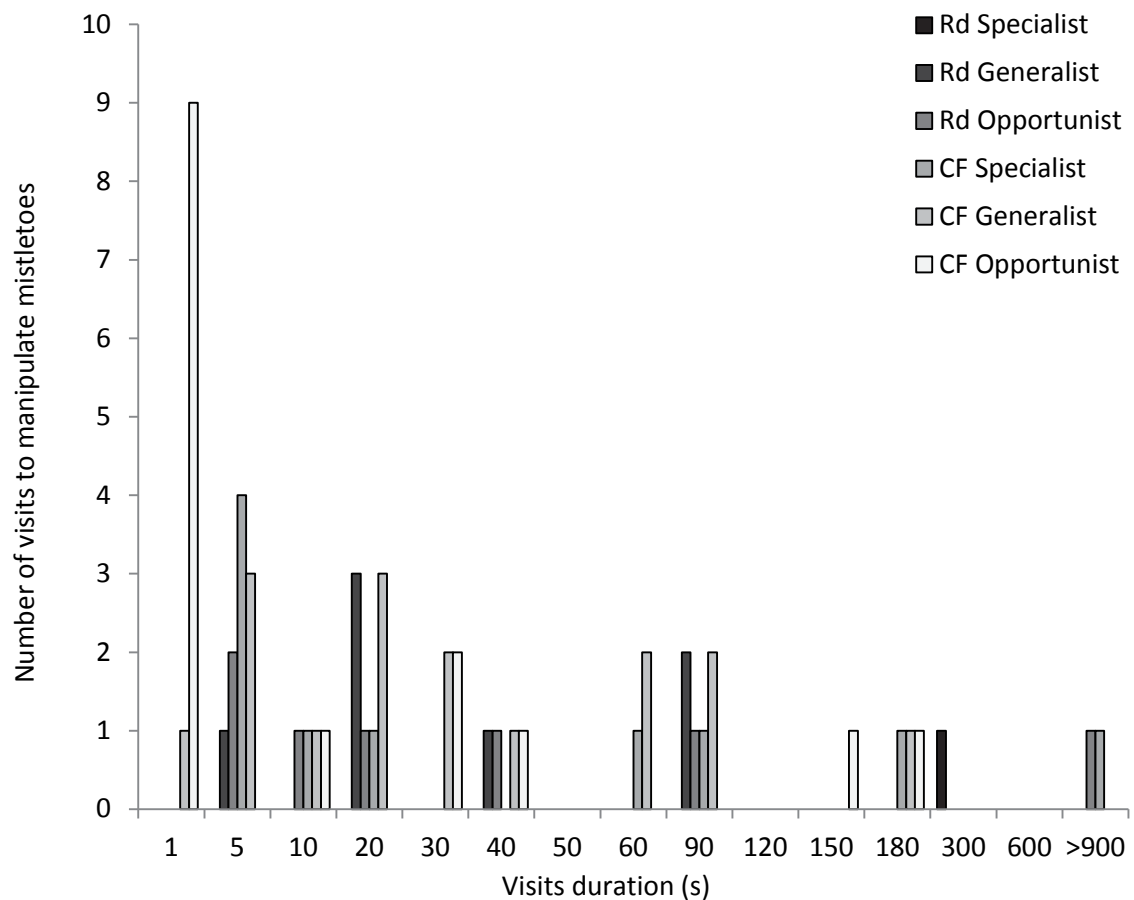


Figure 23. Binned visit durations by guilds (mistletoe specialist, generalist frugivore and opportunist), pooled across treatments (*In-situ* (IS) cut from the original host tree and reattached exactly where it was and, *Same Species* (SS), mistletoe cut and moved to another tree of the same species as the original host). Habitat types: roadside (Rd)/continuous forest (CF).

Table 11. Chapter 4: Suite of GzLMs (negative binomial log link) investigating the effects of habitat variables on habitat type and treatment visitation by birds. AIC and Δ AIC values (as compared to the basic model) presented for model of best fit selection. Habitat types: roadside/ continuous forest. Treatment: *In-situ* cut from the original host tree and reattached exactly where it was and, *Same Species*, mistletoe cut and moved to another tree of the same species as the original host. Interaction: Habitat type x treatment. Selected model in BOLD.

Covariate	AIC	Δ AIC
None	176.919	-
Number of fruits	176.814	0.105
Number of fruits Host canopy cover	178.600	-1.681
Number of fruits Host canopy cover	180.554	-3.635

Number of mistletoes		
Host canopy cover Number of mistletoes	180.660	-3.741
Number of mistletoes	178.883	-1.964
Host canopy cover	178.722	-1.803
Number of fruits Number of mistletoes	178.790	-1.871

Table 12. Chapter 4: Suite of GzLMs (negative binomial log link) investigating effects of habitat variables on specialists visits to habitat type and treatment. AIC and Δ AIC values (as compared to the basic model) presented for model of best fit selection. Habitat variables: number of fruits on manipulated mistletoe, host canopy cover, number of mistletoes on host tree. Habitat type: roadside/continuous forest. Treatment: *In-situ* cut from the original host tree and reattached exactly where it was and, *Same Species*, mistletoe cut and moved to another tree of the same species as the original host. No interaction terms. Selected model in BOLD.

Covariate	AIC	Δ AIC
None	64.881*	-
Number of fruits	64.805	0.076
Number of fruits Host canopy cover	66.801	-1.92
Number of fruits Host canopy cover Number of mistletoes	68.735	-3.854
Host canopy cover Number of mistletoes	68.863	-3.982
Number of mistletoes	66.881	-2
Host canopy cover	66.864	-1.983
Number of fruits Number of mistletoes	66.735	-1.854

*This test was not valid (Omnibus test: $\chi^2 = 8.217$, $df = 2$, $P = 0.016$)

Table 13. Chapter 4: Suite of GzLMs (negative binomial log link) investigating effects of habitat variables on generalist visits to habitat type and treatment. AIC and Δ AIC values (as compared to the basic model) presented for model of best fit selection. Habitat variables: number of fruits on manipulated mistletoe, host canopy cover, number of mistletoes on host tree. Habitat type: roadside/continuous forest. Treatment: *In-situ* cut from the original host tree and reattached exactly where it was and, *Same Species*, mistletoe cut and moved to another tree of the same species as the original host. Interaction: Habitat type x treatment. Selected model in BOLD.

Covariate	AIC	Δ AIC
none	107.098	-
Number of fruits	108.717	-1.619
Number of fruits Host canopy cover	110.349	-3.251
Number of fruits Host canopy cover Number of mistletoes	111.595	-4.497
Host canopy cover Number of mistletoes	109.877	-2.779
Number of mistletoes	108.433	-1.335
Host canopy cover	108.647	-1.549
Number of fruits Number of mistletoes	110.071	-2.973

Appendix 4: Bird species lists

Table 14. Bird species list for Chapter 2. Species recorded visiting treatment mistletoes and recorded in surrounding habitat during observations. Common name, *scientific name* and dietary guild classification.

Species that visited treatment mistletoes		
Mistletoebird	<i>Dicaeum hirundinaceum</i>	Mistletoe specialist
Singing Honeyeater	<i>Lichenostomus virescens</i>	Generalist frugivore
Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	Generalist frugivore
Eastern Yellow Robin	<i>Eopsaltria australis</i>	Opportunist
Inland Thornbill	<i>Acanthiza apicalis</i>	Opportunist
Red-capped Robin	<i>Petroica goodenovii</i>	Opportunist
Southern Whiteface	<i>Aphelocephala leucopsis</i>	Opportunist
Yellow Thornbill	<i>Acanthiza nana</i>	Opportunist
Species recorded during observations in the general area		
Mistletoebird	<i>Dicaeum hirundinaceum</i>	Mistletoe specialist
Painted Honeyeater	<i>Grantiella picta</i>	Mistletoe specialist
Singing Honeyeater	<i>Lichenostomus virescens</i>	Generalist frugivore
Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	Generalist frugivore
Striped Honeyeater	<i>Plectorhyncha lanceolata</i>	Generalist frugivore
Australian (Mallee) Ringneck	<i>Barnardius zonarius</i>	Opportunist
Apostlebird	<i>Struthidea cinerea</i>	Opportunist
Black faced Cuckoo Shrike	<i>Coracina novaehollandiae</i>	Opportunist
Collared Sparrowhawk	<i>Accipiter cirrocephalus</i>	Opportunist
Common Bronzewing	<i>Phaps chalcoptera</i>	Opportunist
Eastern Yellow Robin	<i>Eopsaltria australis</i>	Opportunist
Grey Butcherbird	<i>Cracticus torquatus</i>	Opportunist
Grey Fantail	<i>Rhipidura albiscapa</i>	Opportunist
Grey Shrike Thrush	<i>Colluricincla harmonica</i>	Opportunist
Inland Thornbill	<i>Acanthiza apicalis</i>	Opportunist
Mulga Parrot	<i>Psephotus varius</i>	Opportunist
Noisy Miner	<i>Manorina melanocephala</i>	Opportunist
Parrot sp.		Opportunist
Red-capped Robin	<i>Petroica goodenovii</i>	Opportunist
Rufous Whistler	<i>Pachycephala rufiventris</i>	Opportunist
Sacred Kingfisher	<i>Todiramphus sanctus</i>	Opportunist

Southern Whiteface	<i>Aphelocephala leucopsis</i>	Opportunist
Splendid Fairy Wren	<i>Malurus splendens</i>	Opportunist
Striated Pardalote	<i>Pardalotus striatus</i>	Opportunist
Superb Parrot	<i>Polytelis swainsonii</i>	Opportunist
Thornbill sp.	<i>Acanthiza</i> sp.	Opportunist
Varied Sitella	<i>Daphoenositta chrysoptera</i>	Opportunist
Wattlebird sp.		Opportunist
White-browed Babbler	<i>Pomatostomus superciliosus</i>	Opportunist
Western Gerygone	<i>Gerygone fusca</i>	Opportunist
White-winged Chough	<i>Corcorax melanorhamphos</i>	Opportunist
Willie Wagtail	<i>Rhipidura leucophrys</i>	Opportunist
Yellow Thornbill	<i>Acanthiza nana</i>	Opportunist
Yellow-rumped Thornbill	<i>Acanthiza chrysorrhoa</i>	Opportunist
Unknown sp.		Opportunist

Table 15. Bird species for Chapter 3. Species recorded visiting experimentally manipulated mistletoes and recorded in surrounding habitat during observations. Common name, *scientific name* and dietary guild classification.

Species that visited experimentally manipulated mistletoes		
Mistletoebird	<i>Dicaeum hirundinaceum</i>	Mistletoe specialist
Silvereye	<i>Zosterops lateralis</i>	Generalist frugivore
Singing Honeyeater	<i>Lichenostomus virescens</i>	Generalist Frugivore
Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	Generalist frugivore
Striped Honeyeater	<i>Plectorhyncha lanceolata</i>	Generalist frugivore
Australian (Mallee) Ringneck	<i>Barnardius zonarius</i>	Opportunist
Double-barred Finch	<i>Taeniopygia bichenovii</i>	Opportunist
Grey Shrike-thrush	<i>Colluricincla harmonica</i>	Opportunist
Inland Thornbill	<i>Acanthiza apicalis</i>	Opportunist
Noisy Miner	<i>Manorina melanocephala</i>	Opportunist
Red-capped Robin	<i>Petroica goodenovii</i>	Opportunist
Rufous Whistler	<i>Pachycephala rufiventris</i>	Opportunist
Splendid Fairy Wren	<i>Malurus splendens</i>	Opportunist
Yellow Thornbill	<i>Acanthiza nana</i>	Opportunist
Unknown		Opportunist
Species recorded during observations in the general area		
Mistletoebird	<i>Dicaeum hirundinaceum</i>	Mistletoe specialist
Painted Honeyeater	<i>Grantiella picta</i>	Mistletoe specialist
Silvereye	<i>Zosterops lateralis</i>	Generalist frugivore
Singing Honeyeater	<i>Lichenostomus virescens</i>	Generalist Frugivore
Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	Generalist frugivore
Striped Honeyeater	<i>Plectorhyncha lanceolata</i>	Generalist frugivore
Australian (Mallee) Ringneck	<i>Barnardius zonarius</i>	Opportunist
Black-chinned Honeyeater	<i>Melithreptus gularis</i>	Opportunist
Black faced Cuckoo Shrike	<i>Coracina novaehollandiae</i>	Opportunist
Chestnut-rumped Thornbill	<i>Acanthiza uropygialis</i>	Opportunist
Crested Pigeon	<i>Ocyphaps lophotes</i>	Opportunist
Double-barred Finch	<i>Taeniopygia bichenovii</i>	Opportunist
Eastern Rosella	<i>Platycercus eximius</i>	Opportunist
Eastern Yellow Robin	<i>Eopsaltria australis</i>	Opportunist

Grey Fantail	<i>Rhipidura albiscapa</i>	Opportunist
Grey Shrike-thrush	<i>Colluricincla harmonica</i>	Opportunist
Inland Thornbill	<i>Acanthiza apicalis</i>	Opportunist
Jacky Winter	<i>Microeca fascinans</i>	Opportunist
Little Friarbird	<i>Philemon citreogularis</i>	Opportunist
Magpielark	<i>Grallina cyanoleuca</i>	Opportunist
Mulga Parrot	<i>Psephotus varius</i>	Opportunist
Noisy Miner	<i>Manorina melanocephala</i>	Opportunist
Pardalote sp.	<i>Pardalotus sp.</i>	Opportunist
Parrot sp.		Opportunist
Peaceful Dove	<i>Geopelia striata</i>	Opportunist
Red-capped Robin	<i>Petroica goodenovii</i>	Opportunist
Red Wattlebird	<i>Anthochaera carunculata</i>	Opportunist
Rufous Whistler	<i>Pachycephala rufiventris</i>	Opportunist
Southern Whiteface	<i>Aphelocephala leucopsis</i>	Opportunist
Speckled Warbler	<i>Chthonicola sagitta</i>	Opportunist
Splendid Fairy Wren	<i>Malurus splendens</i>	Opportunist
Striated Pardalote	<i>Pardalotus striatus</i>	Opportunist
Varied Sitella	<i>Daphoenositta chrysoptera</i>	Opportunist
Weebill	<i>Smicrornis brevirostris</i>	Opportunist
Western Gerygone	<i>Gerygone fusca</i>	Opportunist
White-browed Babbler	<i>Pomatostomus superciliosus</i>	Opportunist
White-eared Honeyeater	<i>Lichenostomus leucotis</i>	Opportunist
White-plumed Honeyeater	<i>Lichenostomus penicillatus</i>	Opportunist
White-winged Chough	<i>Corcorax melanorhamphos</i>	Opportunist
Willie Wagtail	<i>Rhipidura leucophrys</i>	Opportunist
Thornbill sp.	<i>Acanthiza sp.</i>	Opportunist
Yellow Thornbill	<i>Acanthiza nana</i>	Opportunist
Yellow-rumped Thornbill	<i>Acanthiza chrysorrhoa</i>	Opportunist
Unknown sp.		Opportunist

Table 16. Bird species recorded in Chapter 4. Species recorded visiting experimentally manipulated mistletoes and recorded in surrounding habitat during observations. Common name, *scientific name* and dietary guild classification.

Roadside		
Species that visited experimentally manipulated mistletoes		
Mistletoebird	<i>Dicaeum hirundinaceum</i>	Mistletoe Specialist
Singing Honeyeater	<i>Lichenostomus virescens</i>	Generalist Frugivore
Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	Generalist Frugivore
Chestnut-rumped Thornbill	<i>Acanthiza uropygialis</i>	Opportunist
Noisy Miner	<i>Manorina melanocephala</i>	Opportunist
Unknown sp.		Opportunist
Yellow Thornbill	<i>Acanthiza nana</i>	Opportunist
Species recorded during observations in the general area		
Mistletoebird	<i>Dicaeum hirundinaceum</i>	Mistletoe Specialist
Painted Honeyeater	<i>Grantiella picta</i>	Mistletoe Specialist
Singing Honeyeater	<i>Lichenostomus virescens</i>	Generalist Frugivore
Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	Generalist Frugivore
Striped Honeyeater	<i>Plectorhyncha lanceolata</i>	Generalist Frugivore
Apostlebird	<i>Struthidea cinerea</i>	Opportunist
Australian Raven	<i>Corvus coronoides</i>	Opportunist
Black-eared Cuckoo	<i>Chalcites osculans</i>	Opportunist
Black faced Cuckoo Shrike	<i>Coracina novaehollandiae</i>	Opportunist
Blue Bonnet Parrot	<i>Northiella haematogaster</i>	Opportunist
Chestnut-rumped Thornbill	<i>Acanthiza uropygialis</i>	Opportunist
Crested Pigeon	<i>Ocyphaps lophotes</i>	Opportunist
Cockatiel	<i>Nymphicus hollandicus</i>	Opportunist
Eastern Rosella	<i>Platycercus eximius</i>	Opportunist
Magpie	<i>Cracticus tibicen</i>	Opportunist
Magpielark	<i>Grallina cyanoleuca</i>	Opportunist
Noisy Miner	<i>Manorina melanocephala</i>	Opportunist
Pardalote sp.	<i>Pardalotus sp.</i>	Opportunist
Parrot sp.		Opportunist
Pied Butcherbird	<i>Cracticus nigrogularis</i>	Opportunist
Rainbow Bee-eater	<i>Merops ornatus</i>	Opportunist

Red-capped Robin	<i>Petroica goodenovii</i>	Opportunist
Red Wattlebird	<i>Anthochaera carunculata</i>	Opportunist
Rufous Whistler	<i>Pachycephala rufiventris</i>	Opportunist
Superb Parrot	<i>Polytelis swainsonii</i>	Opportunist
Thornbill sp.	<i>Acanthiza sp.</i>	Opportunist
White-plumed Honeyeater	<i>Lichenostomus penicillatus</i>	Opportunist
White-winged Chough	<i>Corcorax melanorhamphos</i>	Opportunist
White-winged Triller	<i>Lalange sueurii</i>	Opportunist
Willie Wagtail	<i>Rhipidura leucophrys</i>	Opportunist
Yellow Thornbill	<i>Acanthiza nana</i>	Opportunist
Yellow-rumped Thornbill	<i>Acanthiza chrysorrhoa</i>	Opportunist
Zebra Finch	<i>Taeniopygia guttata</i>	Opportunist
Unknown sp.		Opportunist

Continuous Forest

Species that visited experimentally manipulated mistletoes

Mistletoebird	<i>Dicaeum hirundinaceum</i>	Mistletoe Specialist
Silvereye	<i>Zosterops lateralis</i>	Generalist Frugivore
Singing Honeyeater	<i>Lichenostomus virescens</i>	Generalist Frugivore
Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	Generalist Frugivore
Double-barred Finch	<i>Taeniopygia bichenovii</i>	Opportunist
Inland Thornbill	<i>Acanthiza apicalis</i>	Opportunist
Noisy Miner	<i>Manorina melanocephala</i>	Opportunist
Red-capped Robin	<i>Petroica goodenovii</i>	Opportunist
Rufous Whistler	<i>Pachycephala rufiventris</i>	Opportunist
Splendid Fairy Wren	<i>Malurus splendens</i>	Opportunist
Yellow Thornbill	<i>Acanthiza nana</i>	Opportunist
Unknown sp.		Opportunist

Species recorded during observations in the general area

Mistletoebird	<i>Dicaeum hirundinaceum</i>	Mistletoe Specialist
Painted Honeyeater	<i>Grantiella picta</i>	Mistletoe Specialist
Silvereye	<i>Zosterops lateralis</i>	Generalist Frugivore
Singing Honeyeater	<i>Lichenostomus virescens</i>	Generalist Frugivore
Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	Generalist Frugivore
Striped Honeyeater	<i>Plectorhyncha lanceolata</i>	Generalist Frugivore

Australian (Mallee) Ringneck	<i>Barnardius zonarius</i>	Opportunist
Black-chinned Honeyeater	<i>Melithreptus gularis</i>	Opportunist
Black faced Cuckoo Shrike	<i>Coracina novaehollandiae</i>	Opportunist
Chestnut-rumped Thornbill	<i>Acanthiza uropygialis</i>	Opportunist
Double-barred Finch	<i>Taeniopygia bichenovii</i>	Opportunist
Eastern Rosella	<i>Platycercus eximius</i>	Opportunist
Eastern Yellow Robin	<i>Eopsaltria australis</i>	Opportunist
Grey Fantail	<i>Rhipidura albiscapa</i>	Opportunist
Grey Shrike-thrush	<i>Colluricincla harmonica</i>	Opportunist
Inland Thornbill	<i>Acanthiza apicalis</i>	Opportunist
Jacky Winter	<i>Microeca fascinans</i>	Opportunist
Magpielark	<i>Grallina cyanoleuca</i>	Opportunist
Mulga Parrot	<i>Psephotus varius</i>	Opportunist
Noisy Miner	<i>Manorina melanocephala</i>	Opportunist
Parrot sp.		Opportunist
Peaceful Dove	<i>Geopelia striata</i>	Opportunist
Red-capped Robin	<i>Petroica goodenovii</i>	Opportunist
Rufous Whistler	<i>Pachycephala rufiventris</i>	Opportunist
Southern Whiteface	<i>Aphelocephala leucopsis</i>	Opportunist
Speckled Warbler	<i>Chthonicola sagitta</i>	Opportunist
Splendid Fairy Wren	<i>Malurus splendens</i>	Opportunist
Striated Pardalote	<i>Daphoenositta chrysoptera</i>	Opportunist
Varied Sitella	<i>Daphoenositta chrysoptera</i>	Opportunist
Western Gerygone	<i>Gerygone fusca</i>	Opportunist
White-browed Babbler	<i>Pomatostomus superciliosus</i>	Opportunist
White-eared Honeyeater	<i>Lichenostomus leucotis</i>	Opportunist
White-plumed Honeyeater	<i>Lichenostomus penicillatus</i>	Opportunist
White-winged Chough	<i>Corcorax melanorhamphos</i>	Opportunist
Willie Wagtail	<i>Rhipidura leucophrys</i>	Opportunist
Thornbill sp.	<i>Acanthiza sp.</i>	Opportunist
Yellow Thornbill	<i>Acanthiza nana</i>	Opportunist
Yellow-rumped Thornbill	<i>Acanthiza chrysorrhoa</i>	Opportunist
Unknown sp.		Opportunist

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