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Characteristics of urbanization that influence bird communities in suburban remnant vegetation

A thesis submitted in fulfilment of the requirements for
the award of the degree of Doctor of Philosophy

From

University of Wollongong

By

Patricia Ruth Hodgson

Bachelor of Science in Environmental Biology

Bachelor of Science (Honours) in Biological and Biomedical Sciences

I, Patricia Ruth Hodgson, declare that this thesis, submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the Department of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Patricia Ruth Hodgson

31st August 2005

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Abstract

In many landscapes subject to fragmentation, particularly through the process of urbanization, small remnants of original native vegetation surrounded by a highly modified matrix are often the only suitable habitat for most native species. Management of these small remnants may be the most feasible option for the conservation of regional avian biodiversity and urban-sensitive species. Remnant native vegetation may improve the complexity of urban vegetation, or provide regular habitat or stepping-stones for dispersal in an inhospitable matrix. External factors in the surrounding matrix, or internal constraints related to the size of the remnant may influence bird communities within remnant vegetation. Determining the relative influence between these factors should assist management of conditions that will help to retain urban-sensitive species.

On the Central Coast of New South Wales, Australia, bird communities in remnant vegetation were surveyed to investigate the influence of internal and external factors on composition. The effect of housing density and vegetation type was investigated in relation to remnant size. The foraging behaviour of five insectivorous species (present in low numbers) in remnants surrounded by high-density housing was examined in relation to the vegetation structure. Bird movements across habitat edges were investigated at the interface between remnant vegetation and suburban housing. The proportion of crossings by guilds and individual species were compared between edges of high- and low-density housing.

Bird communities of remnant vegetation were significantly influenced by the surrounding housing density. There was no interaction between remnant size and

surrounding housing density, suggesting external factors were having a greater influence than internal factors. Community composition changed in response to surrounding housing density. Introduced species, granivores and medium nectarivores occurred more often in remnants surrounded by high-density housing. These communities resembled those commonly described for the urban matrix itself. Small insectivores and nectarivores occurred more often in remnants surrounded by low-density housing, giving these communities a closer resemblance to those often described in undisturbed vegetation. It appears that remnants surrounded by low-density housing can support several bird species dependent on native habitat.

The composition of bird communities in remnant vegetation was significantly influenced by vegetation type when remnants were larger than 80 ha. In remnants smaller than 35 ha bird communities were not influenced by vegetation type, suggesting they are influenced more by external factors. Bird density and species richness were influenced by vegetation structure and were positively associated with high-shrub cover. Increasing the cover of high shrubs may be one way to improve bird diversity within remnants smaller than 35 ha. Retaining larger remnants (> 80 ha) that provide resistance to characteristics of the surrounding suburban matrix is likely to be an important way of maintaining urban-sensitive species and bird assemblages specific to particular vegetation types, over the majority of the suburban landscape.

The foraging behavior of small insectivorous birds in remnants surrounded by high-density housing was not adversely affected by urbanization. Canopy- and shrub-foragers showed minimal behavioural changes. Species classified as feeding on or near the ground tended to forage at lower heights in remnants compared with those in

continuous vegetation. These changes were partially explained by structural differences between vegetation in remnants and continuous sites. The rate at which birds attacked prey items was significantly higher in continuous habitat for only two species. Overall, it appears that remnants have potential value as habitat and foraging sources in a suburban landscape. Despite this, small insectivores are still sensitive to urbanization, suggesting that other factors, probably associated with the matrix, are important.

Behavioural responses to edges adjoining the two densities of housing matrix differed significantly among feeding guilds. Guilds of omnivores and nectarivores were significantly more likely than insectivores to penetrate edges adjoining high-density housing. Analysis of individual species revealed several consistent trends. Nectarivorous species appeared more likely to cross at edges of high-density housing, while insectivores were more likely to cross at edges of low-density housing. Regression models suggest these trends were influenced by characteristics within the matrix, principally the proportion of housing and shrub and canopy vegetation. Importantly, by crossing at these habitat edges many species demonstrated, that with appropriate management of the housing matrix, they have the potential for dispersal necessary for the maintenance of meta-populations.

Overall this thesis suggests that characteristics of the surrounding matrix influence both the internal remnant quality and the ability of birds to disperse among remnant vegetation. Therefore management of the matrix is likely to play a pivotal role if small remnants are to function as a habitat network and promote the avian diversity of suburban landscapes.

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Chapter 1

General introduction

1.1 Habitat components of the fragmented landscape

Habitat loss through land clearing or modification results in fragmentation of original native habitat that is reduced to isolated remnants. Lost habitat is replaced by a new matrix, in which the remnants are embedded. Increasing fragmentation reduces the size of remnants and creates proportionally more and more edge environment in the landscape (Merriam & Wegner 1992). The amount of original habitat in a remnant is thus further reduced through the infiltration of edge effects, which occur where previously sheltered, undisturbed habitat becomes exposed to the new matrix. The depth to which edge effects penetrate into the remnant creates an edge zone. The edge zone potentially provides sub-optimal habitat in relation to the remainder of the remnant, which is known as the undisturbed core or effective remnant area for organisms dependent on the original vegetation (Freemark *et al.* 2002).

Edge effects can be created by the physical edge itself and by characteristics of the new matrix. At the physical edge, effective remnant area may be reduced through changes in abiotic factors, such as increased wind, light intensity or temperature (Sisk *et al.* 1997; Beer & Fox 2000). These changes potentially cause direct alteration to the microclimate at the edge of the remnant, or indirect changes through alteration of the vegetation structure (Saunders *et al.* 1991). Structural changes can include a greater number of saplings (Jokimaki *et al.* 1998), or a lower canopy and leaf litter cover accompanied by greater shrub cover (Watson *et al.* 2004).

Effective remnant area may also be reduced through direct and indirect effects of the surrounding matrix. Elements from the matrix can potentially invade remnant vegetation. For instance, the structure and composition of native habitat can be directly altered by land management practices in the matrix which result in the proliferation of weed species, trails, anthropogenic rubbish, urban runoff and activities that compact soil and remove dead wood (Kruger & Lawes 1997; Gilfedder & Kirkpatrick 1998; Sauvajout *et al.* 1998). The edge environment may also reduce effective remnant area by providing conditions that favour some organisms over others. Rates of competition, parasitism or predation from species that invade from the matrix have the potential to increase at remnant edges (Bayne & Hobson 1997; Pell & Tidemann 1997; Chace *et al.* 2003).

As the successor to the original habitat, matrices of different structure can differ substantially in the intensity of the edge effects they impose upon a remnant. The matrix can act as a buffer, reducing the exposure of the remnant edge to abiotic factors (Franklin 1993). Reducing the exposure may reduce the penetration distance of the edge zone, leaving a larger effective remnant area. A matrix of similar composition to the remnant reduces the contrast across habitats and is likely to have a greater buffering capacity than a dissimilar matrix with a high contrast (Lindenmayer & Franklin 2000). Modelling studies suggest that 58 % less habitat is required for population persistence when the quality of the matrix is improved from low to high (Fahrig 2001).

Characteristics of remnants and their surrounding matrix can potentially complement each other and enable populations to persist in a fragmented landscape. A collection of remnants between which organisms can move may form a habitat network. The functionality of habitat networks depends on remnant quality, as well as characteristics that influence the movements of organisms, such as permeability of the matrix, distance between remnants, and the spatial arrangement of remnants (Hobbs 2002; Opdam 2002).

1.2 Species responses to small effective remnant area and the matrix

Continuing habitat loss raises concerns over whether species can survive in the long term using isolated remnants in a fragmented landscape. Many species appear to be fragmentation-sensitive as their population viability is reduced in fragmented landscapes (Kattan *et al.* 1994; Porneluzi & Faaborg 1999; Crooks *et al.* 2001; Luck 2003). Concern for species dependent on the original vegetation is greatest as they are likely to be restricted to remnants, and their loss has the potential to greatly reduce the biodiversity found in fragmented landscapes.

Species dependent on original vegetation need remnants and habitat networks with effective areas large enough to provide their full range of foraging and home range requirements. According to these requirements, fragmentation theoretically creates two classes of remnants; large remnants that contain the full range of conditions necessary for survival, and smaller remnants that suffer shortages unless supplemented from the matrix or other remnants. Species in small remnants have sometimes been shown to experience relative food shortages compared with those in

larger remnants (Burke & Nol 1998; Zarette *et al.* 2000). The greater survival potential in large remnants may partially be reflected by the higher species richness (Brotons & Herrando 2001a; Beier *et al.* 2002; Castelletta *et al.* 2005) which is often connected with greater habitat heterogeneity than is found in small remnants (Hinsley *et al.* 1998; Donnelly & Marzluff 2004).

For species dependent on native vegetation, the influence of the physical edge and matrix composition on effective remnant size can represent a loss of useable habitat and resources. This effect is potentially observed through a reduction in species richness, abundance or changes in guild composition that often occurs from the remnant interior towards the edge (Bolger *et al.* 1997; Baker *et al.* 1998; Restrepo & Gomez 1998; Dale *et al.* 2000; Fernandez-Juricic 2001; Beier *et al.* 2002). Species dependent on remnants may be able to compensate for a small effective remnant size and resource deficiency by supplementing their requirements from nearby resources in the matrix (Saunders 1989). This resource supplementation is potentially demonstrated when small remnants contain more species than large remnants (Loman & Von Schantz 1991) or when there is an overlap in species composition between communities in adjacent habitats (Norton *et al.* 2000). Species unable to use the matrix for supplementation may need to compensate by using multiple remnants to meet their requirements (Dunning *et al.* 1992; Hinsley 2000; Graham 2001; Norris & Stutchbury 2001).

Therefore the fragmentation response of species in remnants with small effective areas may be driven by remnant area, or by characteristics of the matrix. If a species' response varies with remnant size but not with differences in matrix composition, it

suggests that internal conditions in the remnant have an important influence on its survival, while if a species responds to differences in matrix composition but not remnant size, it suggests that factors external to the remnant are more important. External influences potentially have a more widespread effect because many remnants may be embedded in the same matrix, whereas internal influences are potentially confined to a single remnant. Understanding the relative influence of size and matrix on species in remnants is essential if management of fragmented landscapes is to focus effectively on the survival of species dependent on original vegetation, especially if different species respond to different influences within the same landscape (Lee *et al.* 2002).

1.3 Population linkages in fragmented landscapes

Species that can acquire resources for their immediate survival in remnants must also maintain enough individuals and breeding pairs for a genetically viable population. Species may need to occupy several remnants for this purpose (Mortberg 1998). This distribution is often modelled around meta-population and source-sink concepts (Henderson *et al.* 1985; Pulliam 1988; Moilanen & Hanski 1998). Meta-populations are a group of sub-populations where each occupies a habitat patch or remnant of equal quality (Hanski & Gilpin 1991). While these sub-populations may experience stochastic extinctions at the local level, the meta-population is maintained at the regional level through local recolonization by dispersers from another sub-population. Sub-populations in source-sink configurations are distributed throughout habitat patches or remnants of varying quality (Dias 1996). Source populations exist in remnants of good quality and produce an abundance of offspring that exceed the

carrying capacity of the patch. Offspring must disperse in order to find territories of their own. Territories are most often available in remnants of poor quality where the death rate exceeds the birth rate, creating sink populations. The exchange between source and sink remnants maintains the meta-population at a regional level. Both these models rely on all remnants (meta-population model) or several remnants (source-sink model) providing the full range of conditions necessary for the survival of a sub-population of the species (Baillie *et al.* 2000). Meta-populations are synonymous with habitat networks, where network populations are considered viable but the local populations are not (Opdam 2002).

A key element to the use of multiple remnants or habitat networks is the movement and dispersal of individuals (Fahrig & Merriam 1994; Dias 1996). Successful movement is likely to be influenced by the dispersal characteristics of a species such as maximum flight distance (Norris & Stutchbury 2001), as well as conditions such as the isolation distance between suitable remnants. More isolated remnants are less likely to be used or colonized (Dunning *et al.* 1995; Gustafson & Gardner 1996; Fortin & Arnold 1997).

In fragmented landscapes the degree of remnant isolation can be influenced by the connectivity of the matrix. Matrix connectivity can be structural or functional (With 2002). Structural connectivity occurs when vegetation, usually the same type as the remnant, forms a corridor that provides a physical linkage between remnants that leads species between remnants (Freemark *et al.* 2002; Opdam 2002; Uezu *et al.* 2005). Functional connectivity occurs when species are able to use characteristics of the matrix in the absence of corridors.

For individuals that must move through the surrounding matrix to use multiple remnants or habitat networks, successful movement and dispersal is likely to be influenced by the characteristics or permeability of the matrix (Fahrig & Merriam 1994; Tischendorf *et al.* 2003). Ease of movement through different matrix types potentially accounted for a species area effect in remnants surrounded by grassland but not in remnants surrounded by plantations (Wethered & Lawes 2003). Similarly, species sensitive to fragmentation were better able to re-colonize some small remnants than others depending on the dominant plant species of surrounding secondary forest (Antongiovanni & Metzger 2005). Behavioural studies have demonstrated that different matrix types can affect an individuals' rate of movement (Belisle *et al.* 2001; Ricketts 2001; Hein *et al.* 2003).

Matrix permeability can be dependent on physical characteristics such as the amount of hospitable vegetation for use as protection or stepping-stones. For instance the homing abilities of forest-dependent birds decreased as forest cover in a rural fragmented landscape decreased (Belisle *et al.* 2001). In an agricultural matrix containing native vegetation, white-browed treecreepers (*Climacteris affinis*) were able to occupy remnants up to 8 km apart, but could only occupy remnants 3 km apart when native vegetation was absent from the matrix (Radford & Bennett 2004). The distribution of structural resources, rather than food resources, corresponded more closely with the population distribution of Mediterranean blue tits (*Parus caeruleus*) in a patchy environment (Pulido & Diaz 1997).

Alternatively, matrix permeability may be related to behavioural inhibitions that hinder a species dispersal, even though the matrix provides functional connectivity

(Harris & Reed 2002). For example, predation risk is considered an important dispersal cost (Yoder *et al.* 2004) and, as vulnerability to predation is related to structural cover, matrix structure can inhibit dispersal, even though a species has the potential to move through the matrix (Rodriguez *et al.* 2001).

1.4 Species movement and the influence of the edge environment

Individuals on the move make first contact with the matrix at the remnant edge. Therefore edge environments are a vital component of the fragmented landscape that can influence a species' distribution (Wiens 1992; Jokimaki & Huhta 1996). Birds approaching a remnant edge may respond to the altered conditions within the edge zone of the remnant or to matrix characteristics abutting the edge. This response influences their ability to approach the remnant edge in order to cross into the matrix and disperse. Species dependent on original vegetation may be unable to approach if they are edge-sensitive and respond to changes in the remnant edge zone caused by the physical edge environment or invasive matrix elements (Sauvajout *et al.* 1998; Watson *et al.* 2004). Alternatively these species may be tolerant of the edge zone and be able to approach the matrix, but instead may be matrix-sensitive. Physical or behavioural constraints associated with the matrix may then affect their impetus to cross and disperse. Studies of bird densities have detected both edge-sensitive species that responded to structural changes in edge vegetation (Kruger & Lawes 1997; Watson *et al.* 2004) and matrix-sensitive species that were present at the interior and the edge but did not occur in the matrix (Hansson 1983; Beier *et al.* 2002; Antos & White 2004).

Studies of actual edge crossing behaviour often employ playback methods to initiate an edge response. These studies most commonly identify matrix-sensitive species. Matrix quality determined the occurrence of small birds at edges, with their use of the matrix increasing as woody cover increased (Rodriguez *et al.* 2001). Flocks of understorey birds readily crossed roads covered by a partial canopy whereas flocks at roads without a canopy were less likely to cross (Develey & Stouffer 2001). Species given the option of travelling across a gap or through woodland preferred the woodland even though the distance was three times further (Desrochers & Hannon 1997). In the absence of playback methods, behaviour of chickadee flocks suggested they were matrix-sensitive as their association with forest edges was not related to foraging requirements, or vegetation changes at edges (Desrochers & Fortin 2000).

1.5 The urban landscape as a fragmented environment for birds

Fragmentation caused by expansion of an urban matrix creates a vastly different situation from the expansion of other matrices such as agriculture and forestry. Urban landscapes typically contain small remnants (Porter *et al.* 2001; Stenhouse 2004), relative to agricultural and forestry landscapes where comparatively large remnants still occur. Recommendations (based on agricultural and forestry research) suggesting that large remnants will provide a better conservation outcome than small remnants are likely to be inappropriate, as are those suggesting enlargement of small remnants (Renjifo 1999; Cornelius *et al.* 2000; Major *et al.* 2001; Beier *et al.* 2002; Castelletta *et al.* 2005). Opportunities similar to re-claiming and re-vegetating adjacent paddocks may be limited in urban landscapes, where much of the original native vegetation is replaced on a permanent basis with hard impermeable surfaces

(Marzluff & Ewing 2001), and where remnant size may be constrained by buildings and associated infrastructure. These conditions suggest that urbanization has a more detrimental long-term effect that may be harder to reverse. Over time, remnants in an urban landscape can become degraded with a loss of plant species from native habitat (Solinska-Gornicka & Symonides 1995). The limited scope for increasing the size, or optimizing the shape of remnants in urban landscapes suggest that management of the surrounding matrix may provide a more feasible focus for the creation of habitat networks to promote the persistence of species dependent on native vegetation.

Urbanization generally creates a matrix with two opposing spatial gradients that radiate outwards from the city centre. The amount of buildings and associated infrastructure increase towards the city centre and is accompanied by a decrease in the volume and complexity of vegetation (Blair 1996; Clergeau *et al.* 1998). Use of the matrix by birds has been widely researched through the use of urban gradients in most climates including arid (Germaine *et al.* 1998; Green & Baker 2003; Fraterrigo & Wiens 2005), temperate (Clergeau *et al.* 1998; Bennett *et al.* 2004), humid sub-tropical (Sewell & Catterall 1998; Lim & Sodhi 2004), mediterranean (Bolger *et al.* 1997; Fernandez-Juricic 2000a; Crooks *et al.* 2004), tropical (Canaday 1997) and sub-arctic (Jokimaki & Suhonen 1998).

This urban gradient approach has been useful in determining how bird communities change across the urban landscape. It is widely accepted that as the degree of urbanization increases, the avifauna becomes more homogeneous (Blair 2001) through a decline in species richness and a corresponding increase in the abundance or dominance of exotic and native species adapted to the urban environment (Maeda

& Maruyama 1991; Blair 1996; Dulisz & Nowakowski 1996; Clergeau *et al.* 1998; Germaine *et al.* 1998; Jokimaki & Suhonen 1998; Marzluff *et al.* 2001; Sandstrom *et al.* in press). Feeding guild structure shifts from tree- and canopy-foraging insectivores to predominantly ground-foraging omnivores and granivores (Canaday 1997; Sewell & Catterall 1998; Allen & O'Connor 2000; Lim & Sodhi 2004). Similar changes occur over a temporal gradient of urbanization (Mason 1985; Munyenyembe *et al.* 1989; Parody *et al.* 2001) and between communities in the matrix and those in original native forest (Beissinger & Osborne 1982; Nilon *et al.* 1995; Evans *et al.* 1997; Catterall *et al.* 1998; Kluza *et al.* 2000; Parsons *et al.* 2003).

This research within the urban matrix has developed a sound basis on which to conduct research into the potential of remnants in an urban landscape to provide habitat networks for species dependent on native vegetation and sensitive to urbanization. Indications are that remnant vegetation, even small patches, provides important habitat and has potential conservation value (Grover & Slater 1994; Wood 1996; Catterall *et al.* 1997; Crooks *et al.* 2001; Parsons *et al.* 2003).

1.5.1 Species responses to small effective remnant area and the matrix in the urban landscape

The conservation value of remnants in the urban landscape will be influenced by their quality of vegetation. Conservation value is potentially high as remnants contain a significant proportion of the native vegetation in the region. Native vegetation appears to be an important factor influencing urban bird communities. Species richness and abundance increased as vegetation changed from exotic streetscapes to native streetscapes and parks (White *et al.* 2005). Furthermore native vegetation influenced the composition of native and exotic bird species. The number of native bird species increased with native vegetation while exotic bird species decreased (Green 1984).

Conservation potential may also be related to remnant vegetation structure. Structural complexity, often described as increasing shrub and canopy cover, is associated with a greater bird species diversity and abundance of specialist species in the urban matrix of streets, buildings and managed parklands (Fernandez-Juricic 2004; Sandstrom *et al.* in press). A similar trend is described for remnants in the urban landscape (Tilghman 1987; Grover & Slater 1994; Slater 1995). Remnant vegetation is likely to have a higher structural complexity than vegetation of the urban matrix, as its complexity is not compromised through requirements to provide areas of open lawns and walking paths for residential recreation.

Remnant integrity can be degraded through exposure to invasive elements from the matrix. Integrity, measured as the ratio of exotic to native plants species, was significantly associated with the type of surrounding matrix, with suburban remnants

having the highest exotic species richness (Gillfedder & Kirkpatrick 1998). As urbanization increased, vegetation condition decreased, and was accompanied by high levels of weed infestation, higher densities of formal and informal walking paths and disturbance such as fire (Matlack 1993; Stenhouse 2004). Variation in urban matrix composition is known to influence the bird communities in managed parklands (Morneau *et al.* 1999; Fernandez-Juricic 2000a, 2004) so the effects of matrix modification might also extend to remnant vegetation. Several studies indicate that abundance, species richness and species diversity of birds in remnants decrease as nearby urbanization increases (Rottenborn 1999; Miller *et al.* 2001).

The degree of invasion by matrix elements can be dependent on the amount of edge. Smaller remnants have a greater proportion of edge than larger remnants (Saunders *et al.* 1991; Turner *et al.* 2001) so the ability of a remnant to maintain its integrity may be influenced by its size. It is known that an increase in the size of managed parklands and remnants corresponds to an increase in bird abundance and species richness (Sasvari 1984; Tilghman 1987; Grover & Slater 1994; Mortberg 1998; Fernandez-Juricic 2000b; Fernandez-Juricic & Jokimaki 2001; Crooks *et al.* 2004; Drinnan 2005). Remnant size has sometimes been shown to have a stronger influence on species richness than surrounding housing density. Species richness was correlated with both variables, but increasing remnant size, was more strongly correlated than decreasing housing density (Tilghman 1987). Alternatively matrix composition has also been shown to have a greater influence than remnants size. The species richness of neo-tropical migrants decreased in diversity and abundance as building density increased, irrespective of remnant size (Freisen *et al.* 1995). Furthermore, a change in either factor may alter the influence of the other. In three

landscapes of increasing housing density, species richness consistently increased with reserve size, but the benefit of large reserve size only appeared to hold in landscapes with more than 20 % urban land cover (Donnelly & Marzluff 2004).

Given that urban-sensitive species in remnants with a small effective area may respond to internal remnant factors such as vegetation quality or size, or to external characteristics in the matrix, it is important to evaluate the relative effects of these factors to determine where urban conservation efforts should be directed to minimize impacts on bird communities in remnant vegetation.

1.5.2 Population linkages and influence of the edge environment in urban landscapes

Urban-sensitive species in remnants with a small effective area may also utilize multiple remnants or form meta-populations. Use of multiple remnants exposes birds to risks associated with source-sink dynamics and ecological traps, where both sinks and ecological traps result in population decline (Pidgeon *et al.* 2003; Battin 2004; Bro *et al.* 2004). These risk factors and potential population decline become a concern mainly if species are able to move between and access these remnants. Thus it is necessary to investigate their ability to disperse through the urban matrix and their response to matrix characteristics at the remnant edge. Dispersal through the urban matrix is often inferred by comparing the presence of a species, or species richness across remnants in relation to matrix characteristics. The area of tree cover in a 250 m radius around the remnant positively influenced the presence of great tits, as well as the number of other remnants within 1 km also occupied by tits (Hashimoto *et al.* 2005). Species richness of fragmentation-sensitive species

increased as connectivity, described as the amount of useable habitat in the urban landscape, increased (Mortberg & Wallentinus 2000). The matrix elements that dispersing birds appear to use include greater tree growth and increased shrub cover as the number of fragmentation-sensitive species within the matrix itself increased in response to these vegetation structural characteristics (Munyenyembe *et al.* 1989). Similarly, species richness in wooded streets was intermediate between streets with no vegetation and urban parks (Fernandez-Juricic 2000a).

Bird responses to edges in the urban landscape are often investigated by comparing species densities across the edge. The breeding density of edge-sensitive species decreased towards the edge of managed parks, while that of human-habituated species increased (Fernandez-Juricic 2001). Species considered sensitive to urbanization rarely crossed the edge from remnants into the matrix (Catterall *et al.* 1991; Wood 1996) suggesting there is little overlap in the use of remnants and the urban matrix (Parsons *et al.* 2003). However, these studies speculated that the responses of urban-sensitive species might have been influenced by the presence of aggressive urban species recorded near the edges (and subsequent conflicts, see Catterall *et al.* 1991).

1.5.3 Urban behavioural studies are needed

The effects of urbanization and the matrix on bird communities are mostly described by various indices based on species richness or abundance (Marzluff 2001) and more recently on species composition (Parsons *et al.* 2003; White *et al.* 2005). While these indices can describe the distribution of birds throughout remnants they are no guarantee of a continued existence (Saunders *et al.* 1991) and cannot reveal the mechanistic processes influencing the patterns. Furthermore, in an urbanized landscape the presence of a bird species in a remnant may be a function of the quality of the remnant or the permeability of the matrix. These indices cannot distinguish between these functions. Behavioural studies are necessary to determine whether a species' distribution is a response to internal remnant quality or external matrix characteristics.

Remnant vegetation with a small effective area potentially has altered conditions that may affect the direct requirements of a species. Species will often respond to new conditions by changing their foraging (Bell 1985; Forstmeier & Weiss 2004) or breeding behavior (Bowman & Woolfenden 2002; Fleischer *et al.* 2003) in an attempt to optimize their fitness in these conditions. Assessing foraging behavior, as a measure of bird responses to urbanization, involves fewer limitations than life history parameters because it is an ecological process that takes place at the individual level. As a result, conditions in remnants where individuals in the population may be unable to form successful breeding pairs can still be investigated. Foraging behavior is balanced between maximizing time and energy budgets (Stephens & Krebs 1986) and avoiding predators or aggressive competitors.

Therefore if remnant conditions were sub-optimal, measurable changes in foraging behavior in response to these direct and indirect effects could be expected, providing a useful indication about whether remnants have potential short term use as stepping-stones (Fortin & Arnold 1997) or as more medium term use as regular habitat within a habitat network.

Birds may also alter their movement patterns in response to conditions within the matrix. Modelling studies and field research have investigated the effects of different matrix types on species movement. One discrepancy between these modelling studies and field research is that models often incorporate the probability that an individual will cross once the edge has been approached (Stamps *et al.* 1987; Tischendorf *et al.* 2003), while field research focuses on rates of movement once an organism has crossed into the matrix. Field research observing edge crossing behaviour, and investigating the probability of an individual crossing in response to different matrix types is one missing factor.

Behavioural studies in fragmented landscapes are now regularly recommended as the next step towards understanding how mechanisms and landscape features impede or facilitate animal movements and influence their dispersal decisions, especially if habitat networks are to be created to promote the persistence of fragmentation-sensitive species (Baillie *et al.* 2000; Belisle & Desrochers 2002; Harris & Reed 2002).

1.6 Definitions

The gradient of housing density associated with urbanization has generated a wide array of terms throughout the literature (Marzluff *et al.* 2001). These terms are potentially confusing due to different regional and cultural meanings. Marzluff *et al.* (2001) proposed a set of standardized terms with reference to building density per hectare, suggesting that urban areas contain > 10 buildings, suburban areas contain between 2.5 and 10 buildings and rural areas contain < 2.5 buildings. In the study region in which the following work was conducted, housing density ranged between 0.1 and 13 houses per hectare. It is therefore discussed as a suburban landscape with areas of low- and high-density housing. The term of ‘urban’ has been avoided in discussion of my study system, as urban areas typically incorporate multi-storied housing and areas of industrial or commercial development (Marzluff *et al.* 2001). The study region was characterized by single- and double-storey housing, while industrial or commercial areas were avoided. However, I still use the term ‘urban’ when discussing the findings of other researcher, as the majority have used this term in discussing their own work. The definition of rural has also been avoided as it is potentially associated with agricultural areas where the predominant land use involves primary industry, such as wheat growing or dairy farming, rather than residential housing.

1.7 Thesis aims and outline

This thesis aimed to investigate the relative influence of internal and external factors on the bird communities in remnant vegetation of a suburban environment. These investigations intended to help determine where conservation efforts should be directed in order to minimize impacts on remnant bird communities, and to establish habitat networks to promote the persistence of urban-sensitive species.

This thesis initially investigated the effects of internal and external factors on community composition in remnants. In chapter two I examine how bird communities in remnants change in relation to remnant size and the surrounding housing density in the matrix. In chapter three I examine how bird communities change in relation to remnant vegetation characteristics and remnant size.

Having described the pattern of bird distributions in relation to the landscape, I then investigated the influence of internal and external factors on bird behaviour. Chapter four is the first study to examine the foraging behaviour, in suburban remnants, of small Australian insectivores known to be sensitive to fragmentation and urbanization. The behaviour of conspecifics inhabiting continuous vegetation and those inhabiting remnant vegetation were compared to identify differences that might indicate variation in internal remnant quality. Chapter five is the first study to examine the influence of external factors by documenting the edge crossing behaviour of bird species appearing at the interface between remnant vegetation and the adjoining housing matrix. Birds sensitive to urbanization were expected to demonstrate a different response to those more tolerant of suburban conditions.

Responses were also expected to vary between matrix types and with characteristics in the matrix.

Each chapter, addressing a specific aim of the thesis, is a self-contained unit that has been submitted as a journal article. As such, there is some repetition of concepts and methods from one chapter to the next. In the final chapter I discuss the implications for management of the suburban landscape to promote habitat networks for the continued existence of species sensitive to fragmentation and urbanization.

1.8 Study region

Wyong Shire (Lat 33°17', Long 151°26') provided an ideal region to investigate the influence of urbanization on characteristics of bird communities. Located 100km north of Sydney, the largest city in Australia, the state government has stipulated that Wyong should provide new housing for Sydney's expanding population. Consequently the shire has the second highest population growth rate in NSW at 2.9 % in 1996 (ABS) and is under increasing pressure from urbanization.

The process of urbanization began after the 1950's when land use shifted from forestry and farming in the mountains and valleys to the coastal plain where the lakes and beaches became popular residential areas. This shift is reflected by land use in the shire with forestry covering the largest area of 37 %, farming covering 20 % and urban housing covering 10 %. Clearing associated with these uses have left bushland cover (excluding forestry) at 29 % (Anon 2000).

Popularity of the coastal plain was assisted by the construction of major roads, most significantly both the north-south Pacific highway and the Sydney freeway. Two thirds of Wyong shire lands lie to the west of the freeway. In contrast the majority of suburban areas has been restricted to the eastern side and now contains 90 % of the population. Consequently the remaining bushland cover to the west of the freeway is extensive while that to the east is limited. To the east only eight areas are recognized as having a sufficiently large size to provide potential long term conservation. The remainder is highly fragmented creating many remnants surrounded by suburban housing with remnants having unknown conservation value.

Chapter 2

Changes in bird communities of remnant bushland in response to suburban housing density and remnant size in an urbanized landscape

2.1 Introduction

Urbanization can remove large tracts of original native habitat, replacing it with two new environments for bird communities; the new man-made matrix of streets and structures with managed parklands and gardens, and the remnants of native vegetation embedded in the new matrix. Remnants in the urban landscape have the potential to be strongholds for native species that might be able to extend their range into the matrix, even though they may be unable to survive in streets and parklands remote from remnants. Therefore remnants may play an important role in the biodiversity of the urban landscape.

In contrast to bird communities in large tracts of native habitat, bird communities in the streets or parkland environments have more introduced species, more omnivores and more granivores (Beissinger & Osborne 1982; Sasvari 1984; Zalewski 1994; Clergeau *et al.* 1998; Marzluff 2001) and, within Australia, more medium-sized nectarivores (Jones 1983; Sewell & Catterall 1998; Parsons *et al.* 2003). A higher abundance of introduced species, omnivores and granivores is often accompanied by a loss or decrease in the abundance of small insectivores in the streets or parkland environments (Beissinger & Osborne 1982; Zalewski 1994; Parsons *et al.* 2003) and can result in an increase in homogeneity of bird communities (Blair 2001). This characteristic of urban bird communities appears to be modified by the degree of

urbanization. An increase in building density causes an increase in abundance and a decrease in species richness (Maeda & Maruyama 1991; Dulisz & Nowakowski 1996; Clergeau *et al.* 1998; Germaine *et al.* 1998; Jokimaki & Suhonen 1998), while an increase in vegetation in the matrix improves species richness (Sasvari 1984; Sewell & Catterall 1998; Fernandez-Juricic 2000b). Bird communities in managed parklands are further influenced by the size of the park, increasing in species richness and abundance with increased park size (Sasvari 1984; Fernandez-Juricic 2000b; Fernandez-Juricic & Jokimaki 2001).

If bird communities in the urban matrix are directly influenced by housing density, then variation in housing density might also influence the communities of nearby remnants. If changes in the remnant community are observed in response to housing density, then factors external to the remnant are influential in shaping this community. Importantly, external influences can have a potentially widespread effect considering that many remnants may be embedded in the same matrix. Several studies, mainly in agricultural and forestry landscape, have demonstrated that variation in matrix composition can influence communities in remnant vegetation, with changes evident in abundance, species richness and community composition (Sisk *et al.* 1997; Renjifo 2001; Wethered & Lawes 2003). Studies in an urban landscape have shown that species richness and density in riparian corridors decreased as the degree of urbanization increased (Rottenborn 1999; Miller *et al.* 2000). Mechanisms proposed to explain matrix effects include invasive edge effects, such as increased predation (Danielson *et al.* 1997), parasitism (Chace *et al.* 2003), or the introduction of exotic species (Pell & Tidemann 1997). Invasive edge effects

have the potential to reduce both remnant quality and the species' chance of survival and reproduction.

External influences may limit the capacity of species to move between remnants, thereby reducing the dispersal and recruitment necessary for the functioning of meta-populations, resulting in population isolation and decline across the urban landscape. In agricultural landscapes differences in matrix composition can influence individual movement rates (Belisle *et al.* 2001; Ricketts 2001; Hein *et al.* 2003). Reductions in avian dispersal capacity may operate through several mechanisms in the matrix, including predation rates (Rodriguez *et al.* 2001; Lepczyk *et al.* 2003; Yoder *et al.* 2004), human disturbance (Fernandez-Juricic 2000a) and vegetation characteristics (Belisle *et al.* 2001; Hashimoto *et al.* 2005) that provide structural or functional connectivity (With 2002). Structural connectivity is created through corridors that link remnants, and lead species between remnants. Functional connectivity occurs when species are able to move through the matrix in the absence of corridors, using matrix characteristics as stepping-stones.

Processes occurring within a remnant may also influence species composition e.g. remnant size, vegetation quality, competitive species. Bird communities of remnant vegetation in an urbanized landscape have been shown to respond to remnant size, with larger remnants supporting greater species richness (Tilghman 1987; Grover & Slater 1994; Mortberg 1998; Crooks *et al.* 2004). Theoretically remnant size can moderate influences from the surrounding matrix type, as larger remnants usually have lower edge to area ratios and therefore a larger core area unaffected by edge effects associated with the matrix (Saunders *et al.* 1991; Turner *et al.* 2001).

If remnant vegetation is to play an important role in the biodiversity of the urban landscape then it is important to determine the relative influence of housing density and remnant size on the bird communities. This will help to understand the processes by which remnant communities are structured, and should allow better management of conditions within remnants that will help to retain native species sensitive to urbanization. Several studies have investigated the relative influence of matrix composition and remnant size. Freisen *et al.* (1995) demonstrated that matrix composition had a greater influence with species richness of neo-tropical migrants decreasing in diversity and abundance as building density increased, irrespective of remnant size. Conversely an increase in species richness was better explained by an increase in remnant size, followed by an increase in matrix vegetation (Bennett *et al.* 2004) or a decrease in surrounding housing density (Tilghman 1987). In three landscapes of increasing housing density, species richness increased with reserve size however the benefit of large reserve size only appeared to hold in the landscapes with more than 20 % urban land cover (Donnelly & Marzluff 2004). In these and the majority of other studies, the influence of matrix type and remnant size has been described by species richness indices, which can mask species composition. However, if remnants are expected to support more native species than the streets and parklands, then species composition could provide a better indication of the influence of these factors, especially as they may vary in importance for different species (Lee *et al.* 2002).

This study focuses on how bird communities in remnants change in relation to surrounding housing density and remnant size in an urbanizing landscape. I initially investigate the relative effects of housing density and remnant size on species

richness and bird density. I then evaluate the relative effects of these factors on species composition to determine whether conservation efforts are better directed towards management of internal or external factors to minimize impacts on composition of remnant bird communities.

2.2 Methods

2.2.1 Study region

The study was undertaken in a suburban area with significant surrounding natural vegetation. Wyong Shire (827 km²) forms part of the Central Coast of New South Wales (NSW), Australia. The climate is temperate, with temperatures ranging from 12° C - 24° C (mean daily minimum and maximum). Average annual rainfall ranges from 1200-1800 mm. The geography ranges from plateaus in the west, to hills and valleys, and a coastal plain in the east. The coastal plain contains a system of three connected tidal lakes. The native vegetation of the shire is predominantly woodland to the north and moist forest to the south. This vegetation is in various stages of fragmentation and now covers 29 % of the land (Anon 2000). Land uses contributing to fragmentation include forestry (37 %), farming (20 %) and urban housing (10 %) (Anon 2000).

Wyong Shire's position midway between two major cities (Newcastle and Sydney) has resulted in the New South Wales State Government stipulating that Wyong should provide new housing for Sydney's expanding population. As a result the shire has the second highest annual population growth rate in NSW at 2.9 % in 1996 (ABS 1996) and is becoming rapidly urbanized.

2.2.2 Study sites

A total of thirty-four remnants ranging in size from 1 to 32.5 hectares (average 7.1 ha \pm 7.7 sd) were selected based on surrounding housing density and remnant size (Table 1). Surrounding housing density and remnant size were calculated from 1:25000 topographic maps and aerial photos. Housing density was calculated as the number of residential houses per hectare in a 200 m zone around the edge of the remnant (average zone area 34.9 ha \pm 14.2) and was classified as either high (≥ 4 houses ha⁻¹) or low (< 4 houses ha⁻¹). Remnant size was classified in this way as 4 ha appears to be a threshold for maintaining biodiversity in remnants in urban areas (Drinnan 2005). Remnant vegetation generally consisted of a eucalypt canopy with allocasuarina and melaleuca shrubs.

Characteristics of remnant vegetation were sampled at three points spread evenly along one transect (see below) in each remnant. At each point a 20 m x 20 m quadrat (NPWS 1998) was established. Four vegetation layers were defined as ground, low-shrub, high-shrub and canopy. Due to the different vegetation types surveyed, these layers were defined by vegetation profile not by pre-determined height classes. Vegetation characteristics were collected by visually estimating the height and percent cover for each of these vegetation layers and were averaged across samples for each transect.

Table 1: Distribution of remnants according to surrounding housing density and remnant size

House Density	n	Remnant Size	n
High (> 4 /ha)	18	Large (> 4 ha)	8
		Small (< 4 ha)	10
Low (< 4 /ha)	16	Large	10
		Small	6

2.2.3 Bird surveys

Bird surveys were conducted in each remnant between October 2001 and January 2002. One survey per site was conducted within 3 hrs of sunrise on days of dry weather and little or no wind. The number and species of diurnal land birds seen or heard were recorded. Birds flying overhead were not included in the survey. Bird survey transects in suburban and agricultural landscapes of Australia are typically conducted over 200 to 400 m for between 20 and 40 mins (Munyenymbe *et al.* 1989; Evans *et al.* 1997; Fisher 2001; Major *et al.* 2001). Remnant size (average 7.1 ± 7.7) was a limiting factor in the suburban landscape of Wyong. Transect length was restricted to 150 m in length and 50 m width, and surveys were conducted for 45 min, so that survey effort would be equal for all remnants and allow a direct comparison of the similarities between bird communities in the same area of small and large remnants.

To determine the effectiveness of the restricted survey in the larger remnants, surveys were extended for a further 45 min along another 150 m to investigate the adequacy of the survey design to detect most species. The restricted survey was considered adequate detecting, on average, 71.5 % of the species detected in the extended surveys.

2.2.4 Data analysis

To ensure that potential differences in bird communities could be attributed to remnant size and housing density and not to changes in the vegetation structure within remnants, I initially compared four variables (percent cover of ground layer, low-shrub layer, high-shrub layer and canopy layer) using ANOSIM (analysis of similarity). Remnant vegetation structure was not significantly different among remnant size class (Global R = -0.011, P = 0.49) or housing density (Global R = 0.079, P = 0.074).

Differences in species richness and bird density across levels of housing density and remnant size were tested, using two-factor ANOVA. Community composition was compared using non-parametric multivariate techniques based on a similarity matrix that describes relationships between samples (PRIMER: Clarke 1993). The similarity matrix was created using the Bray-Curtis similarity index (Clarke & Warwick 1994). Remnants were plotted on a non-metric multi-dimensional scaling plot for visual assessment, and were tested for significance using the ANOSIM procedure. This procedure is a permutation test that generates a Global R test statistic which reflects the differences within remnants contrasted with differences among remnants. A value of 0.05 indicates that groups of remnants are clearly different from other groups (Clarke and Gorley 2000). Differences in composition across housing density and remnant size were tested for significance using two-factor ANOSIM. Presence/absence data were used so that uncommon species, which may be more strongly affected by urbanization, were given equal importance to common species.

Significant compositional differences were investigated by similarity percentage analysis (SIMPER), which uses the same Bray-Curtis similarity index to calculate the average percent dissimilarity between factors, and to identify species making the greatest contribution to that index.

Species can make a contribution to the similarity index either by discriminating between levels of each treatment or by being characteristic of remnants within particular levels of housing density or remnant size. The degree to which a species discriminates or characterizes a community is determined by their Dissimilarity/SD or Similarity/SD ratio, which indicates how consistently they contribute to the Bray-Curtis dissimilarity or similarity index between pairs of samples. Clarke & Warwick (1994) suggest that species with a ratio above 1.5 make a consistent contribution. All species contributing to a cumulative total of 60 % of the similarity index within a level were investigated to determine their contribution.

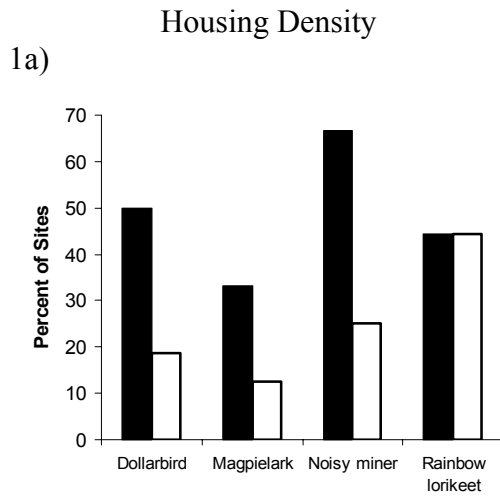
Different feeding guilds show differential susceptibility to urbanization (Beissinger & Osborne 1982; Parsons *et al.* 2003). Therefore, all species occurring at more than 20 % of remnants were grouped into guilds, which were analyzed individually. Introduced birds were grouped into a single 'guild' and native birds were grouped into feeding guilds. Differences in occurrence between housing density and between remnant sizes were investigated using chi-square analysis.

2.3 Results

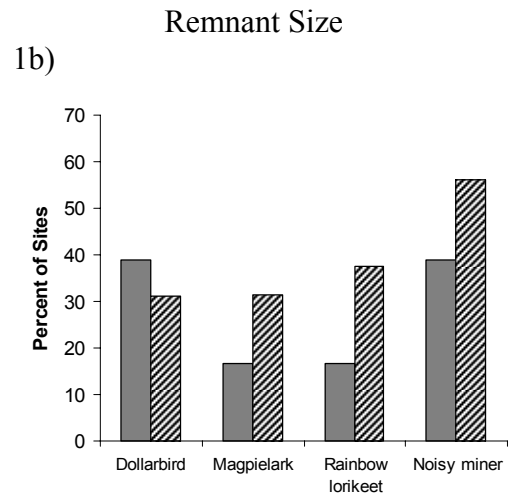
A total of 60 species were recorded from 34 remnants. Transects had an average of 9.1 (± 4.6 sd) species and 25.2 (± 11.1) individuals. The presence of bird species occurring at more than 20 % of sites is displayed across housing density and remnant size in Figure 1.

Species richness was not significantly different between remnants surrounded by high-density and low-density housing ($F_{1,30} = 0.11$, $P = 0.75$) or between large and small remnants ($F_{1,30} = 0.16$, $P = 0.69$). There was no interaction between housing density and remnant size ($F_{1,30} = 1.15$, $P = 0.29$). Bird density showed the same pattern, with no significant difference in relation to housing density ($F_{1,30} = 1.69$, $P = 0.20$), remnant size ($F_{1,30} = 0.12$, $P = 0.73$) or an interaction between housing density and remnant size ($F_{1,30} = 0.05$, $P = 0.82$).

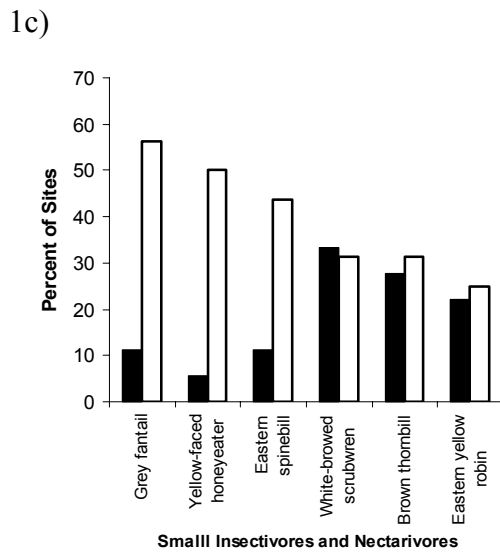
Bird community composition, however, was significantly associated with housing density (Global $R = 0.230$, $P = 0.005$, Figure 2a). Communities in remnants surrounded by high-density housing were more homogeneous than communities in remnants surrounded by low-density housing (average Bray-Curtis similarity of 28.0 % and 16.8 % respectively). There was no difference in composition between large and small remnants (Global $R = -0.003$, $P = 0.34$).



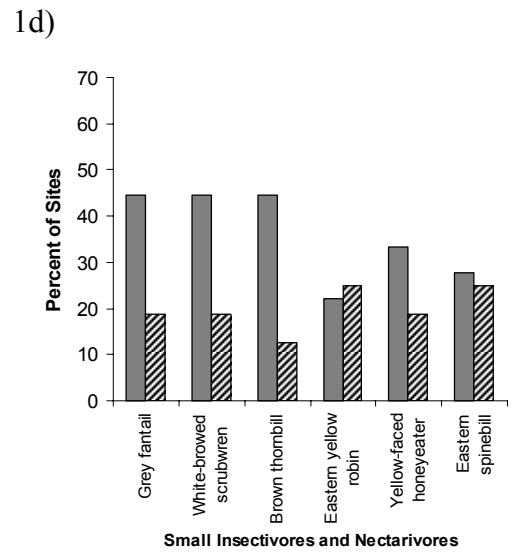
Medium Insectivores and Nectarivores



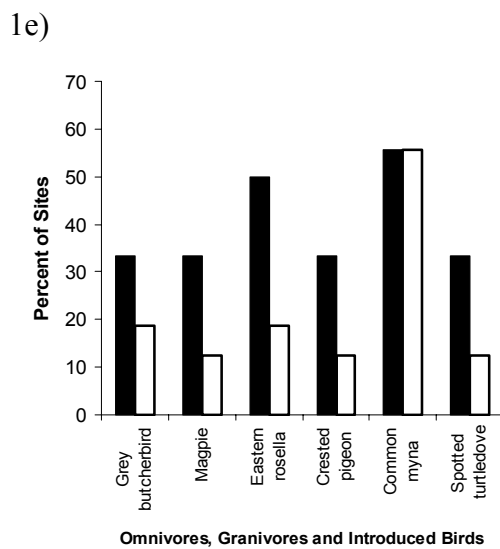
Medium Insectivores and Nectarivores



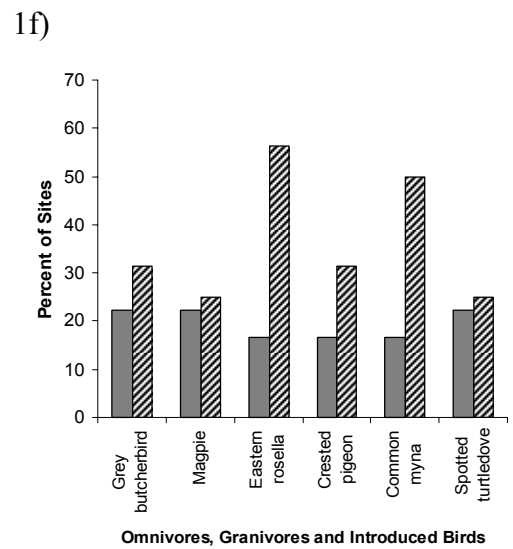
Small Insectivores and Nectarivores



Small Insectivores and Nectarivores

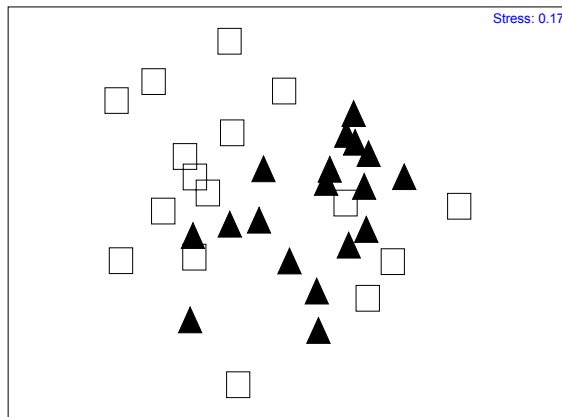


Omnivores, Granivores and Introduced Birds

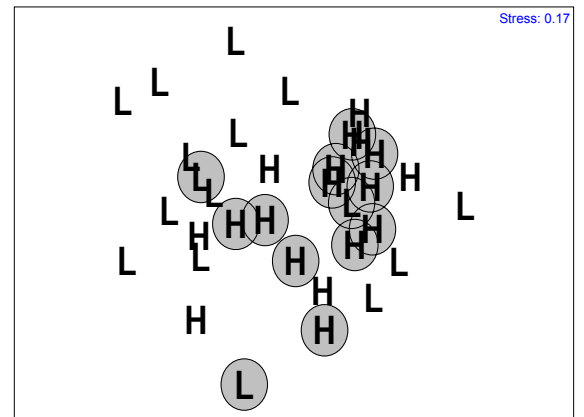


Omnivores, Granivores and Introduced Birds

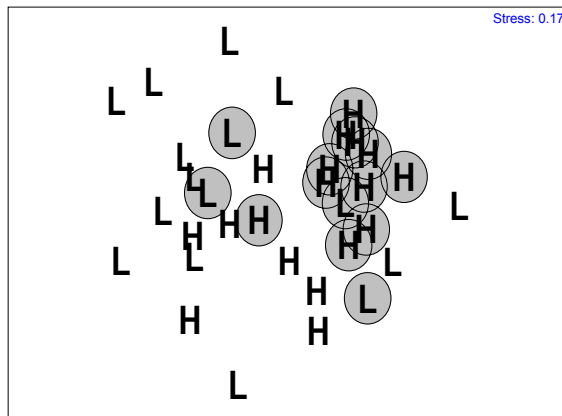
Figure 1: Presence of birds at sites according to housing density (a, c, e). Filled columns represent high-density ($n = 18$), unfilled columns represent low-density ($n = 16$). Presence of birds at sites according to remnant size (b, d, f). Shaded columns represent large remnants ($n = 18$), striped columns represent small remnants ($n = 16$).



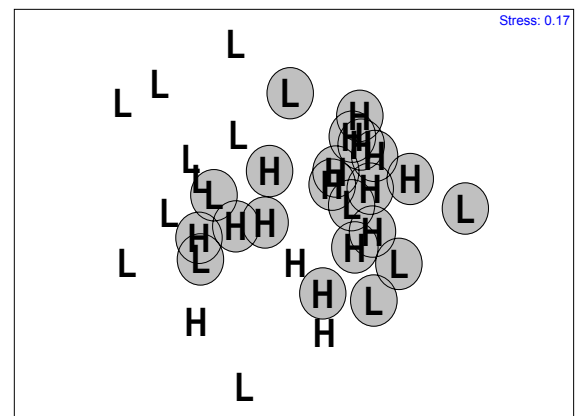
2a) Housing density



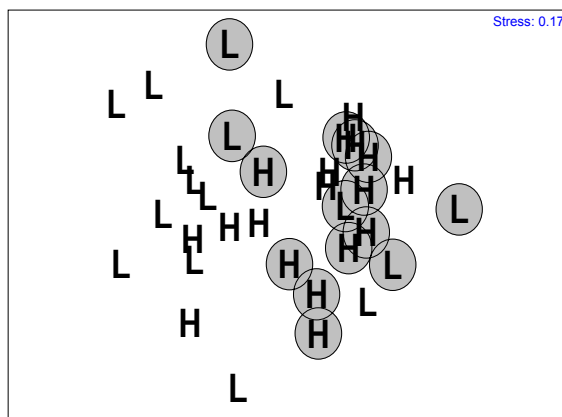
2b) Introduced birds (2 species)
 $\chi^2_{1,32} = 6.57, P = 0.0104$



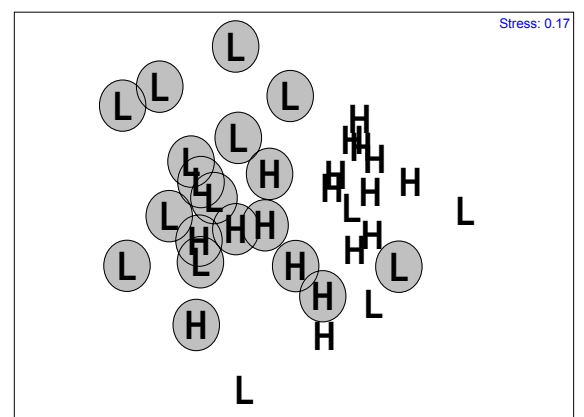
2c) Granivores (2 species)
 $\chi^2_{1,32} = 4.61, P = 0.0318$



2d) Medium insectivores and nectarivores
 (4 species) $\chi^2_{1,32} = 8.32, P = 0.0039$



2e) Omnivores (2 species)
 $\chi^2_{1,32} = 1.24, P = 0.2652$



2f) Small insectivores and nectarivores
 (6 species) $\chi^2_{1,32} = 4.61, P = 0.0318$

Figure 2: Non-metric multi-dimensional scaling plots of remnant bird communities ($n = 34$) showing (a) response to matrix housing density and (b) – (f) the association between bird guilds and matrix housing density. Points that are closer together represent remnants with more similar bird communities. ▲ Remnants surrounded by high-density housing, □ Remnants surrounded by low-density housing. Shaded circles indicate presence of guilds at remnants surrounded by high- density (H) and low density (L) housing.

Analysis of feeding guilds (Table 2) demonstrated that the presence of introduced birds and native feeding guilds was significantly associated with housing density. Introduced birds, granivores, medium-sized insectivores and medium-sized nectarivores were present at significantly more remnants surrounded by high-density housing than those surrounded by low-density housing ($\chi^2 \geq 4.61$, $P \leq 0.03$; Figure 2b-d). Small insectivores and small nectarivores were present at significantly more remnants surrounded by low-density housing ($\chi^2 = 13.69$, $P = 0.008$; Figure 2f). Omnivores (Figure 2e) were not significantly associated with housing density.

Table 2: Habitat preferences of guilds comprised of species occurring in at least 20 % of sites. Preferences for remnants surrounded by high-density or low-density housing as determined in this study are compared with occurrence of the species in the urban matrix as described in the literature.^

* Species contributed up to 60 % of the similarity of communities within a housing density type.

Species contributed up to 60 % of the similarity of communities with or without noisy miners.

+ Species listed after 50 % cut off for contribution to dissimilarity index

^ Mason 1985; Catterall *et al.* 1997; Sewell & Catterall 1998; Parsons *et al.* 2003

Birds classified as generalist showed no preference for suburban or bushland

Fifteen of the sixteen species in Table 2 accounted for 48.6 % of the average Bray-Curtis dissimilarity (84.7 %) between remnants surrounded by high- and low-density housing. Five bird species of medium-size (23-31 cm; Simpson & Day 1996) contributed 59.4 % of the Bray-Curtis similarity index of communities in remnants surrounded by high-density housing. All species occurred at more than 20 % of sites and are presented in Table 2. One species was the introduced common myna, *Acridotheres tristis*, two were the nectarivorous rainbow lorikeet, *Trichoglossus haematodus* and noisy miner, *Manorina melanocephala*, one was the granivorous eastern rosella, *Platycercus eximius*, and one was the insectivorous dollarbird, *Eurystomus orientalis*. Noisy miners demonstrated a very strong relationship with matrix density ($\chi_1^2 = 6.11$, $P = 0.014$), occurring at 67 % of remnants surrounded by high-density housing and 25 % of those surrounded by low-density housing. No relationship existed with remnant size ($\chi_1^2 = 1.09$, $P = 0.31$). As this species influences bird communities in rural remnants (Grey *et al.* 1997), differences in community composition between sites with and without noisy miners was tested by one-factor ANOSIM, following the removal of noisy miners from the dataset. Community composition was significantly different (Global $R = 0.331$; $p = 0.001$) between sites with and without noisy miners.

Six bird species contributed to 59.8 % of the Bray-Curtis similarity index of communities in remnants surrounded by low-density housing. Five were bird species of small-size (13-18 cm). Two species were nectarivores (yellow-faced honeyeater; *Lichenostomus chrysops*, eastern spinebill; *Acanthorhynchus tenuirostris*), three were insectivores (grey fantail; *Rhipidura fuliginosa*, yellow thornbill; *Acanthiza nana*, and variegated fairy-wren; *Malurus lamberti*). Only the yellow-faced honeyeater,

eastern spinebill and grey fantail occurred at more than 20 % of sites and are presented in Table 2. The noisy miner also featured, but unlike remnants surrounded by high-density housing, it only made a small individual contribution (5.3 %) to the similarity index of remnants surrounded by low-density housing.

None of the species that were present in more than 20 % of remnants had a Diss/SD or Sim/SD ratio above 1.5. Therefore none occurred consistently with one level of housing density, indicating they were not characteristic of a particular housing density. However, they did contribute to the average Bray Cutis dissimilarity index by occurring more regularly at one housing density than the other. This community overlap is reflected in the weak (Global $R < 0.5$) but highly significant Global R value (0.230; $P = 0.005$).

The species explaining the dissimilarity between sites with and without noisy miners were the same species that explained the difference between sites surrounded by a high-density and low-density matrix (Table 2). Species occurring more often at remnants surrounded by high-density housing occurred more often at sites where noisy miners were present. Species occurring more often at remnants surrounded by low-density housing also occurred more often at sites where noisy miners were absent.

2.4 Discussion

In contrast to other studies, I found that remnant bird communities in the urbanized landscape did not respond to variation in remnant size, showing no change in bird density, species richness, or species composition. Remnant size has been shown to be the most universal factor explaining patterns of bird distribution (Brotons & Herrando 2001a; Major *et al.* 2001; Santos *et al.* 2002; Castelletta *et al.* 2005), however, most of this research has been in agricultural landscapes, where a much broader range of remnant sizes is often available. In such landscapes, the remnant area threshold at which significant changes in bird communities occur has been found to lie in the range between 20 ha (Barrett *et al.* 1994) and 200 ha (Major *et al.* 2001). Watson *et al.* (2000) concluded that the lack of a size relationship in their study was because their largest size class was less than 20 ha. In urban landscapes, remnant size tends to be smaller and it seems likely that the absence of a size effect in the present study was because the majority of sites were smaller than the typical size threshold. All the remnants in this study were less than 32 ha (av. 7.1 ha). The absence of a size effect, suggests that internal factors are having a relatively minor impact on community composition when measured at this scale. At a larger scale (0.2 to 172 ha) Drinnan (2005) found a threshold occurred in urban bird communities at a remnant size of 4 ha.

Instead, species composition was influenced by variation in surrounding housing density. Moreover, there was no interaction between remnant size and surrounding housing density, suggesting that remnant size was not modulating influences from the matrix over the range of remnant sizes present in this study.

Small insectivores and small nectarivores occurred more often in remnants surrounded by low-density housing. These species were regularly recorded in large tracts of native vegetation (unpubl.data) and are commonly classified as bushland-dependent species (Sewell & Catterall 1998; Parsons *et al.* 2003; Antos & White 2004). The presence of these bushland species increases the similarity of remnants surrounded by low-density housing to those of undisturbed native vegetation, demonstrating that small remnants in suburban areas are capable of supporting at least some species dependent on native habitat providing that surrounding housing density is low. These results suggest that external factors associated with the matrix are influencing communities occurring in remnants, potentially through several processes.

Immigration of species into remnant areas is likely to be associated with matrix connectivity and a species' capacity to move through the matrix. Changes in matrix structure are likely to change the species that are capable of dispersing. If this is the case then meta-population dynamics associated with matrix structure becomes a key factor influencing composition of remnants. Introduced species, granivores and medium nectarivores occurred more often in remnants surrounded by high-density housing and are species that regularly occur in the streets and parklands of the high-density housing matrix (Wood 1996; Catterall *et al.* 1998; Sewell & Catterall 1998; Parsons *et al.* 2003). The similarities of the bird communities of remnants surrounded by high-density housing with those in the streets and parklands suggest that species common in the matrix disperse easily into remnants.

Small insectivores and small nectarivores may only be capable of dispersing into remnants through a matrix of low-density housing. This suggests that in the absence of structural connectivity, i.e. corridors, the low-density matrix still provides functional connectivity for these birds (With 2002). Functional connectivity of the low-density matrix may be related to vegetation features in the matrix, especially as the volume and complexity of vegetation increases as urbanization decreases (Blair 1996; Clergeau *et al.* 1998). Within remnants of an urban landscape species richness of fragmentation-sensitive species increased as connectivity, described as the amount of useable habitat in the landscape, increased (Mortberg & Wallentinus 2000; Drinnan 2005). The area of tree cover in a 250 m radius around the remnant positively influenced the presence of great tits, as well as the number of other remnants within 1 km also occupied by great tits (*Parus major minor*; Hashimoto *et al.* 2005). Within the urban matrix itself the number of fragmentation-sensitive species increased in response to vegetation structure such as greater tree growth and increased shrub cover (Munyenymbe *et al.* 1989), and species richness in wooded streets was intermediate between streets with no vegetation and urban parks.

Some studies have found that species richness in remnants did not respond to surrounding vegetation, suggesting that vegetation in the matrix does not increase functional connectivity (Yeoman & Mac Nally 2005). A lack of responses to vegetation (which may or may not be sufficient in the high-density matrix) might occur if these birds exhibit behavioural inhibitions to external factors and are deterred from entering the matrix. Possible deterrent factors included human disturbance (Fernandez-Juricic 2000a), road proximity (Brotons & Herrando 2001b), noise levels (Katti & Warren 2004), or domestic pets (Lepczyk *et al.* 2003). These

factors may be less prevalent in a low-density matrix and have less of an effect on functional connectivity.

The presence of the noisy miner also had an influence on the distribution of small insectivores and nectarivores. This medium nectarivore is a co-operatively breeding species that aggressively defends its territory from heterospecifics (Dow 1977) thereby excluding small birds from remnants (Grey *et al.* 1997). This behaviour is implicated in similar reductions in small bird abundance in urban landscapes (Catterall *et al.* 1997; Parsons *et al.* 2003). The presence of noisy miners in remnants is likely to reduce the abundance of small birds through interference competition. While competitive species are usually considered to be an internal process that might influence community composition, the noisy miner demonstrated a very strong relationship with high-density housing suggesting their effect may be an extension of external matrix influences. Noisy miners occurred at 67 % of remnants surrounded by high-density housing and only 25 % of remnants surrounded by low-density housing. Furthermore noisy miners are often present in the streets and parklands of the high-density housing matrix (Wood 1996; Catterall *et al.* 1998; Sewell & Catterall 1998; Parsons *et al.* 2003).

This potential contribution of noisy miners to both internal and external effects may have dual impact on meta-population dynamics in a suburban landscape. The reluctance of small insectivores and nectarivores to use remnants in which noisy miners are present suggests that remnant availability, particularly in a low-density matrix, through which these small birds can still disperse, may be a limiting factor. Reduced remnant availability decreases the number of sub-populations in a region

ultimately lowering the resilience of the meta-population to stochastic events. Reduced remnant availability may also reduce the number of stepping-stones, thereby increasing the chances of dispersing individuals perishing in the matrix. In the high-density matrix, through which small insectivores and small nectarivores are potentially unable to disperse, the presence of the noisy miner in the matrix itself may act as a behavioural deterrent that prevents these birds leaving the remnant to disperse.

Overall these results suggest that a small but highly significant portion of the avian community of small remnants in a suburban landscape are more likely to be influenced by external factors related to the matrix, than to internal factors related to remnant size. Management of matrix characteristics to promote dispersal and remnant access for urban-sensitive species appears to be a practical way to strengthen meta-populations. Implications for urban planning and design include limitations to housing density and improvement of matrix conditions, potentially through the provision of vegetation, or control of species that exploit the matrix at the expense of urban-sensitive species. The presence of urban-sensitive species in remnants surrounded by low-density housing, suggests that low-density housing has the potential to act as a buffer zone between heavily urbanized environments and undisturbed native vegetation. The degree to which the matrix is managed may depend on whether urban-sensitive species use these remnants as brief stepping-stones on their way through matrix (Fortin & Arnold 1997), or as more substantial habitat for foraging and breeding, an area that requires further research.

Chapter 3

Compositional differences in bird communities of remnant bushland in response to vegetation type and remnant size in an urbanized landscape

3.1 Introduction

Bird communities in urban landscapes are considered to be more homogeneous than bird communities in undisturbed landscapes. Homogeneity is created through a decline in species richness and a corresponding increase in the abundance or dominance of exotic and native species adapted to the urban environment (Green 1984; Maeda & Maruyama 1991; Blair 1996; Dulisz & Nowakowski 1996; Clergeau *et al.* 1998; Germaine *et al.* 1998; Jokimaki & Suhonen 1998; Marzluff *et al.* 2001; Sandstrom *et al.* in press). These changes are often associated with an increase in buildings and structural development and a decrease in the volume and complexity of vegetation (Blair 1996; Clergeau *et al.* 1998; Savard 2001; Antos & White 2004; Antongiovanni & Metzger 2005). Consequently it is frequently recommended that avian diversity and the presence of urban-sensitive species can be promoted through improvements to the quality of vegetation in the urban landscape.

Vegetation in the urban landscape ranges from household gardens and planted streetscapes though to managed parklands and remnants of native vegetation in which different combinations of exotic and native plant species occur. Native vegetation appears to be an important factor influencing urban bird communities. Avian species richness and abundance increases when vegetation changes from exotic streetscapes to native streetscapes and parks (White *et al.* 2005). The total

amount of native vegetation also influences the composition of native and exotic bird species. The number of native bird species has been shown to increase with increased native vegetation in streets and backyards, while the number of exotic bird species has been shown to decrease (Green 1984). Furthermore, the influence of the amount of native vegetation extends to foraging behaviour, with native birds foraging proportionately more than exotic birds on native plants (Green 1984) and native birds foraging proportionately more on native plants than exotic plants (French *et al.* 2005).

In urban landscapes, remnants of native vegetation have the potential to contribute to the conservation of biodiversity through several mechanisms. Firstly they contain a significant proportion of the native vegetation in the region. Secondly, they can contribute to regional vegetation complexity. In the urban matrix of streets, buildings and managed parklands, increasing shrub and canopy cover provide a greater vegetation complexity, resulting in a greater bird species diversity and abundance of specialist species (Fernandez-Juricic 2004; Sandstrom *et al.* in press). Remnants in the urban landscape demonstrate a similar trend in which remnants with greater understorey cover have been shown to contain a greater bird species diversity, or more understorey specialists (Tilghman 1987; Grover & Slater 1994; Slater 1995). In comparison to the matrix and parklands, remnants potentially make a greater contribution, as their complexity is not compromised through requirements to provide areas of open lawns and walking paths for residential recreation. Emphasis on maintaining native vegetation, both as plants in streets and gardens, and as remnants in the landscape is suggested as a way of reducing the effects of urbanization on bird communities (Green & Baker 2003).

Remnant vegetation can also contribute to regional vegetation complexity by providing a variety of different vegetation types. Different vegetation types are known to support different assemblages of birds (Mac Nally 1990) and can influence the species richness and species composition of bird communities in remnants of agricultural landscapes (Bentley & Catterall 1997; Major *et al.* 2001; Santos *et al.* 2002). Within urban remnants species density and composition can vary among vegetation types (Wood 1995; Parsons *et al.* 2003).

The ability of a remnant to contribute to the conservation value of vegetation in an urban landscape may be affected by the surrounding matrix. Remnant integrity can be degraded through exposure to invasive elements from the matrix. Integrity, measured as the ratio of exotic to native plants species, was shown to be significantly associated with the type of surrounding matrix, with suburban remnants having the highest exotic species richness (Gilfedder & Kirkpatrick 1998). As urbanization increased, vegetation condition decreased, and was accompanied by high levels of weed infestation, higher densities of formal and informal walking paths and disturbance such as fire (Stenhouse 2004). Over time, remnants can become further degraded through a loss of original native plant species (Matlack 1993; Solinska-Gornicka & Symonides 1995).

Invasion of matrix elements occurs at the remnant edge. Therefore the degree of invasion can be dependent on the amount of edge. Smaller remnants have a greater proportion of edge than larger remnants (Saunders *et al.* 1991; Turner *et al.* 2001) so the ability of a remnant to maintain its integrity may be reflected by the size thresholds often reported in literature. In agricultural landscapes significant changes

in bird communities occur between 20 ha (Barrett *et al.* 1994) and 200 ha (Major *et al.* 2001). In urban landscapes the threshold appears to be lower occurring in the range between 2 to 50 ha (Tilghman 1987; Catterall *et al.* 1997; Drinnan 2005). The number of bushland-dependent birds appears to decrease while the number of birds characteristic of the urban matrix appears to increase around these threshold values (Catterall *et al.* 1997; Drinnan 2005). An increase in the number of birds characteristic of the urban matrix may introduce similarities between the communities in different vegetation types, potentially reducing the effectiveness of multiple vegetation types in enhancing regional biodiversity. This suggests that the value of remnant vegetation may only be in adding structural complexity, rather than a variety of vegetation types to the urban landscape.

This research focused on the role of remnant size, vegetation type and vegetation structure in influencing bird community composition in suburban remnants. Two vegetation types were studied. I initially investigated, whether any changes in vegetation structure occurred in relation to remnant size. Then I investigated whether vegetation type influenced bird communities in remnants, and how changes in vegetation structure affected the community. I also investigated whether changes in vegetation structure influenced species richness and bird density.

3.2 Methods

3.2.1 Study region

Wyong Shire (827 km²) forms part of the Central Coast region of NSW. The temperature ranges from 12°C to 24°C (mean daily minimum to maximum), with mean annual rainfall ranging from 1200 to 1800 mm. Plateaus form the west of the shire and are connected to the coastal plain in the east by a series of hills and valleys. Fragmentation has reduced the cover of native vegetation to 29 % of the landscape. Woodland predominates in the north and moist forest predominates in the south of the shire (Anon 2000). Urbanization has been the dominant fragmentation force since the 1950's (Anon 2000) with the majority of the coastal fringe and parts of the coastal plain now developed.

3.2.2 Survey sites

The two dominant vegetation types on the fragmented coastal plain of Wyong Shire are moist forests and woodlands. Moist forest is characterized by *Eucalyptus saligna*, *E. pilularis*, *Syncarpia glomulifera*, and *Glochidion ferdinandi*. Canopy height averages between 25 to 28 m. The mesic understorey averages 8 m in height and contains a diverse range of climbing vines while the ground layer is characterized by ferns. Woodlands are characterized by *Angophora costata*, *E. haemostoma*, *Corymbia gummifera*, and *E. capitellata*. Canopy height ranges from 15 to 25 m with a dry shrubby understorey averaging 4 m in height. The ground layer is characterized by grasses (NPWS 2000). Thirty-nine remnants ranging in size from 1 to 4125 ha (average 458 ha \pm 1259 sd) were selected and grouped into vegetation classes (moist forest or woodland; Table 3) and size classes (< 4 ha, 4-35 ha, > 80 ha; no remnants 35-80 ha were available). These sizes relate to apparent thresholds for maintaining

biodiversity in remnants (Catterall *et al.* 1997; Martin & Catterall 2001; Watson *et al.* 2001; Drinnan 2005).

Table 3: Distribution of remnants across factors of size and vegetation type.

Vegetation Type	Small (< 4 ha)	Large (4-35 ha)	Continuous (> 80 ha)
Moist forest	5	5	6
Woodland	9	10	4

Characteristics of remnant vegetation were measured to represent the vegetation structure of each transect where bird observations were conducted. Samples were collected at three points spread evenly along each transect (see below) in each remnant. At each point a 20 m x 20 m quadrat (NPWS 1998) was established. Four vegetation layers were defined as ground, low-shrub, high-shrub and canopy. Due to the different vegetation types surveyed, these layers were defined by vegetation profile not by pre-determined height classes. Vegetation characteristics were collected by visually estimating the height and percent cover for each of these vegetation layers and were averaged across samples for each transect.

3.2.3 Bird surveys

Bird surveys were conducted in each remnant between October 2001 and January 2002. One survey per site was conducted within 3 hrs of sunrise on days of dry weather and little or no wind. The number and species of diurnal land birds seen or heard were recorded. Birds flying overhead were not included in the survey. Bird survey transects in suburban and agricultural landscapes of Australia are typically conducted over 200 to 400 m for between 20 and 40 mins (Munyenymbe *et al.* 1989; Evans *et al.* 1997; Fisher 2001; Major *et al.* 2001). Remnant size (average 7.1 ± 7.7) was a limiting factor in the suburban landscape of Wyong. Transect length was

restricted to 150 m in length and 50 m width, and surveys were conducted for 45 min, so that survey effort would be equal for all remnants and allow a direct comparison of the similarities between bird communities in the same area of small and large remnants.

To determine the effectiveness of the restricted survey in the larger remnants, surveys were extended for a further 45 min along another 150 m to investigate the adequacy of the survey design to detect most species. The restricted survey was considered adequate detecting, on average, 68.7 % of the species detected in the extended surveys.

3.2.4 Data analysis

Initially I tested whether vegetation structure differed across remnant size classes within vegetation types using an ANOSIM (analysis of similarity) procedure (PRIMER: Clarke 1993). This is a non-parametric multivariate technique based on a similarity matrix that describes relationships between samples.

Community composition of birds was compared across all remnants. Initially, a similarity matrix was created using the Bray-Curtis similarity index (Clarke & Warwick 1994) and assessed visually by plotting remnants on a non-metric multi-dimensional scaling plot (nMDS). Differences in composition across vegetation type were tested using one-factor ANOSIM on presence/absence data rather than abundance, so that uncommon species, which may be more strongly affected by urbanization, were given equal importance to common species. The community composition of birds was then compared across size for each vegetation type using a one-factor ANOSIM. The ANOSIM procedure is a permutation test that generates a Global R test statistic which reflects the differences within remnants contrasted with differences among remnants. A value of 0.05 indicates that groups of remnants are clearly different from other groups (Clarke and Gorley 2000).

Significant compositional differences were investigated by similarity percentage analysis (SIMPER), which uses the same Bray-Curtis similarity index to calculate the average percent dissimilarity between factors, and to identify species making the greatest contribution to that index.

To examine the effect of vegetation structure regardless of vegetation type, I investigated relationships of vegetation structure with species richness and bird density using multiple regression (SYSTAT 10). This separated the effect of floristic differences found between vegetation types from broader effects of differences in vegetation structure which are considered important influences on avian communities (Mac Nally 1990). Remnant size was also removed as ANOSIM results suggested that any differences in vegetation structure were not associated with remnant size. Eight variables of vegetation height and percent cover for the ground, low-shrub, high-shrub and canopy layers were entered into the model. Data were checked for normality and homogeneity of variance. No transformation of data was necessary. Residuals of the models after analysis were also checked for normality. Correlated variables were excluded from regression models if their Pearson correlation value was less than 0.7 (Tabachnick & Fidell 1996). Variables with high P values and/or low tolerance (≤ 0.1) were sequentially removed from the full model until those remaining established a model that significantly explained the variation.

3.3 Results

Remnant vegetation structure was not significantly different among remnant size class for moist forest remnants (Global $R = -0.073$, $P = 0.818$), or for woodland remnants (Global $R = -0.021$, $P = 0.547$). Therefore any differences in bird community composition across size classes could be attributed directly to remnant size, not to potential changes in vegetation structure related to size.

A total of 65 bird species were recorded from 39 remnants. Transects had an average of $9.0 (\pm 4.7 \text{ sd})$ species and $22.8 (\pm 11.6)$ individuals. The presence of bird species occurring at more than 20 % of sites is displayed across vegetation types in Figure 3.

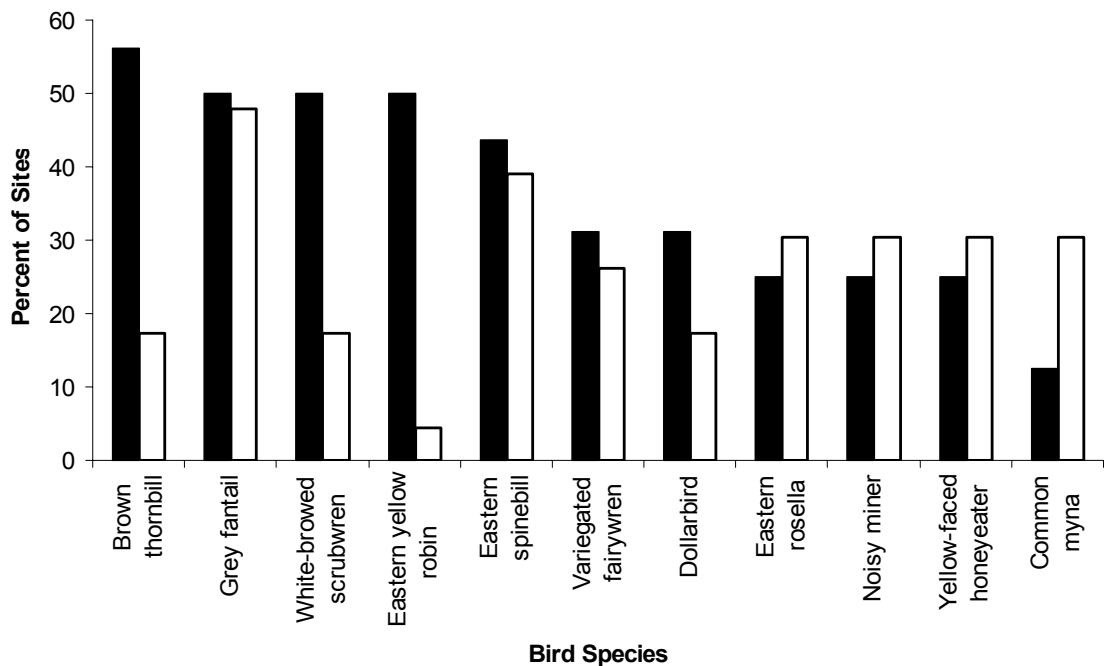


Figure 3: Presence of birds at sites according to vegetation type. Filled columns represent moist vegetation ($n = 16$), unfilled columns represent woodland vegetation ($n = 23$).

Bird communities in moist forest remnants were different to those in woodland remnants (Global $R = 0.17$, $P = 0.001$). Associations with vegetation type were very strong in remnants larger than 80 ha (Global $R = 0.76$, $P = 0.005$), but were absent in remnants smaller than 35 ha (Global $R = 0.13$, $P = 0.11$), indicating that as remnant size decreases, differences in bird communities between vegetation types diminishes.

It appeared that differences in communities associated with remnant size occurred more consistently in moist forest than in woodland (Figure 4). When vegetation types were analyzed separately, the differences between communities in moist forest remnants remained, with communities in remnants larger than 80 ha still significantly different from those in remnants smaller than 4 ha and from those between 4 and 35 ha (Global $R = 0.41$, $P = 0.003$; Figure 5). Communities in remnants smaller than 4 ha and remnants between 4 and 35 ha were not different from each other. However, while bird communities in woodland remnants still demonstrated the trend, this vegetation type did not show significantly distinct communities among the remnant size classes (Global $R = 0.11$, $P = 0.095$; Figure 6). Interestingly, when both size classes of remnants smaller than 35 ha were combined and compared with remnants larger than 80 ha, this trend became significant (Global $R = 0.23$, $P = 0.01$), indicating a clear threshold of change between 35 and 80 ha. I consider the pooling of remnants smaller than 35 ha to be a reasonable step as it is in keeping with the non-significant difference between remnants smaller than 4 ha and those between 4 and 35 ha described by the primary analysis of these remnants.

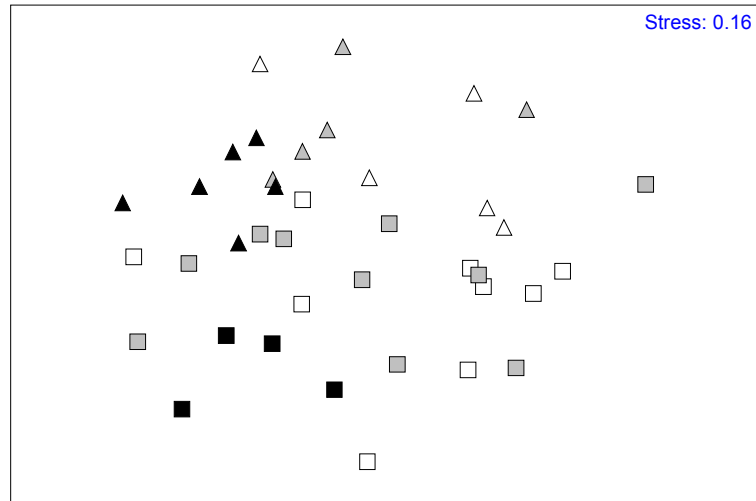


Figure 4: Non-metric multi-dimensional scaling plot of remnant bird communities (n = 39) showing response to vegetation type and remnant size. Points that are closer together represent remnants with more similar bird communities. Triangles represent moist forest. Squares represent woodland. Filled symbols represent remnants > 80 ha. Shaded symbols represent 4-35 ha remnants. Unfilled symbols represent < 4 ha remnants.

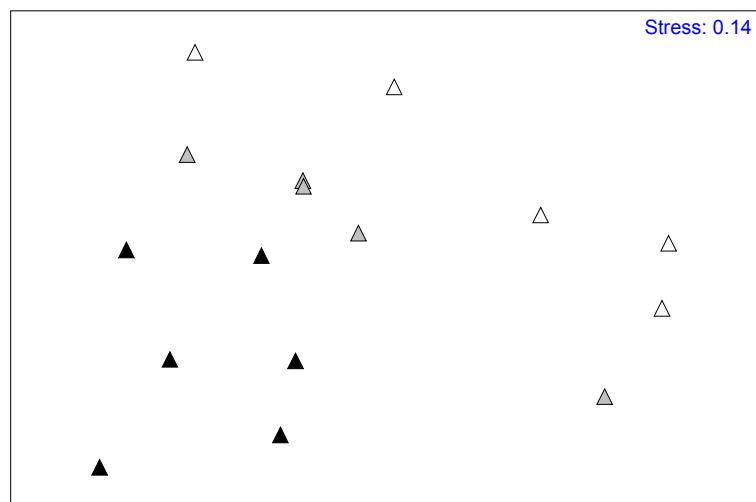


Figure 5: Non-metric multi-dimensional scaling plot of bird communities in moist forest remnants (n = 16) showing response to remnant size. Points that are closer together represent remnants with more similar bird communities. Filled symbols represent remnants > 80 ha. Shaded symbols represent 4-35 ha remnants. Unfilled symbols represent < 4 ha remnants.

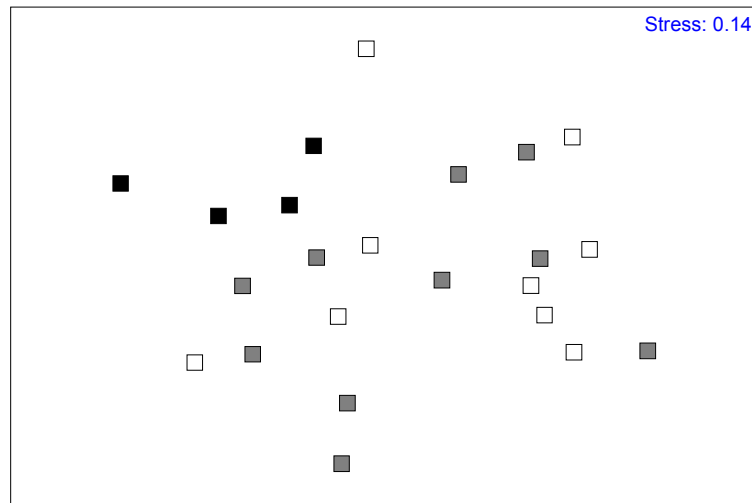


Figure 6: Non-metric multi-dimensional scaling plot of bird communities in woodland remnants ($n = 23$) showing response to remnant size. Points that are closer together represent remnants with more similar bird communities. Filled symbols represent remnants > 80 ha. Shaded symbols represent 4-35 ha remnants. Unfilled symbols represent < 4 ha remnants.

Both size classes of remnants smaller than 35 ha were subsequently combined and compared with remnants larger than 80 ha for the SIMPER analysis within vegetation types. The majority of bird species that contributed to the size difference were small insectivores (13-18 cm) including the white-throated treecreeper (*Cormobates leucophaeus*), golden whistler (*Pachycephala pectoralis*) and thornbills (*Acanthiza* spp.; Table 4), which were more commonly encountered in large than small remnants. In moist forest remnants smaller than 35 ha, three species more typical of woodland than of moist forest (Simpson & Day 1996) were often present: noisy miner (*Manorina melanocephala*), grey butcherbird (*Cracticus torquatus*) and dollarbird (*Eurystomus orientalis*). The noisy miner and butcherbird are also common birds of the urban matrix. Interestingly, bird communities in remnants larger than 80 ha, were more homogeneous than those in remnants smaller than 35 ha, with an average Bray-Curtis similarity of 38.9 % compared with 23.0 %.

Table 4: Remnant size preferences of bird species in remnants of moist forest vegetation.

Bird species contributed to a cumulative total of 50 % of the Bray-Curtis dissimilarity index between size classes.

Bird Species		Contribution to dissimilarity index (%)
Species more commonly encountered in remnants smaller than 35 ha		
White-browed scrubwren	<i>Sericornis frontalis</i>	3.31
Eastern yellow robin	<i>Eopsaltria australis</i>	3.05
Brown gerygone	<i>Gerygone mouki</i>	3.02
Noisy miner	<i>Manorina melanocephala</i>	2.82
Grey butcherbird	<i>Cracticus torquatus</i>	2.82
Dollarbird	<i>Eurystomus orientalis</i>	2.73
Species more commonly encountered in remnants larger than 80 ha		
White-throated treecreeper	<i>Cormobates leocophaeus</i>	4.80
Golden whistler	<i>Pachycephala pectoralis</i>	4.14
Variegated fairy-wren	<i>Malurus lamberti</i>	4.06
Grey fantail	<i>Rhipidura fuliginosa</i>	3.92
Eastern spinebill	<i>Acanthorhynchus tenuirostris</i>	3.36
Striated thornbill	<i>Acanthiza lineata</i>	3.29
Yellow-faced honeyeater	<i>Lichenostomus chrysops</i>	3.15
Brown thornbill	<i>Acanthiza pusilla</i>	3.11
Lewins honeyeater	<i>Meliphaga lewinii</i>	2.82

For woodland remnants, bird species that contributed to the differences amongst remnants of different sizes were again small insectivores such as the southern emu-wren (*Stipiturus malachurus*) and grey fantail (*Rhipidura fuliginosa*; Table 5), which were more common in large than small remnants. Several species more commonly encountered in woodland remnants smaller than 35 ha are also common birds of the urban matrix (Simpson & Day 1996): noisy miner, spotted turtledove (*Streptopelia chinensis*) and Australian magpie (*Gymnorhina tibicen*). As was the case for moist forest remnants, bird communities in woodland remnants larger than 80 ha were more homogeneous than those in remnants smaller than 35 ha, with an average Bray-Curtis similarity of 35.3 % compared with 18.9 %. Interestingly the noisy miner was the only species more commonly encountered in remnants smaller than 35 ha in size for both moist and woodland remnants.

Univariate analysis investigating the response of both bird species richness and density to vegetation structure produced significant regression models (Table 6). Species richness responded to two variables which explained 33.2 % of variation. High-shrub cover made the largest contribution (standard coefficient = 0.354) followed by the height of the tree layer (standard coefficient = 0.305). Bird density also responded to two variables which explained 21.8 % of variation. High-shrub cover made the largest contribution (standard coefficient = 0.393), followed by tree cover (standard coefficient = 0.236).

Table 5: Remnant size preferences of bird species in remnants of woodland vegetation. Bird species contributed to a cumulative total of 50 % of the Bray-Curtis dissimilarity index between size classes.

Bird Species		Contribution to dissimilarity index (%)
Species more commonly encountered in remnants smaller than 35 ha		
Eastern rosella	<i>Platycercus eximius</i>	4.08
Noisy miner	<i>Manorina melanocephala</i>	3.99
Yellow-faced honeyeater	<i>Lichenostomus chrysops</i>	3.68
Spotted turtledove	<i>Streptopelia chinensis</i>	3.58
Variegated fairy-wren	<i>Malurus lamberti</i>	3.53
Australian magpie	<i>Gymnorhina tibicen</i>	3.50
Species more commonly encountered in remnants larger than 80 ha		
Southern emu-wren	<i>Stipiturus malachurus</i>	7.87
Eastern spinebill	<i>Acanthorhynchus tenuirostris</i>	6.05
Grey fantail	<i>Rhipidura fuliginosa</i>	5.82
Mistletoebird	<i>Dicaeum hirundinaceum</i>	4.92
Sacred kingfisher	<i>Todiramphus sanctus</i>	3.60

Table 6: Standard multiple regression models of vegetation structure with species richness and bird density.

Variables	Coefficient	Standard Error	Standard Coefficient	Tolerance	<i>t</i>	P
Species richness <i>a</i>						
High-Shrub Cover	0.139	0.063	0.354	0.718	2.202	0.034
Tree Height	0.195	0.103	0.305	0.718	1.895	0.066
Bird density <i>b</i>						
Constant						
High-Shrub Cover	0.382	0.144	0.393	0.998	2.662	0.012
Tree Cover	0.296	0.185	0.236	0.998	1.596	0.119
<i>a</i> R ² = 0.332; df = 2,36; P = 0.001						
<i>b</i> R ² = 0.218; df = 2,36; P = 0.012						

3.4 Discussion

Bird communities in remnants larger than 80 ha were significantly influenced by vegetation type, with communities in moist forest remnants differing from those in woodland remnants. Bird communities in remnants smaller than 35 ha were significantly different from those in remnants larger than 80 ha, however they were not influenced by vegetation type. Interestingly, the difference in bird communities between remnants smaller than 35 ha and larger than 80 ha was more consistent for moist forest remnants than woodland remnants. This suggests a differential impact of remnant size on bird communities associated with different vegetation types. This impact does not appear to be associated with remnant quality, as vegetation structure did not differ across remnant size within a vegetation type. Of further interest is the non-significant difference between bird communities in different vegetation types in remnants smaller than 35 ha. This suggests that factors in common to the two vegetation types, such as external factors related to the surrounding matrix, may also be having an influence on the composition of the bird communities. It appears that several factors may have been operating in the suburban landscape to produce these different responses.

Firstly, bird communities in large remnants are less likely to be disturbed by fragmentation in general. Remnants with this more natural plant community retain small bushland-dependent insectivorous species that differentiate the bird communities in each vegetation type. In moist forest, species more typical of moist forest, such as the white-throated treecreeper, occurred in remnants larger than 80 ha but were mostly absent from remnants smaller than 35 ha. In woodland, species more typical of woodland, such as the southern emu-wren similarly occurred in remnants

larger than 80 ha and were mostly absent from remnants smaller than 35 ha. These distributions suggest that some of the species that differentiate the bird communities of these vegetation types in a natural state are not found in small remnants.

Secondly, bird communities in moist forest and woodland remnants smaller than 35 ha share common elements. The surrounding matrix might be one potential source of common elements. The noisy miner, the species in common between moist and woodland remnants smaller than 35 ha, is a common inhabitant of the urban matrix (Sewell & Catterall 1998), so its presence is consistent with the potential of matrix elements to invade remnants (Pell & Tidemann 1997; Marzluff & Ewing 2001; Chace *et al.* 2003). Woodland remnants were additionally inhabited by an introduced species, the spotted turtledove, and moist forests were additionally inhabited by the grey butcherbird, a species not typical of moist vegetation. This indicates that species from the matrix were responsible for some of the variation in the bird community between large and small remnants.

The loss of bushland-dependent species, often characteristic of a vegetation type in its natural state, and the invasion by species adapted to the surrounding matrix into small remnants is consistent with other fragmented landscapes. In variegated landscapes consisting of agricultural and urban areas, remnants up to 2 ha in size had lowered densities of bushland-dependent species and a high abundance of matrix specialists (Martin & Catterall 2001). This pattern has also been observed in remnants up to 10 ha in size (Catterall *et al.* 1997). In an urban landscape, bushland-dependent birds only became dominant over urban birds when remnants were larger than 5 ha, with a further increase up to 50 ha required before urban species became

absent (Drinnan 2005). These studies suggest a threshold effect between 2 and 50 ha in which small remnants express a similar change in bird community composition. While this study did not investigate size thresholds, these results suggest that the threshold is between 35 and 80 ha.

The density and species richness of birds was influenced by changes in vegetation structure. High-shrub cover was a common and dominant factor in both moist and woodland habitats influencing both bird density and species richness. Cover or complexity of shrub and understorey vegetation is known to have a positive influence on bird density and species richness both in the urban matrix (Beissinger & Osborne 1982; Munyenymbe *et al.* 1989; Blair 1996; Dulisz & Nowakowski 1996) and within remnant vegetation (Tilghman 1987; Hinsley *et al.* 1998), particularly on species that are forest or understorey specialists, or sensitive to fragmentation (Grover & Slater 1994; Slater 1995; Bolger *et al.* 2001; Brotons & Herrando 2001a). High-shrub cover in this study represents a more complex understorey structure and probably provides more habitat or shelter to accommodate more individual birds as well as greater habitat heterogeneity to provide for more species. A more complex understorey may also benefit bird communities in remnant vegetation by reducing the permeability of the remnant to invasive elements from the matrix, such as introduced or urban-adapted species that potentially compete with the species more dependent on native vegetation. In a fragmented landscape where remnant vegetation structure was known to differ, matrix-adapted species had an elevated abundance in remnants with no understorey, while bushland-dependent species were reduced in abundance (Catterall *et al.* 1997). Maintaining the structural integrity of remnant vegetation is

one recommendation aimed at improving the urban landscape for bushland-dependent species (Catterall *et al.* 1997; Watson *et al.* 2001).

I found that within woodland remnants, the differences in bird community composition associated with remnant size bordered on significance depending on how remnant size was grouped. This may indicate that bird communities in some habitats are more vulnerable to fragmentation than others. Communities in woodland remnants appear less vulnerable than those in moist remnants. Woodland potentially has a more simple vegetation structure (in comparison with moist forest), creating less of a contrast with the surrounding suburban matrix. Woodland remnants may therefore be fundamentally similar to suburban areas and their bird communities may share species and be more easily maintained across size classes. This community overlap is reflected in the weak but significant Global R value (0.23, $P = 0.01$). Communities in moist remnants appear to be more vulnerable and more difficult to maintain, having less community overlap (Global R value = 0.41, $P = 0.003$).

This study suggests that vegetation type is an important determinant of the species composition of bird communities in remnants larger than 80 ha. Including remnants larger than 80 ha will be important for the conservation of biodiversity and specific species assemblages in suburban environments at a landscape level. Remnants smaller than 35 ha appear to lose their integrity, with external factors becoming influential in the composition of bird communities, potentially through the invasion of species associated with the surrounding matrix. In these smaller remnants maintaining structural complexity of the vegetation, especially the shrub layer, will provide a better focus through which to improve the diversity of bird communities.

Overall, while small remnants can be mapped and included in any target for retention of that vegetation type, these results indicate that the potential value of retaining a diversity of vegetation types may be lost if their size or the surrounding matrix composition in the landscape compromises their distinct wildlife value. Retaining larger remnants of a size that provides resistance to characteristics of the surrounding suburban matrix may be one way of maintaining birds that are characteristic of native vegetation types and enhancing biodiversity within the suburban landscape.

Chapter 4

A comparison of foraging behaviour of small, urban-sensitive insectivores in continuous woodland and woodland remnants in a suburban landscape

4.1 Introduction

In many fragmented landscapes, small remnants of original native vegetation, surrounded by a highly modified matrix, are often the only habitat available for most native species. Therefore management of these remnants is often the most feasible option for the conservation of biodiversity (Shafer 1995; Fauth 2001; Fischer & Lindenmayer 2002). Theoretically, small remnants can contribute to the conservation of species that are sensitive to fragmentation through the provision of stepping-stones for dispersal, shelter from predators, or regular habitat (Forman 1999) in an inhospitable matrix. These functions have been demonstrated in agricultural landscapes with remnants acting as stepping-stones (Brooker & Brooker 1997; Fortin & Arnold 1997; Cale 2003; Fraser & Stutchbury 2004) or as habitat for populations in source/sink configurations (Zanette 2000; Fauth 2001).

However, remnant vegetation may be subject to a variety of pressures from the surrounding matrix, including an increase in exotic or native competitors (Gilfedder & Kirkpatrick 1998), removal of key resources, and disruption of nutrient and hydrological cycles (Marzluff & Ewing 2001; Stenhouse 2004). As a result, vegetation in small remnants may be altered and unlikely to contain the full range of conditions necessary for the survival of a population of a single species, or a suite of species. Therefore, it is possible that remnants will play a role in conservation by

complementing larger vegetation tracts through the provision of secondary habitat for many species, rather than fully maintaining sustainable populations of these species.

Altered conditions within a remnant can affect the direct requirements of a species through reduction of food resources (Burke & Nol 1998; Zann *et al.* 2000), nesting material and sites (Ford *et al.* 2001), and shelter. As a consequence breeding success, which can depend on territory quality (Przybylo *et al.* 2001), is often reduced in remnants in an agricultural landscape (Poneluzi & Faaborg 1999) relative to large vegetation tracts.

Altered remnant conditions may alternatively have an indirect effect on species by providing conditions more favourable to their competitors or predators. Remnant species may then suffer increased predation during nesting (Huhta *et al.* 2004), juvenile and adult stages (Elchuk & Wiebe 2002), or be out-competed for food (Davis & Recher 1993; Grey *et al.* 1997) or nesting resources (Pell & Tidemann 1997). Species will often respond by changing their behavior in an attempt to optimize their fitness in the new conditions (Bell 1985; Forstmeier & Weiss 2004).

Foraging behavior is balanced between maximizing time and energy budgets (Stephens & Krebs 1986) and avoiding predators or aggressive competitors. Therefore if remnant conditions were sub-optimal, measurable changes in foraging behavior in response to these direct and indirect effects could be expected. Foraging behavior has been widely examined in birds in continuous habitats (Recher & Holmes 1985; Pulido & Diaz 2000; Murakami & Nakano 2001) and is known to respond to seasonal fluctuations (Cameron 1985; Recher & Holmes 1985; Cale

1994), habitat structure (Robinson & Holmes 1982; Recher *et al.* 2002), and adverse conditions including drought (Bell & Ford 1990), fire (Chapman & Harrington 1997) and food shortage (Bell 1985). In remnant vegetation, Miller & Cale (2000) found that characteristics such as remnant size influenced bird foraging methods. Furthermore, assessing foraging behavior, as a measure of bird responses to fragmentation, involves fewer limitations than life history parameters because it is an ecological process that takes place at the individual level. As a result, conditions in remnants can still be investigated even where individuals in the population may be unable to form successful breeding pairs.

Species sensitive to fragmentation in urban landscapes have not been studied as intensively as those in agricultural landscapes. Surveys have shown that, relative to the matrix, remnants in urban landscapes often contain a greater density of these sensitive birds (Wood 1996; Catterall *et al.* 1998; Parsons *et al.* 2003; Crooks *et al.* 2004) and a greater diversity of species (Green 1984; Tilghman 1987; Wood 1996; Sewell & Catterall 1998), yet the extent to which they are able to utilize the remnants is not known.

Behavioural studies by Breininger (1999) have demonstrated that scrub-jays permanently inhabited a remnant but had lower reproductive success than those in continuous vegetation. Bowman & Woolfenden (2002) found scrub-jays in urban remnants built their nests higher above the ground than those in continuous habitat. Relatively few foraging studies have been undertaken in the urban landscape (but see Fleischer *et al.* 2003). None have investigated the quality of isolated remnants

although some studies have investigated the use of native versus exotic plant species within the urban matrix (Green 1984; Green *et al.* 1989; French *et al.* 2005).

Small insectivorous species are often the species that are most affected by urbanization (Beissinger & Osborne 1982; Zalewski 1994; Catterall *et al.* 1998; Clergeau *et al.* 1998; Allen & O'Connor 2000). Isolated remnants within the urban matrix are often considered important refuges for these species, however no study has determined whether these habitats are equivalent to larger tracts of vegetation or whether they represent sub-optimal habitat. This paper compares the foraging behaviour of small urban-sensitive insectivores in remnant vegetation with those in continuous vegetation to determine whether changes are occurring in their foraging behaviour and whether these changes represent adverse effects within a suburban landscape.

4.2 Methods

4.2.1 Study region

The predominantly open woodland vegetation of the Wyong Shire (95 km north of Sydney, 33°17'S, 151°26'E) is in various stages of fragmentation and now covers only 29 % of the land surface (Anon 2000). Land uses contributing to this fragmentation include forestry (covering 37 %), farming (20 %) and urban housing (10 %). Urban development has been concentrated in 56 square kilometers of the coastal plain, and the density of housing within this area reaches 20 to 25 house blocks per hectare. Fragments of eucalypt woodland within the urban area are either Smooth-barked Apple Woodland (*Angophora costata*) or Scribbly Gum Woodland (*Eucalyptus haemastoma*). These two woodland types, which often merge, are closely related and floristically similar, sharing many shrub species (NPWS 2000) e.g. *Allocasuarina littoralis*, *Banksia spinulosa*, *Lambertia formosa*, *Pimelia linifolia*, *Lomandra obliqua* and *Entolasia stricta*. Riparian Melaleuca Swamp Woodland (*Melaleuca sieberi*) is also associated with both these woodlands along narrow drainage lines.

4.2.2 Survey species

I investigated the foraging behavior of the white-browed scrubwren (*Sericornis frontalis*), eastern yellow robin (*Eopsaltria australis*), brown thornbill (*Acanthiza pusilla*), striated thornbill (*Acanthiza lineata*) and grey fantail (*Rhiphidura fuliginosa*). These species commonly occur in Australian woodlands and have been relatively well studied in continuous habitat. They have also been recorded in native remnants occurring within the urban landscape (Green 1984; Wood 1995, 1996; Evans *et al.*

1997; Catterall *et al.* 1998; Sewell & Catterall 1998; Parsons *et al.* 2003), and were known to occur in remnants of the study region (chapter two).

These species forage at a range of different heights (Recher & Holmes 1985; Mac Nally 1994). Both the white-browed scrubwren and eastern yellow robin forage mainly on the ground (Marchant 1985; Recher & Holmes 1985; Cale 1994). The brown thornbill forages mainly at the shrub level (Bell 1985; Bell & Ford 1990) while the striated thornbill and grey fantail predominantly forage in the canopy (Bell 1985; Cameron 1985).

Individual birds were observed in seven remnants and four sites within a tract of continuous woodland (now referred to as remnants and continuous respectively). All remnants backed onto suburban areas, and the majority of remnants were surrounded by suburban matrix. Remnants ranged in size from 4 – 30 ha and were between 0.1 and 6 km apart. The continuous woodland was approximately 800 ha with the four sites between 0.2 and 2.5 km apart.

4.2.3 Bird observations

The behavior of the five bird species was recorded over the warmer months from September 2002 to March 2003. Observations were recorded within 4 hours of sunrise, finishing by 10:00 EDST. The behavior of individual birds was recorded only once per day. For flocking species, the behavior of no more than half the flock was recorded to reduce the possibility of recording the same bird twice.

The behavior of individual birds (except those known to be breeding) was timed continuously for a minimum of 20 seconds to a maximum of 20 minutes (average = 176 sec). Each timed recording noted the birds' behavior, position in the vegetation, and each time these attributes changed.

Bird behavior was recorded under four categories: foraging, preening, vocalizing or vigilance. The number of times a bird attacked its prey and the substrate on which the attack occurred were recorded, regardless of whether the bird successfully obtained the prey. The length of a prey attack was not recorded, as they were usually brief, spontaneous events.

The position in the vegetation for each behavior category was described by three variables: plant species (smooth-barked eucalypt, rough-barked eucalypt, melaleucas, casuarinas, other tree, bare ground, grass, or leaf litter), vegetation substrate (trunk, branches, or foliage) and height. Dead vegetation and substrates were distinguished from those that were live, and height was estimated to the nearest meter.

4.2.4 Habitat measurements

Vegetation characteristics of sites were recorded in order to identify any difference in habitat between remnants and continuous vegetation, so that variations in bird behavior could be interpreted meaningfully. Habitat structure and composition of each site were sampled at the points at which behavioural observations were conducted. Four, 20 m x 20 m survey quadrats were marked out in each site. This quadrat size was compatible with bird behavior as most individuals covered the same or less area for the duration of their recordings.

Twenty-five sampling points were assessed in each quadrat. At each point the cover of vegetation was measured using a vertical 3-m pole (18 mm diameter) and recording the presence of touching vegetation at a series of height levels (ground, 0-0.2 m, 0.2-0.5 m, 0.5-1 m, 1-2 m, 2-3 m, 3-4 m, 4-5 m, 6-10 m, and > 10 m). Vegetation above 3 m was measured by visually sighting up the rod. The plant species (i.e. rough-bark gum, casuarina etc) touching at each height level was recorded as a measure of vegetation composition.

The percent cover of vegetation at every height level was calculated as the proportion of touches out of a possible 25. The total number of touches for habitat composition could equal more than 25 because several plant species may have been touching in one height level. To assess the habitat composition of each quadrat, plant species at every height level were converted to a proportion of the total number of touches of all plant species at that height level.

4.2.5 Data analysis

Foraging behavior of each species was analyzed in relation to position in the vegetation. The foraging time spent by an individual in each plant type was calculated as a proportion of the individuals' total foraging time. Data distributions violated the assumptions of ANOVA so the Kruskal-Wallis procedure was used to compare all individuals foraging in remnants with all individuals foraging in continuous vegetation for each plant type. Only plant types in which foraging behaviour accounted for 5 % or more of total foraging time were tested for significance. This was repeated for both foraging time in vegetation substrates and

the height in vegetation. An individuals' rate of prey attack was calculated as the number of attacks per minute of their total sample time. Prey substrate frequency was calculated as the proportion of prey attacks on each substrate. The Kruskal-Wallis procedure was again used to test for significance between the prey substrate frequency of all individuals in remnants and those in continuous vegetation.

Habitat structure and composition were analyzed using non-parametric multivariate techniques based on a similarity matrix that describes relationships between samples (PRIMER: Clarke 1993). The similarity matrix was created using the Bray-Curtis similarity index (Clarke & Warwick 1994). Remnants were plotted on a non-metric multi-dimensional scaling plot for visual assessment, and were tested for significance using the ANOSIM procedure. This procedure is a permutation test that generates a Global R test statistic which reflects the differences within remnants contrasted with differences among remnants. A value of 0.05 indicates that groups of remnants are clearly different from other groups (Clarke and Gorley 2000). The SIMPER procedure was used to describe which categories made the highest contribution to any significant differences. For structural differences, understorey species were usually pooled. However, the exotic species lantana (*Lantana camara*) was analyzed separately for differences between habitats (using a Kruskal-Wallis test) as behavioural observations suggested that this plant species contributed to variation in bird behavior. Lantana was of particular interest, as remnant sites are often considered to have increased exotic species, which can significantly increase cover at shrub level (Wood 1996).

4.3 Results

The habitat structure of remnants was significantly, but weakly (Global $R < 0.5$), different from that of continuous vegetation (Global $R = 0.119$, $P = 0.024$) (Figure 7) with a low dissimilarity index (average Bray-Curtis dissimilarity = 20.13 %). Four height levels accounted for 55 % of this dissimilarity (Table 7). Low vegetation at 0.2-0.5 m and 0.5-1 m was more prominent in continuous vegetation while high vegetation at 6-10 m and > 10 m were more prominent in the remnants.

There were no significant differences in habitat composition between remnants and continuous vegetation (Global $R = 0.051$, $P = 0.128$) and no difference in the percentage cover of lantana ($F = 2.18$, $p = 0.1474$).

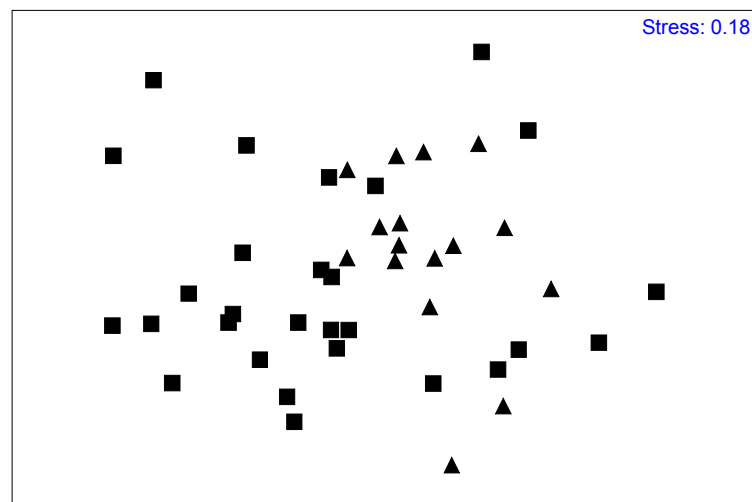


Figure 7: Non-metric multi-dimensional scaling plot of differences in vegetation structure between remnants, using four replicate quadrats at each site ($n = 44$). Points that are closer together represent remnants with more similar habitat structure. ■ Remnant sites, ▲ Continuous sites.

Table 7: Structural differences between remnants and continuous vegetation based on differences identified in multivariate comparisons (SIMPER procedure). Height levels ordered in decreasing height to give a visual representation of structural dissimilarities. + indicates that the particular level was more prominent in that habitat type.

Height Level (m)	Remnants	Continuous vegetation	Percent dissimilarity contribution
>10	+		13.44
6-10	+		13.49
4-5	+		5.20
3-4	+		5.73
2-3	+		9.07
1-2		+	9.21
0.5-1.0		+	14.02
0.2-0.5		+	15.01
0.0-0.2	+		11.63

Two hundred and eighty-six bird records were made for a total of 1135.3 min. In continuous vegetation 153 bird records were made for 552 min; and 133 bird records were made in remnant vegetation for 583.3 min (Table 8). All target species, except the striated thornbill, occurred in at least 75 % of sites for both remnants and continuous vegetation. The striated thornbill occurred in 43 % of remnant sites. Within remnant vegetation, the white-browed scrubwren, brown thornbill, and grey fantail were observed on ≥ 60 % of visits to all except one site (Table 9). The eastern yellow robin was observed on ≥ 60 % of visits to three sites while the striated thornbill was observed on ≥ 50 % of visits for only two sites.

Table 8: Number of bird records and total observation time for target species.

Species		All sites	Remnants (n = 7)	Continuous vegetation (n = 4)
White-browed scrubwren	Samples	67	37	30
	Total Time (min)	279.20	175.75	103.45
	Range (sec)	24 - 1200	39 - 1200	24 - 1074
Eastern yellow robin	Samples	42	15	27
	Total Time (min)	266.56	129.68	136.88
	Range (sec)	30 - 1200	64 - 1200	30 - 1200
Brown thornbill	Samples	80	45	35
	Total Time (min)	131.97	83.97	48.00
	Range (sec)	21 - 410	22 - 410	21 - 379
Striated thornbill	Samples	46	19	27
	Total Time (min)	63.52	24.80	38.72
	Range (sec)	20 - 299	27 - 143	20 - 299
Grey fantail	Samples	51	17	34
	Total Time (min)	394.05	169.12	224.93
	Range (sec)	22 - 1200	40 - 1200	22 - 1089

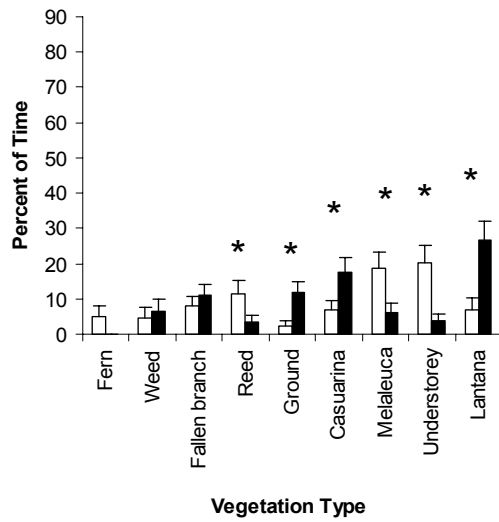
Table 9: Species occurrence at remnant sites and continuous vegetation. Occurrence is expressed as a percentage of all visits to that site between October 2002 and March 2003.

Species disappeared after reconnaissance visits and one recording visit.

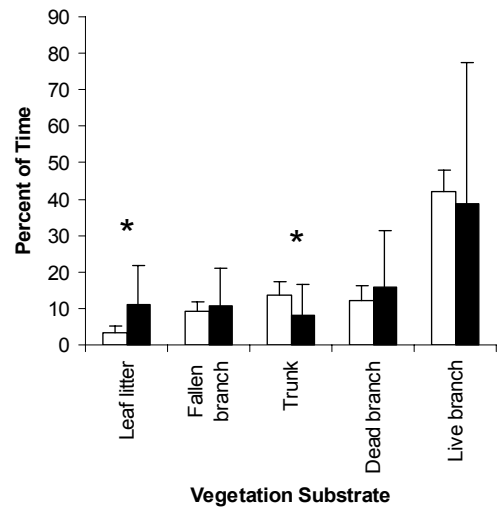
Site	Number of visits	White-browed scrubwren	Eastern yellow robin	Brown thornbill	Striated thornbill	Grey fantail
Remnant						
1	7	100	71	100	29	100
2	6	83	83	83	50	100
3	5	67	17	100	67	67
4	6	100	0	67	0	17
5	7	100	14 [#]	0	0	0
6	5	60	40	40	0	80
7	5	20	60	100	0	80
Continuous vegetation						
1	8	88	100	88	75	100
2	7	71	71	100	57	100
3	7	86	71	100	0	100
4	6	0	33	83	50	100

White-browed scrubwrens spent significantly more time in casuarinas ($\chi_1^2 = 4.34$, $P = 0.034$), lantana ($\chi_1^2 = 15.12$, $P = 0.0001$) and on the ground ($\chi_1^2 = 11.13$, $P = 0.0008$) (Figure 8a) in remnants compared with continuous vegetation. In continuous vegetation, they spent significantly more time in melaleucas ($\chi_1^2 = 10.40$, $P = 0.0013$), reeds ($\chi_1^2 = 8.33$, $P = 0.0039$) and the understorey ($\chi_1^2 = 13.04$, $P = 0.0003$). White-browed scrubwrens spent 60 % of their time foraging on branches (both dead and alive) in both habitats. They spent significantly more time in leaf litter ($\chi_1^2 = 8.01$, $P = 0.0047$) in remnants and more time on trunks in continuous vegetation (Figure 8b). They foraged below 1 m for most of the time, and only very rarely foraged at heights above 6m (Figure 8c). Prey was commonly collected from bark, foliage and leaf litter. In remnants significantly more prey was collected from leaf litter ($\chi_1^2 = 3.94$, $P = 0.0470$) (Figure 8d). The rate of prey attack was not significantly different (Table 10) between remnant and continuous sites.

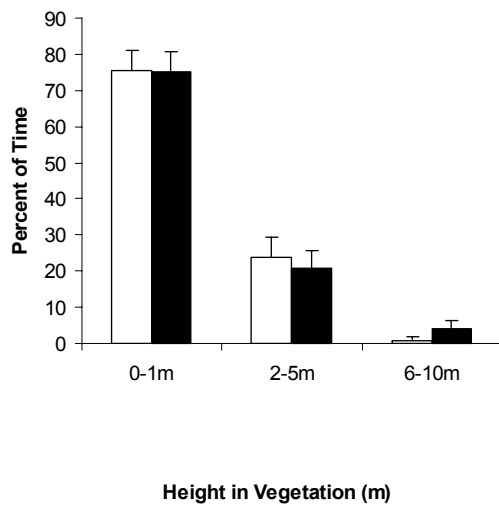
8a)



8b)



8c)



8d)

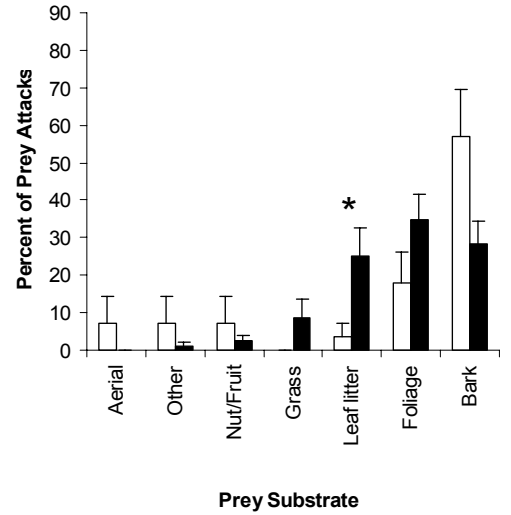


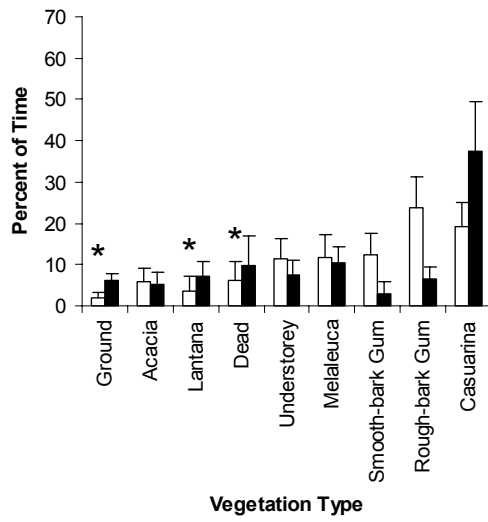
Figure 8: White-browed scrubwren foraging behavior. Filled bars represent remnants, unfilled bars represent continuous vegetation. (a) – (c) mean percent of time spent by individual birds in vegetation categories and (d) mean percent of prey attacks taken from prey substrate type by individual birds. Error bars show standard error. Asterisk indicates a significant difference by the Kruskal-Wallis test.

Table 10: Comparison of prey attack rates (attacks/min) in remnant sites and continuous vegetation. Statistical significance is determined by the Kruskal-Wallis test.

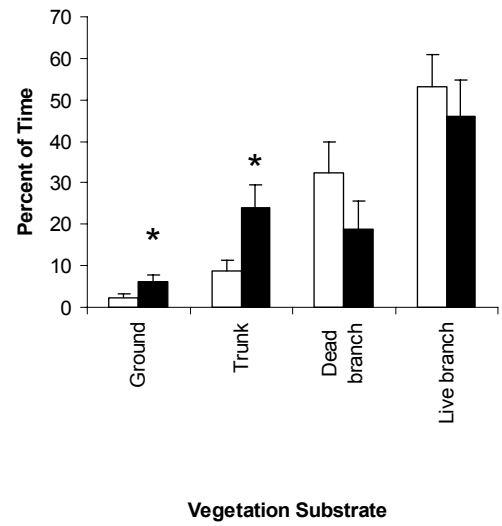
Species	Remnants	Continuous vegetation	P
White-browed scrubwren	0.87	0.57	0.070
Eastern yellow robin	0.75	0.31	0.008
Brown thornbill	2.32	1.88	0.108
Striated thornbill	2.70	1.84	0.028
Grey fantail	1.35	0.91	0.167

Eastern yellow robins spent most time in casuarinas (particularly in remnants) and rough-bark gums (particularly in continuous vegetation), however they spent significantly more time in lower-level vegetation in lantana ($\chi_1^2 = 4.72$, $P = 0.0298$), dead vegetation ($\chi_1^2 = 4.70$, $P = 0.0302$) and on the ground ($\chi_1^2 = 8.89$, $P = 0.0029$) in remnants than in continuous vegetation (Figure 9a). This is further reflected in the height analysis where eastern yellow robins spent significantly more time at 0-1 m in remnants than in continuous vegetation ($\chi_1^2 = 8.66$, $P = 0.0033$) (Figure 9c). Most of their time was spent on branches (both dead and alive), although in remnants they increased their usage of trunks and the ground ($\chi_1^2 = 5.95$, $P = 0.0148$) (Figure 9b). They also obtained more prey from leaf litter ($\chi_1^2 = 4.27$, $P = 0.0389$) (Figure 9d) and performed significantly more prey attacks per minute ($\chi_1^2 = 7.07$, $P = 0.0078$) in remnants than in continuous vegetation (Table 10).

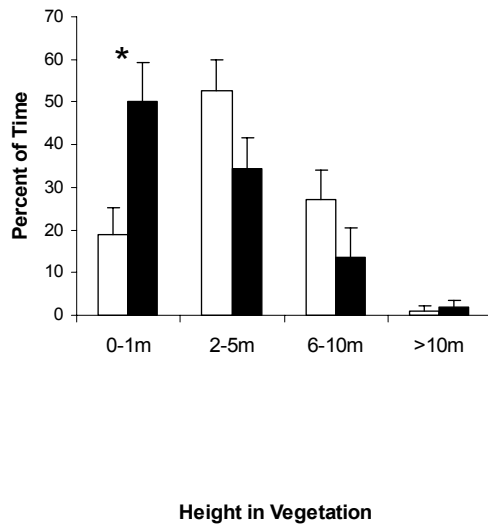
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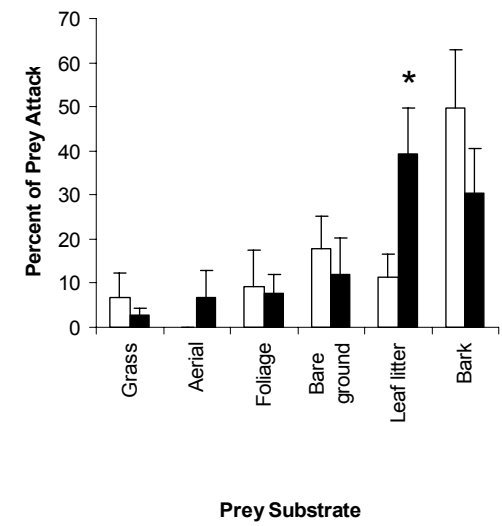
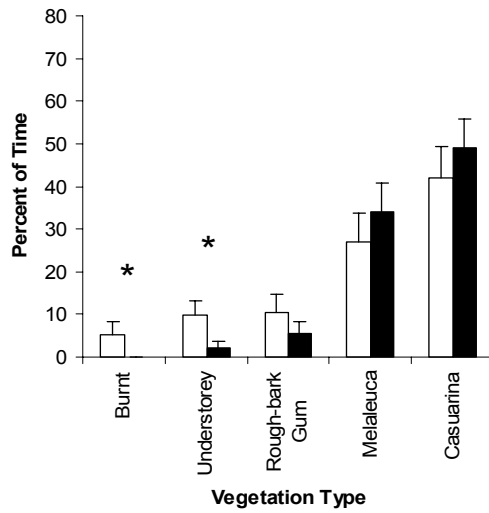


Figure 9: Eastern yellow robin foraging behavior. Filled bars represent remnants, unfilled bars represent continuous vegetation. (a) – (c) mean percent of time spent by individual birds in vegetation categories and (d) mean percent of prey attacks taken from prey substrate type by individual birds. Error bars show standard error. Asterisk indicates a significant difference by the Kruskal-Wallis test.

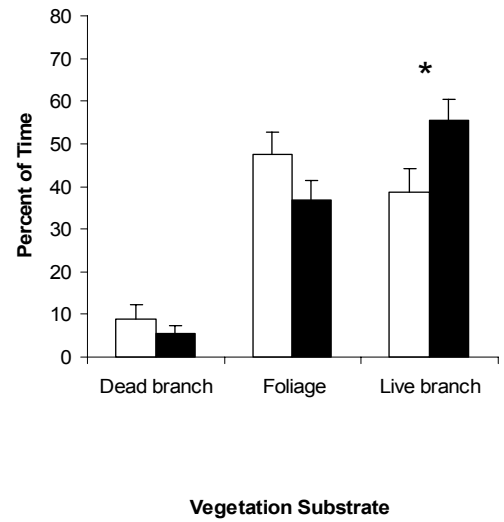
Brown thornbills spent most of their time in melaleucas and casuarinas in both habitats. In continuous vegetation they spent more time in burnt vegetation ($\chi_1^2 = 3.96$, $P = 0.0467$), and the understorey ($\chi_1^2 = 8.37$, $P = 0.0038$) (Figure 10a). Brown thornbills in remnant vegetation spent more time in live branches ($\chi_1^2 = 5.37$, $P = 0.0205$) (Figure 10b) but less time at 6-10 m ($\chi_1^2 = 3.89$, $P = 0.049$) (Figure 10c). Overall, they mostly collected prey from bark and foliage, however, brown thornbills performed more aerial prey attacks ($\chi_1^2 = 6.37$, $P = 0.0116$) (Figure 10d) in remnants - although there was no difference in rate of prey attack (Table 10).

In contrast, striated thornbills foraged in both smooth and rough bark gums amongst the foliage (Figure 11). They tended to be in the canopy above 6 m, collecting prey from bark and foliage. Striated thornbills in remnants had a significantly higher rate of prey attack ($\chi_1^2 = 4.82$, $P = 0.0282$) (Table 10). There was no significant difference in foraging behavior between continuous vegetation and remnants for any other category (Figure 11).

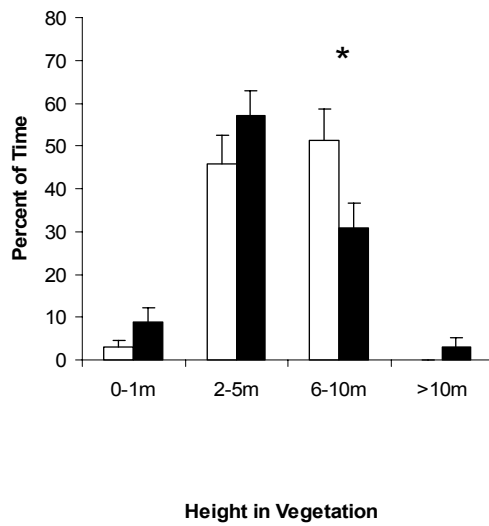
10a)



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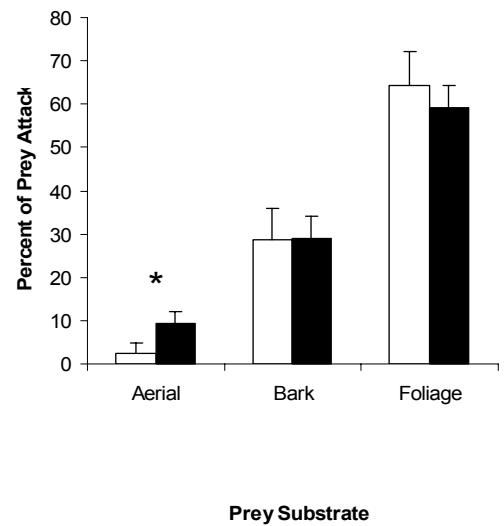
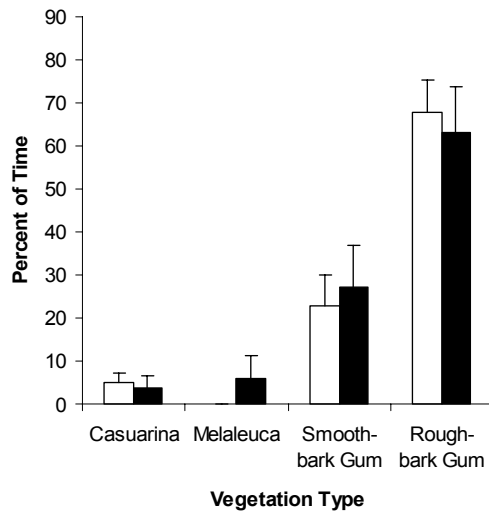
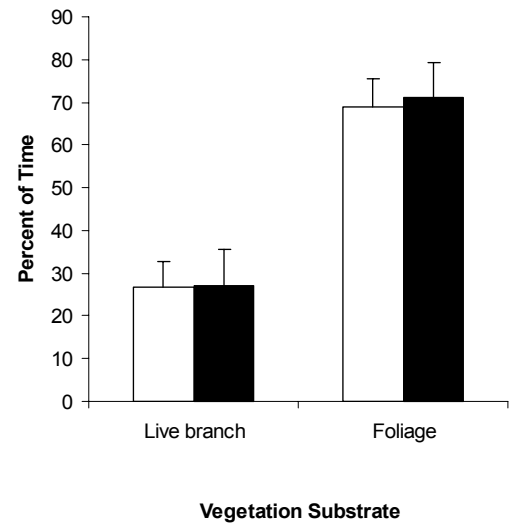


Figure 10: Brown thornbill foraging behavior. Filled bars represent remnants, unfilled bars represent continuous vegetation. (a) – (c) mean percent of time spent by individual birds in vegetation categories and (d) mean percent of prey attacks taken from prey substrate type by individual birds. Error bars show standard error. Asterisk indicates a significant difference by the Kruskal-Wallis test.

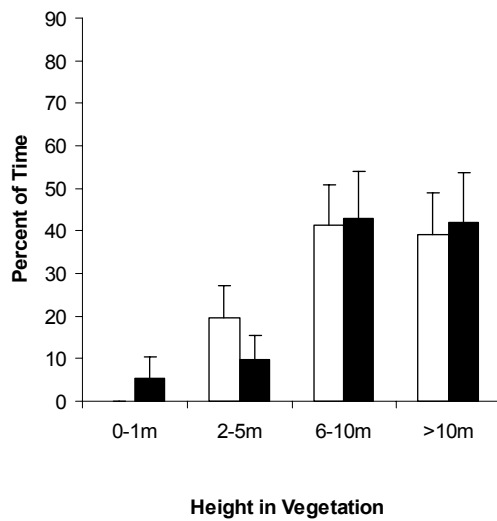
11a)



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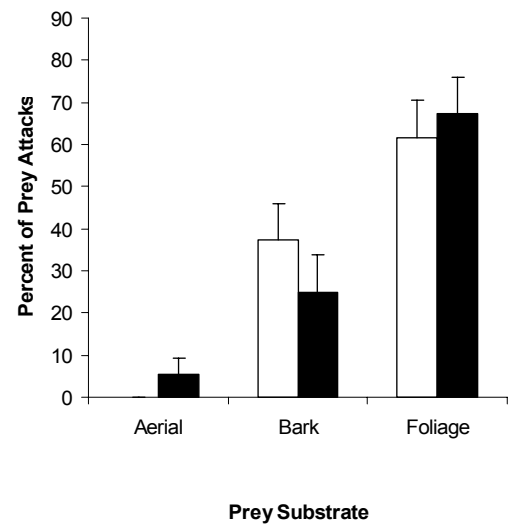


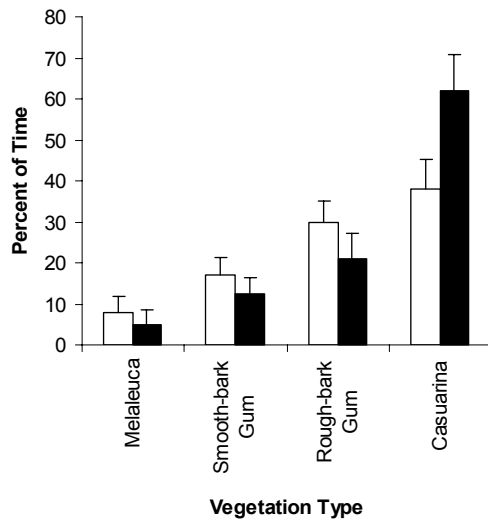
Figure 11: Striated thornbill foraging behavior. Filled bars represent remnants, unfilled bars represent continuous vegetation. (a) – (c) mean percent of time spent by individual birds in vegetation categories and (d) mean percent of prey attacks taken from prey substrate type by individual birds. Error bars show standard error. No differences were significant by the Kruskal-Wallis test.

Grey fantails tended to forage on branches in casuarinas and rough bark gum between 2 and 10 m collecting prey from both foliage and bark. Grey fantails performed more prey attacks on bark ($\chi^2_1 = 4.67$, $P = 0.0307$) (Figure 12d) in remnants than in continuous vegetation, but there was no significant difference in foraging behavior between continuous vegetation and remnants for any other category (Figure 12).

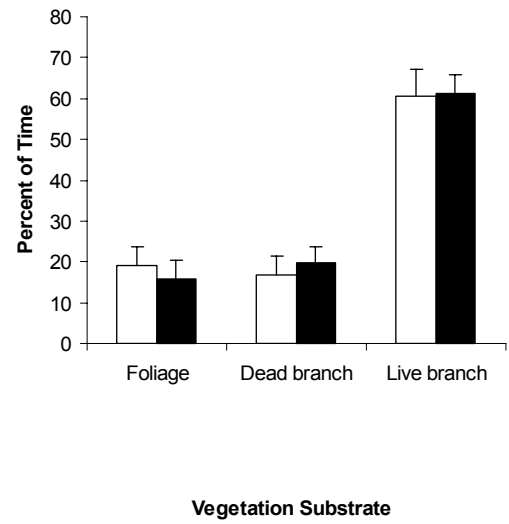
Preening behavior did not vary significantly between remnants and continuous vegetation for any species. Vocalization varied significantly only for brown thornbills, which vocalized significantly more in remnants ($\chi^2_1 = 4.5212$, $P = 0.0335$). Vigilance could only be distinguished from foraging behavior for two species, the eastern yellow robin and the grey fantail, however neither species spent a significantly different proportion of time on vigilance between habitats).

These results have been interpreted conservatively. Firstly there were a large number of individual tests applied to the data. Secondly, for most species observed, significant differences in behaviour occurred in the less frequented vegetation types, heights, and substrates. This conservative approach has had the same effect as applying Bonferroni corrections. These corrections if they had been applied, would have increased the level at which tests reached significance and would not have changed the overall conclusion that behavior involving the more common vegetation types and more common foraging heights varied little between the two habitats.

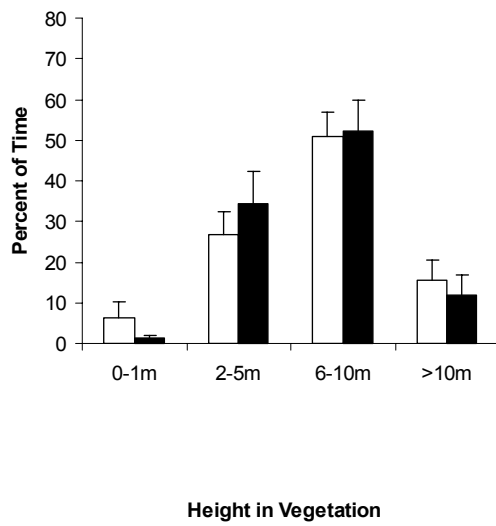
12a)



12b)



12c)



12d)

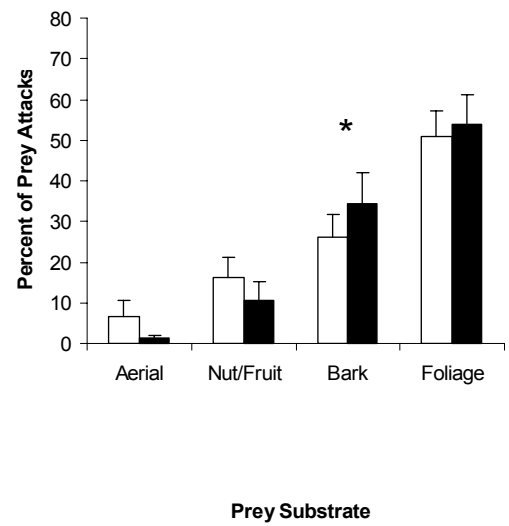


Figure 12: Grey fantail foraging behavior. Filled bars represent remnants, unfilled bars represent continuous vegetation. (a) – (c) mean percent of time spent by individual birds in vegetation categories and (d) mean percent of prey attacks taken from prey substrate type by individual birds. Error bars show standard error. Asterisk indicates a significant difference by the Kruskal-Wallis test.

4.4 Discussion

Remnant vegetation characteristics were not strongly different from those of continuous vegetation, and appeared to provide small insectivorous birds with suitable conditions that enabled them to maintain a presence in the suburban landscape. This suitability was demonstrated by the regular occurrence of all study species within the remnants, and particularly by the similarity in foraging behavior between remnants and continuous vegetation. For most species observed, behavior involving the more common vegetation types and more common foraging heights varied little between the two habitats. Most differences in behavior were in the less frequented vegetation types and heights, and on the less frequently utilized substrates. Similarly, the substrate from which prey was most frequently captured varied little with habitat, and differences were due to the small proportion of prey attacks executed on uncommon prey substrates.

Species varied in the extent to which they exhibited differences in behavior between the two habitats. Shrub- and canopy-foragers used half as many plant species and exhibited fewer differences in foraging behavior between woodland and continuous sites compared with ground foraging species. The brown thornbill was the only shrub- and canopy-forager to show significant changes in foraging behavior. However, several of these changes, i.e. more time at 6-10 m and in burnt vegetation in continuous vegetation, were only just significant ($p = 0.0486$ and 0.0467 respectively), and given the large number of individual tests applied to the data, I consider conclusions should be drawn conservatively. Therefore I consider that only the greater time spent in understorey vegetation and on live branches in continuous vegetation represents a significant change. This suggests that understorey shrubs in continuous vegetation may

provide a better habitat than they do in remnants, although in both habitats, brown thornbills preferred the more complex branches and foliage of casuarinas and melaleucas at heights above 2 m. This compliments the observation that cover provided by low understorey was more prominent in continuous vegetation, and provides evidence, although weak, for the importance of this structural element. Understorey density has been related to the presence of understorey invertebrate-foragers (Slater 1995). In remnants, understorey density has been related to the number of bird species (Tilghman 1987), the number of understorey species (Grover & Slater 1994), the number of foraging guilds (Miller & Cale 2000) and the number of species sensitive to fragmentation (Bolger *et al.* 2001).

Ground- and shrub-foraging species showed a number of minor changes in foraging behavior that support the idea of a depleted understorey resource. White-browed scrubwrens utilized a wide range of vegetation types in both habitats, but tended to forage more on the ground and in leaf litter in remnants, while utilizing the shrub layers in continuous vegetation. Eastern yellow robins in remnants spent more time at 1 m and below, in dead vegetation, in lantana, perching on trunks and on the ground, than did robins in continuous vegetation. Correspondingly, each species in remnants also performed more prey attacks in leaf litter.

Furthermore, the sparser vegetation cover below 1 m in remnants may have enabled eastern yellow robins to exploit the conditions. Eastern yellow robins typically feed on the ground by pouncing from horizontal perches and vertical tree trunks (Marchant 1985), so sparser vegetation cover may have reduced visual obstructions (Chapman & Harrington 1997). Recher *et al.* (2002) have previously found that habitat structure of

the ground surface had a strong influence on foraging behavior of ground-pouncing robins.

An increase in cover in the upper strata in remnants may also have impacted on foraging behavior. For example, greater cover in the upper levels of remnant vegetation may have reduced light levels and foraging efficiency for shrub-foragers like the brown thornbills (Bell 1985) resulting in less time spent in understorey plants of remnants compared with continuous vegetation.

These variations in foraging behavior have been partially explained by slight structural differences in vegetation but not composition. Nevertheless investigation of the use of plant species while foraging has helped to highlight the importance of canopy trees such as eucalypts, casuarinas and melaleucas for insectivores. All birds in remnants and continuous vegetation, utilized these species regularly. Loss of these plant species and their associated structural elements is likely to result in very significant changes in movement and foraging ability. Other studies similarly highlight the importance of canopy trees in the matrix (Munyenymbe *et al.* 1989; Law *et al.* 2000; Grabham & Klomp 2001) and in remnants, with most bird species being observed in the tree canopy of riparian remnants (Fisher 1997), and along a regeneration gradient (Fisher 2001).

Factors other than differences in vegetation structure have been associated with behavioural variation in other studies, but they were not evident in this study. Vegetation composition did not vary between habitats in this study and no aggressive interactions were observed for any species so it seems unlikely that inter-specific competition forced birds to adjust their use of plant species. Increased predation levels

may have caused birds to select plant species offering better protection. However, time spent on vigilance (usually associated with predator detection, Fernandez-Juricic *et al.* 2004) was not greater in remnants, suggesting predation levels were not a driving factor behind plant selection.

Changes in bird foraging behaviour may have been related to spatial or compositional variations in the insect supply on different substrates. Insect communities are known to be affected by habitat complexity (Lassau and Hochuli 2004) and fragmentation (Didham *et al.* 1996). Insect abundance can be greater in small patches of vegetation, and at their edges than interiors (Jokimaki *et al.* 1998; Major *et al.* 2003). Insect community compositions can vary between remnants and continuous vegetation (Major *et al.* 1999; Gibb & Hochuli 2002). Recher & Majer (1994) found that thornbill foraging substrate selection was correlated with the abundances and types of invertebrates present.

If changes to prey composition occur, then changes to prey attack rates are also likely to vary. Studies comparing remnants with continuous tracts of vegetation have found that the rate of provisioning to nestlings was the same, but that nestlings received fewer large prey items (Zanette *et al.* 2000), or that the provisioning rate was lower but nestlings received similar sized items (Luck 2003). Both scenarios represent decreased food intake and availability in remnant vegetation. In contrast Bell (1985) found that when food was less abundant within a remnant, prey attack rate increased, with individuals consuming more small prey items.

Both shrub- and canopy-foragers and ground-foragers in this study showed higher rates of prey attack in remnant vegetation. Rates were between 1.2 and 1.5 times higher than in continuous vegetation, but this was only statistically significant for two species, the striated thornbill and the eastern yellow robin. This change in prey attack rate might suggest that remnants had lower food availability, and that birds increased their prey attack rate to maintain food intake, possibly selecting from a broader variety of prey items. Further research investigating prey availability is needed.

Overall, it would seem that remnants were not limiting in terms of foraging opportunities for small insectivorous birds, given that (1) behavioural changes in relation to vegetation composition usually occurred only in the least common vegetation types, (2) some species with changes related to vegetation structure might have been exploiting improved conditions, and (3) changes in prey attack rate were not consistently significant. However, it would be important to continue to test these ideas throughout all seasons, as insect abundance varies seasonally (Woinarski & Cullen 1984) and would be expected to produce variation in foraging patterns (Bell 1985). Furthermore, other behaviors such as vocalization and vigilance varied little between habitats, suggesting that remnant conditions were not affecting small insectivores through indirect influences such as increased competition or predation.

Remnants in the study region were quite young, as urbanization in this region began between 35 and 50 years ago (Anon 2000). Remnants with a longer time since encapsulation by an urban matrix show greater levels of disturbance such as high weed infestation and poor vegetation condition (Stenhouse 2004). Maintaining structural complexity in remnants is likely to be important, given the weak indication of a loss of

understorey resources identified in the relatively young remnants of this study. Investigating the foraging behavior of birds in older remnants in other regions would be informative.

These results suggest that remnants can provide suitable habitat and foraging resources in a suburban landscape, provided structural complexity is maintained. A number of studies of remnants in an agricultural matrix conclude that the absence of a species from remnants had more to do with isolation than conditions within the remnant (Bellamy *et al.* 1998; Walters *et al.* 1999; Cooper & Walters 2002). These results suggest a similar situation may occur in the suburban environment; the sensitivity of the small insectivorous guild may have more to do with other factors external to the remnant such as isolation and the permeability of the suburban matrix. Therefore remnant vegetation in a suburban environment has the potential to play an important role in maintaining biodiversity. Further research investigating the permeability of the suburban matrix is necessary if this potential is to be fully realized.

Chapter 5

Avian movement across abrupt ecological edges: differential responses to housing density in a suburban matrix

5.1 Introduction

The persistence of animal populations inhabiting remnant vegetation in fragmented landscapes is often modelled around source-sink and meta-population concepts (Henderson *et al.* 1985; Pulliam 1988; Moilanen & Hanski 1998). A key element in these models is the linking of populations through movement and dispersal of individuals (Fahrig & Merriam 1994; Dias 1996). In fragmented landscapes, individuals must move through the surrounding matrix, with successful dispersal likely to be dependent on the vagility of the species and the characteristics of the habitat within the matrix (Fahrig & Merriam 1994; Dias 1996; Tischendorf *et al.* 2003).

Individuals on the move make their first contact with the matrix at the remnant edge. Edges created by anthropogenic disturbance are often separated by an abrupt transition (Murcia 1995). Edge habitat is likely to cause a variety of responses in animals as it may act as a conduit, filter or barrier to animal movement (Forman & Moore 1992).

Despite this range of responses, research at remnant edges has primarily focused on the infiltration of edge effects into remnants (Murcia 1995) with the conservation of communities within the remnant of foremost importance. Results so far have not identified any consistent patterns in relation to community structure or demographic processes, regardless of edge types (Murcia 1995; Sisk & Battin 2002). Some studies

indicate that species richness or abundance can decrease towards the remnant edge (Baker *et al.* 1998; Dale *et al.* 2000; Beier *et al.* 2002), while nest predation or parasitism can increase at the edge (Berry 2002; Chace *et al.* 2003). Guild composition can also change (Restrepo & Gomez 1998; Dale *et al.* 2000; Fernandez-Juricic 2001). However, a similar number of studies have found that these parameters did not change with distance from the edge (Kruger & Lawes 1997; Campi & Mac Nally 2001; Piper *et al.* 2002; Boulton & Clarke 2003).

Importantly this lack of change found in some studies suggests that within the remnant, species still approach the edge and, therefore, have the potential to cross into the matrix. A better understanding of the potential to cross into the matrix is required, as it seems likely that movement and dispersal will become critical parameters if species in patchy populations are to connect and persist in increasingly fragmented landscapes. This potential is affected by an individual's behavioural response to edges. Several studies investigating edge responses have compared species densities on either side of an edge to infer responses (Catterall *et al.* 1991; Sisk & Margules 1993; Gascon *et al.* 1999), or have initiated responses using playback tapes (Desrochers & Hannon 1997; Develey & Stouffer 2001; Rodriguez *et al.* 2001; Belisle & Desrochers 2002). Studies making direct observations of crossings initiated without disturbance by the researcher are needed if knowledge of behavioural responses are to be used to create landscape and matrix conditions that assist movement and dispersal (Baillie *et al.* 2000; Harris & Reed 2002).

Matrices of different types influence bird communities in remnants (Tilghman 1987; Freisen *et al.* 1995; Sisk *et al.* 1997; Rottenborn 1999; Poague *et al.* 2000; Wethered &

Lawes 2003) and are predicted to influence behavioural responses. Modelling studies indicate that edge permeability (related to matrix type) alters the level of emigration (Stamps *et al.* 1987), that matrix composition impacts on immigration rate (Tischendorf *et al.* 2003), and that a higher quality matrix buffers against extinction in meta-populations (Vandermeer & Carvajal 2001). In the field, several studies have demonstrated that different matrix types can affect an individuals' rate of movement (Belisle *et al.* 2001; Ricketts 2001; Hein *et al.* 2003). One discrepancy between these modelling studies and field research is that models often incorporate the probability that an individual will cross once the edge has been approached (Stamps *et al.* 1987; Tischendorf *et al.* 2003), while field research focuses on rates of movement once an organism has crossed into the matrix. Field research observing actual crossings of the edge, and investigating the probability of an individual crossing in response to different matrix types is the missing factor.

This research investigates avian behavioural responses at edges in a suburban landscape, by determining the crossing rates of individual species, once they have approached an edge. Specifically, the proportions of crossings are investigated in relation to species feeding guilds and matrix housing density. In the urban landscapes of Australia, omnivores and nectarivores appear more tolerant of the matrix than insectivores (Sewell & Catterall 1998; Parsons *et al.* 2003), and so I aimed to test whether omnivores and nectarivores would exhibit a greater crossing potential than insectivores, especially at edges interfacing with high-density housing. I also aimed to test whether the number of crossings would be related to the proportion of buildings and vegetation at the edge, and whether nectarivores would respond to a different set of these characteristics compared with insectivores.

5.2 Methods

5.2.1 Study region

This study was conducted on the Central Coast of New South Wales, Australia in two adjacent local government areas (Gosford City Council – 1028 km² and Wyong Shire Council – 827 km²). The climate is temperate, with temperatures ranging from 12° C to 24° C (mean daily minimum and maximum). Average annual rainfall ranges from 1200 to 1800 mm. The geography of the region is predominantly steeply sloping hills separated by narrow valleys adjoining a coastal plain in the east. The region contains a variety of vegetation types including woodland and forest (Benson 1986).

Gosford and Wyong local government areas have undergone rapid urbanization, supplying new residential land for the population of Sydney since 1975. Population growth (3.6 % and 2.9 % respectively) is higher than the state average of 1.1 % (ABS 1996), and the natural vegetation has become highly fragmented. Additional processes contributing to fragmentation include forestry and farming. National parks and reserves contain most of the remaining 30 % of original vegetation.

Planning policies have resulted in a landscape in which large patches of vegetation are surrounded on all sides by areas of high- and low-density housing. This pattern, covering two thirds of the study region, provided an opportunity to compare bird movement at the edges of high-density and low-density housing.

5.2.2 Study sites

Study sites were located around the perimeter of five large vegetation patches set aside as regional reserves and national parks. Four of the five patches were larger than 800 ha and the fifth was 65 ha. Ten sites were established at edges of high-density housing where there were 20-25 house blocks per hectare, and ten sites were established at edges of low-density housing where there were 1-2 house blocks per hectare. The majority of edges at low-density housing had bush interfacing with grassed paddocks and houses within 100 m, whereas edges at high-density housing interfaced with typical suburban building blocks of houses, hard driveways, lawn and scattered plants. All sites were separated by a minimum of 500 m. Sites with colonies of noisy miners (*Manorina melanocephala*) or bell miners (*Manorina melanophrys*) were avoided as these species have the potential to discourage small birds from foraging at patch edges (Loyn *et al.* 1983; Catterall *et al.* 1991; Grey *et al.* 1997).

5.2.3 Habitat measurements

The survey edge was defined as the point where the shrub layer became absent from the vegetation profile. This lack of shrub layer was generated by council and landowner clearing activities for property management and represents an anthropogenic feature. Therefore some sites had sections where the canopy extended beyond the edge. One transect of 40 m width and 50 m length was established, centered lengthways along this edge.

Habitat features of the matrix were characterized using two methods: 1) the average perpendicular distance from the edge was measured for built objects (buildings and solid fences combined), trees in the matrix, shrubs in the matrix, and the extended canopy; 2) the percentage of the transect length covered by the first line of housing, as well as the canopy cover and shrub cover occurring between the edge and the first line of housing. Measurements using method 2) were intended to represent a two-dimensional picture of barriers (houses) and habitat cover (trees and shrubs) as seen by a bird at the edge of bushland.

5.2.4 Bird observations

Bird movement was recorded on both sides of each transect, i.e., observations were made within 20 m of each side of the edge. Bird observations were conducted within 4 hours of sunrise from mid-Dec 2003 to mid-March 2004. The order of site visitation was determined randomly at the beginning of field work. Each site had an equal number of early-morning and mid-morning visitation times. Each of the 20 sites was surveyed four times, with each observation period lasting 40 min. Birds present on either side of the transect were recorded. When birds crossed the edge, I recorded their direction of movement (to the matrix or bush), the height and type of structure on which they landed, and the distance beyond the edge.

5.2.5 Data analysis

The number of crossings and the number of species at each site were pooled across the four surveys and tested for differences between edges of high-density and low-density housing using one-factor ANOVAs.

The number of surveys at which a species was present, and the proportion of these surveys at which a species crossed the edge, were calculated for both edge types. This proportion effectively indicates the presence or absence of a crossing event by that species during each survey and is not influenced by the abundance of a species or the number of crossings during a survey. The proportion of times a species crossed was grouped by foraging guilds based on Blakers *et al.* (1984). Fisher's exact tests were used to compare the proportions of crossings between guilds at each edge type.

Species were selected for individual analysis if they occurred in 10 or more surveys. One factor ANOVAs were used to test whether presence at an edge differed between edge types. Fisher's exact tests were used to compare the proportions of crossings between edge types for each species. Individual species tests on the proportions of crossings suggested that species had a tolerance for one edge type compared with another. Individual tests were not strong enough to regress against matrix characteristics. Therefore to determine which matrix characteristics may have been influencing these tolerance responses, species with similar responses were grouped into a set that showed the general pattern. The proportion of crossings by each set was then related to the seven matrix variables, across all sites, using multiple regression (SYSTAT 10). Data were checked for normality and homogeneity of variance. No

transformation of data was necessary. Residuals of the models after analysis were also checked for normality. Correlated variables were excluded from regression models if their Pearson correlation value was less than 0.7 (Tabachnick and Fidell, 1996). Variables with high P values and/or low tolerance (≤ 0.1) were sequentially removed from the full model until those remaining established a model that significantly explained the variation.

Several criteria were established for analysis of crossing behaviour. The influence of flocking behaviour within a species was removed by considering each flock crossing as one event regardless of the number of individuals in the flock. Furthermore an individual that crossed in one direction was assumed to be equally capable of crossing in the return direction, therefore all crossing events were pooled regardless of their direction.

5.3 Results

A total of 55 species were recorded from all edge sites. Fifty-one percent of species were insectivores, with nectarivores (20 %), granivores (12 %), omnivores (10 %), and frugivores (7 %) being less common.

A total of 298 crossings of the edge were observed, 166 at edges of high-density housing and 132 at edges of low-density housing. There was no significant difference in the total number of crossings between edges types ($F_{1,18} = 0.55$, $P = 0.47$), or the number of species crossing ($F_{1,18} = 0.60$, $P = 0.45$). Unidentified birds made 21 of these crossings and were removed from further analysis. Of the 277 crossings analyzed, insectivores made 39 %, nectarivores 35 %, omnivores 21 %, granivores 3 % and frugivores 2 %. Frugivores were not sufficiently common to include in further analysis.

When present at an edge, omnivores were most likely to cross, showing the highest proportion of crossings (0.50), followed by nectarivores (0.34), granivores (0.29), and insectivores (0.20). Omnivores and nectarivores were significantly more likely to cross than insectivores (Table 11). At edges of high-density housing the order in which guilds were likely to cross was the same, with omnivores and nectarivores still significantly more likely to cross than insectivores. At edges of low-density housing nectarivores were no longer significantly more likely to cross than insectivores, while omnivores became significantly more likely to cross than both insectivores and nectarivores (Table 11).

When individual guilds were compared across edge types (Table 12), nectarivores and granivores were more likely to cross at edges of high-density housing, while omnivores and insectivores were more likely to cross at edges of low-density housing. None of these relationships were significant within guilds, however the trend matches that revealed by analysis of individual species.

There were sufficient data for individual analysis of 19 of the 55 species recorded (Latin binomials presented in Table 13). Seventeen of these species were recorded crossing edges. Of these species, 47 % were insectivores, 35 % were nectarivores, 12 % were omnivores and 6 % were granivores. Despite several species having a significantly greater occurrence at one edge type than another (Table 13), none of these species showed a significant difference in crossing rate between edges of high-density housing and edges of low-density housing (Figure 13). Responses of these individual species' correspond to the pattern described in Tables 11 and 12. Crossing behaviour could not be compared for two species; the common myna, which occurred only at edges of high-density housing, and the brown gerygone, which never crossed the edge.

Table 11: Comparison of proportions of crossings between guilds at edges of high-density and low-density housing. P values determined by Fishers Exact Test 2-tail distribution

Guild 1	Proportion of crossings	Guild 2	Proportion of crossings	P value
All Edges				
Insectivore	0.20	Nectarivore	0.34	0.0039
Insectivore	0.20	Omnivore	0.50	0.0001
Insectivore	0.20	Granivore	0.29	0.250
Nectarivore	0.34	Omnivore	0.50	0.064
Nectarivore	0.34	Granivore	0.29	0.675
Edges of high-density housing				
Insectivore	0.15	Nectarivore	0.41	0.0002
Insectivore	0.15	Omnivore	0.49	0.0002
Insectivore	0.15	Granivore	0.35	0.077
Nectarivore	0.41	Omnivore	0.49	0.539
Nectarivore	0.41	Granivore	0.35	0.789
Edges of low-density housing				
Insectivore	0.24	Nectarivore	0.25	1.000
Insectivore	0.24	Omnivore	0.53	0.018
Insectivore	0.24	Granivore	0.21	1.000
Nectarivore	0.25	Omnivore	0.53	0.038
Nectarivore	0.25	Granivore	0.21	1.000

Table 12: Comparison of proportions of crossings across edges of high-density and low-density housing within guilds. Species are grouped into guilds according to feeding preferences.

P values determined by Fishers Exact Test 2-tail distribution

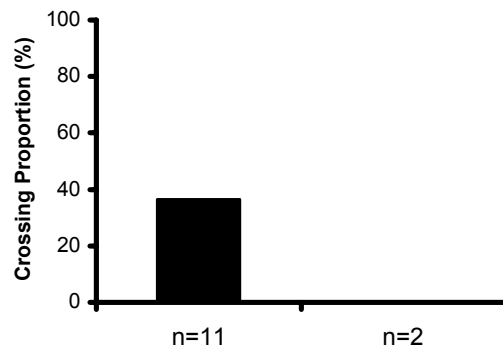
Feeding Guild	Edges of high-density housing			Edges of low-density housing			P value
	Occurrence	Crossings	Proportion	Occurrence	Crossings	Proportion	
Insectivore	89	13	0.15	139	33	0.24	0.127
Nectarivore	79	32	0.41	53	13	0.25	0.064
Omnivore	35	17	0.49	17	9	0.53	1.000
Granivore	17	6	0.35	14	3	0.21	0.456

Table 13: Comparison of individual species frequency at edges of high-density and low-density housing. P values determined by ANOVA.

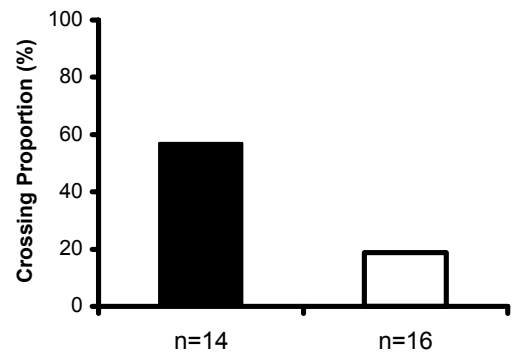
G = granivore, I = insectivore, N = nectarivore, O = omnivore. Edge with greater crossing potential based on Figure 13.

Species		Feeding Guild	Frequency at edges of high-density housing (n = 40)	Frequency at edges of low-density housing (n = 40)	P Value	Edge with greater crossing potential
Tolerant of high-density housing						
Eastern spinebill	<i>Acanthorhynchus tenuirostris</i>	N	15	14	0.84	High-density
Lewins honey-eater	<i>Meliphaga lewinii</i>	N	14	16	0.68	High-density
Red wattlebird	<i>Anthochaera carmunculata</i>	N	12	2	0.02	High-density
Noisy miner	<i>Manorina melanocephala</i>	N	11	4	0.19	High-density
Little wattlebird	<i>Anthochaera chrysoptera</i>	N	11	2	0.005	High-density
Rainbow lorikeet	<i>Trichoglossus haematodus</i>	N	11	2	0.004	High-density
Black-faced cuckoo-shrike	<i>Coracina novaehollandiae</i>	I	7	3	0.33	High-density
Golden whistler	<i>Pachycephala pectoralis</i>	I	4	7	0.34	High-density
Tolerant of low-density housing						
Grey fantail	<i>Rhipidura fuliginosa</i>	I	8	20	0.02	Low-density
Brown thornbill	<i>Acanthiza pusilla</i>	I	11	19	0.09	Low-density
Eastern yellow robin	<i>Eopsaltria australis</i>	I	8	14	0.30	Low-density
Mixed fairy-wrens	<i>Malurus sp</i>	I	8	8	1.00	Low-density
White-browed scrubwren	<i>Sericornis frontalis</i>	I	3	8	0.15	Low-density
Australian magpie	<i>Gymnorhina tibicen</i>	O	2	8	0.19	Low-density
Eastern rosella	<i>Platycercus eximius</i>	G	10	5	0.23	Low-density
No Preference						
Grey butcherbird	<i>Cracticus torquatus</i>	O	12	5	0.09	Equal
Striated thornbill	<i>Acanthiza lineata</i>	I	7	14	0.08	Equal
Common myna	<i>Acridotheres tristis</i>	O	10	0	0.01	na
Brown gerygone	<i>Gerygone mouki</i>	I	4	11	0.11	na

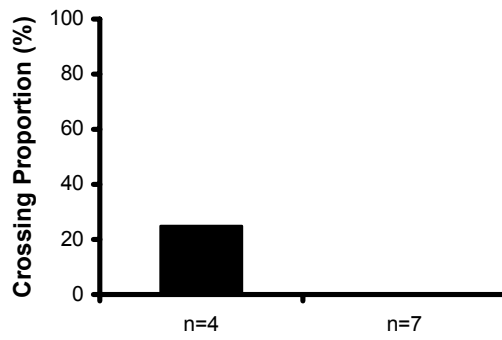
Rainbow Lorikeet (p=1.00)



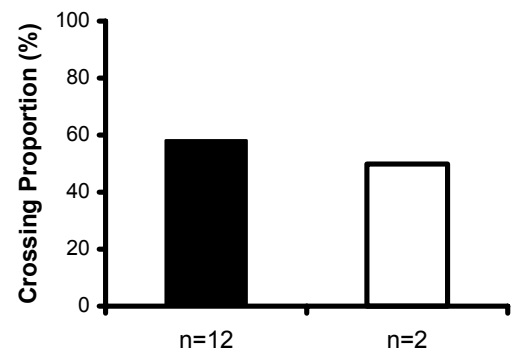
Lewins Honeyeater (p=0.06)



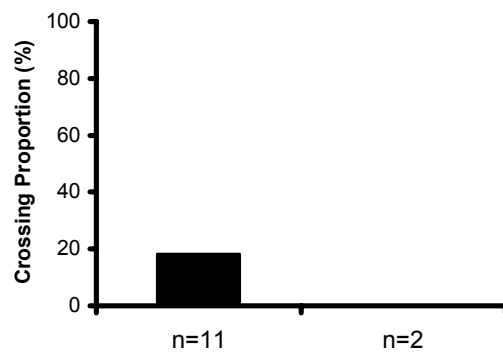
Golden Whistler (p=0.36)



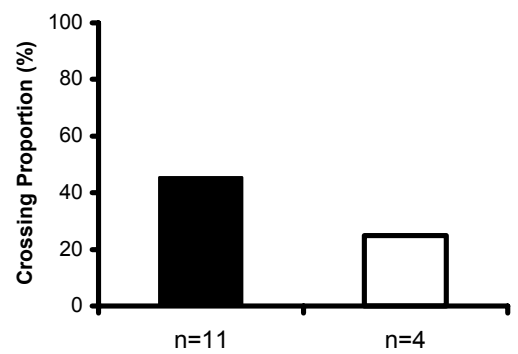
Red Wattlebird (p=1.00)



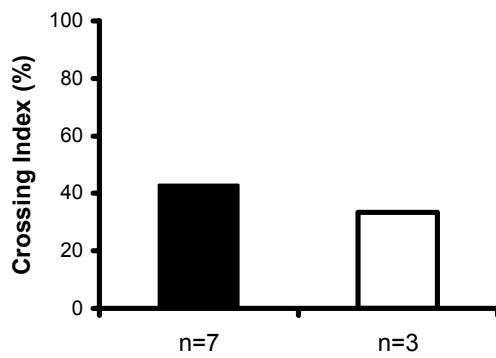
Little Wattlebird (p=1.00)



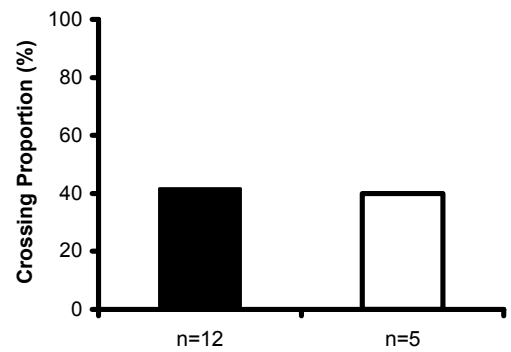
Noisy Miner (p=0.60)



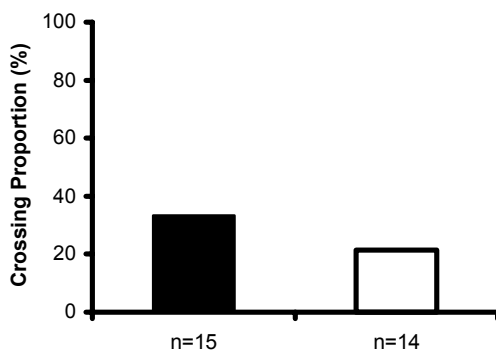
Black-faced Cuckoo-shrike (p=0.33)



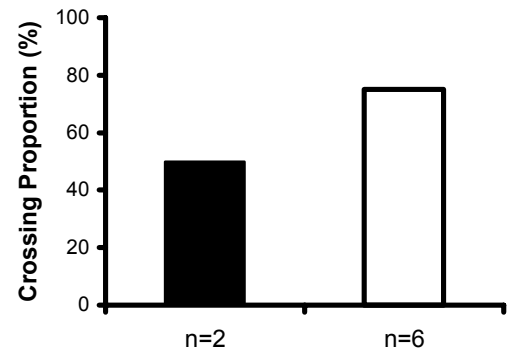
Grey Butcherbird (p=1.00)



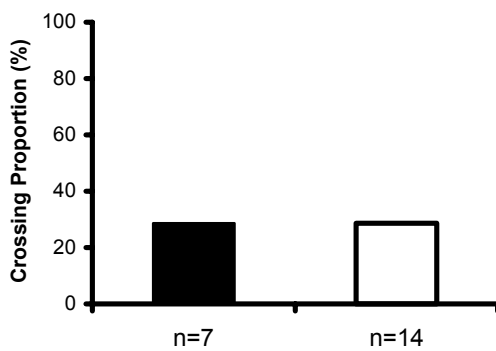
Eastern Spinebill (p=0.68)



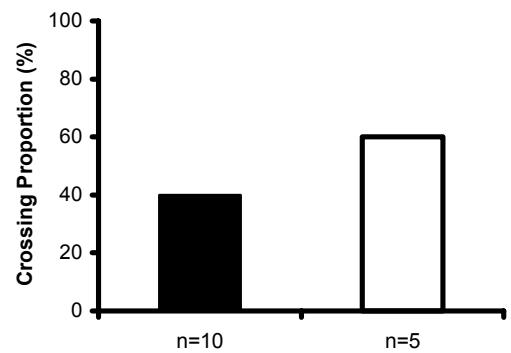
Australian Magpie (p=1.00)



Striated Thornbill (p=1.00)



Eastern Rosella (p=0.61)



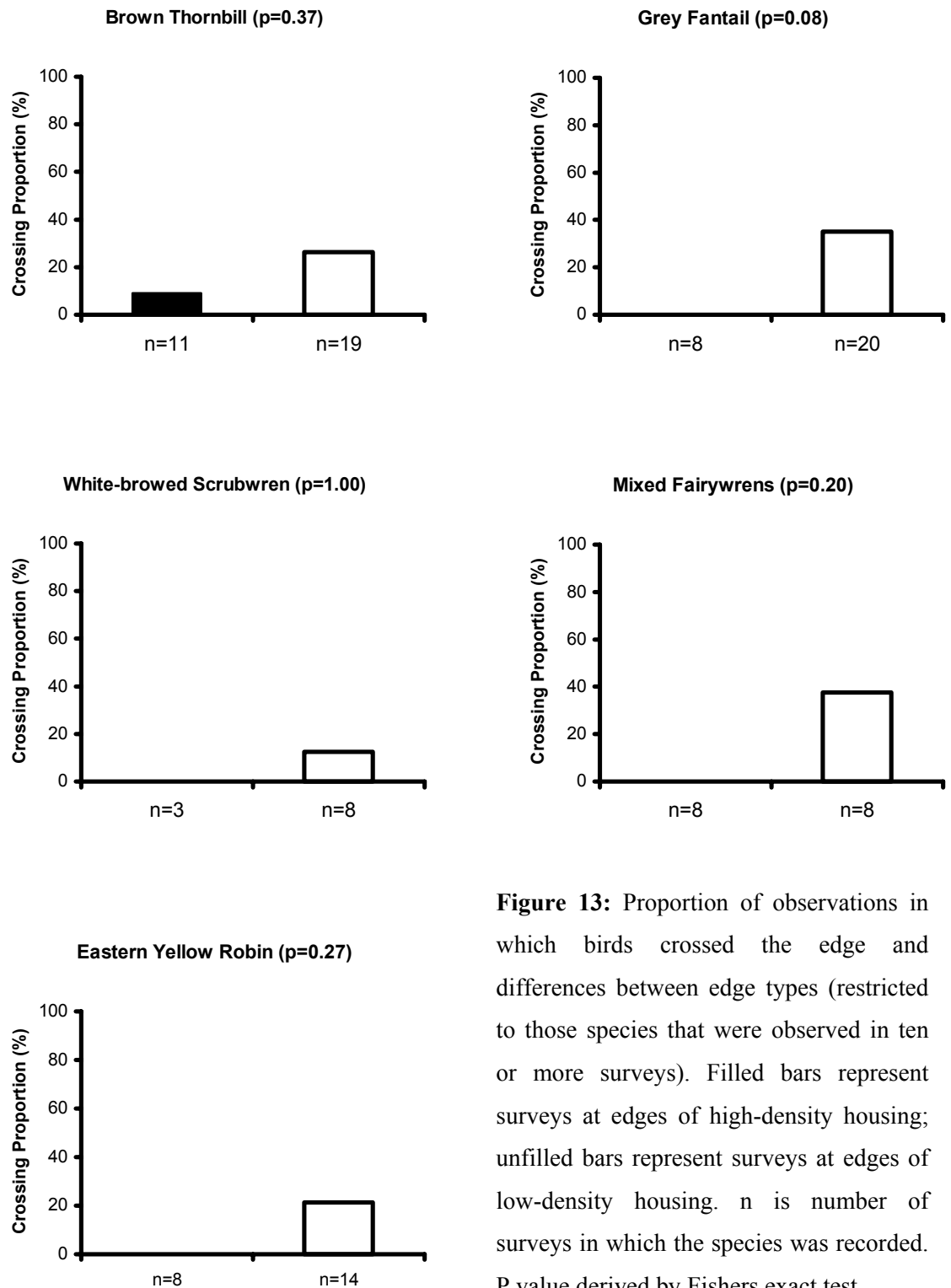


Figure 13: Proportion of observations in which birds crossed the edge and differences between edge types (restricted to those species that were observed in ten or more surveys). Filled bars represent surveys at edges of high-density housing; unfilled bars represent surveys at edges of low-density housing. n is number of surveys in which the species was recorded. P value derived by Fishers exact test.

Despite no significant differences, many species exhibited patterns consistent with a tolerance of one edge over another. Eight species were tolerant of high-density housing. Six of these species were honeyeaters including the little wattlebird, noisy miner, rainbow lorikeet, red wattlebird, lewins honeyeater and eastern spinebill. Two were insectivores; the black-faced cuckoo-shrike and golden whistler. Five species were medium in size (23-39 cm; Simpson & Day 1996) and were typical of birds found in the urban matrix (Jones 1983; Sewell & Catterall 1998; Parsons *et al.* 2003; White *et al.* 2005).

Seven species were tolerant of low-density housing. Five of these species were insectivores including the brown thornbill, eastern yellow robin, grey fantail, white-browed scrubwren, and fairy-wrens. One species was an omnivore; Australian magpie, and one was a granivore; eastern rosella. All insectivores were small in size (13-18 cm; Simpson & Day 1996) and were typical of birds known to be sensitive to the urban matrix (Jones 1983; Sewell & Catterall 1998; Parsons *et al.* 2003; White *et al.* 2005).

Species tolerant of high-density housing and species tolerant of low-density housing appeared to be influenced by several matrix characteristics (Table 14). As a group, species tolerant of high-density housing increased their proportion of edge crossings as the amount of housing increased and the distance to shrubs increased. This model explained 41 % of variance, with the amount of housing making the strongest contribution. The proportion of crossings by species tolerant of low-density housing increased as the amount of canopy increased but decreased as the amount of housing increased. This model explained 54 % of variance, with the amount of canopy making the strongest contribution.

Table 14a: Regression model showing best fit of birds tolerant of high-density housing with matrix characteristics.

Variables in model	Coefficient	Standard Coefficient	Standard Error	Tolerance	t	P (2 Tail)
Proportion of House	0.004	0.460	0.002	0.980	2.445	0.026
Distance to Shrub	0.012	0.385	0.006	0.980	2.049	0.056
Whole model: $R^2 = 0.411$; $df = 2,17$; $P = 0.011$						

Table 14b: Regression model showing best fit of birds tolerant of low-density housing with matrix characteristics.

Variables in model	Coefficient	Standard Coefficient	Standard Error	Tolerance	t	P (2 Tail)
Proportion of House	-0.003	-0.382	0.001	0.849	-2.146	0.047
Proportion of Canopy	0.003	0.500	0.001	0.849	2.810	0.012
Whole model: $R^2 = 0.544$; $df = 2,17$; $P = 0.001$						

5.4 Discussion

This study is among the first to investigate the behaviour of birds at habitat edges in a fragmented suburban landscape. I found that behavioural responses to the edge differed significantly among feeding guilds at edges of high-density housing and edges of low-density housing. These results support the prediction, based on species distribution (chapter two), that omnivores and nectarivores would be more likely than insectivores to penetrate edges adjoining high-density housing. Within each guild, the proportion of crossings was not significantly different across edges of high-density and low-density housing, initially suggesting that matrix type did not affect avian behavioural responses. However, closer analysis of individual species revealed they were more likely to cross one edge type over another, and several consistent trends emerged. Nectarivores appeared more likely to cross at edges of high-density housing, while insectivores were more likely to cross at edges of low-density housing. Regression models suggest these trends may be influenced by characteristics within the matrix.

Eucalypt bird communities of Australia are typically dominated by the insectivorous guild (Keast 1985; Recher & Holmes 1985; Mac Nally 1994). Insectivores were the most speciose guild at the edges of native vegetation in this study, suggesting that the bird community in the remnants studied was fairly typical of other areas of native vegetation. However in a matrix of high-density housing, bird community composition is different. Insectivores, particularly those of small body size, seem to be at a disadvantage, and are often described as sensitive to urbanization, with a reduction in species and abundance (Beissinger & Osborne 1982; Sewell & Catterall

1998; Parsons *et al.* 2003; White *et al.* 2005). The low proportion of crossings in this study (0.15 of edge visitations) at edges of high-density housing corresponds well with their rarity in the suburban matrix and indicates that edges or characteristics of the matrix may potentially be significant barriers for the dispersal of these species.

One reason why insectivores may avoid crossing into the matrix is a lack of food resources within the matrix. In this study, species tolerant of low-density housing, many of which were small insectivores, decreased their proportion of crossings as canopy cover decreased. This may reflect a response based on food resources if the amount of canopy is proportional to the supply of canopy insects. However, insect resources in the suburban matrix are yet to be quantified. Explanations based on foraging behaviour may relate to daily movements. Daily foraging movements most likely represent the behaviour of local sub-populations from which a regional meta-population is composed. These results suggest that sub-populations of small insectivores, which make few crossings, may be completely reliant on internal remnant resources.

Alternatively, insectivores may utilize canopy cover for shelter and protection to assist their movements in the matrix. The importance of canopy trees has been highlighted previously both in the matrix (Munyenembe *et al.* 1989; Law *et al.* 2000; Grabham & Klomp 2001) and in remnants with most bird species being observed in the tree canopy (Fisher 1997, 2001). The probability of great tits occurring in small urban parks (5.5 ha) has been associated with the area of tree cover in a 250 m radius from the park center (Hashimoto *et al.* 2005), and the homing abilities of forest dependent birds decreased as forest cover in a rural

fragmented landscape decreased (Belisle *et al.* 2001). Without this shelter birds may be at much higher risk of negative interactions with predators and aggressive species. For instance, the type of habitat into which small birds would move when crossing forest edges was influenced by predation risk (Rodriguez *et al.* 2001).

In contrast nectarivores, which were more likely to cross, may regularly use the matrix as a supplementary food resource. Nectarivores often become prominent components of the community in a matrix of high-density housing in Australia (Sewell & Catterall 1998; Martin & Catterall 2001; Parsons *et al.* 2003; White *et al.* 2005). In this study, the significantly greater proportion of crossings performed by nectarivores at edges of high-density housing corresponds well with this prominence.

Medium-sized nectarivorous species are known to feed on native and exotic nectar-producing shrubs in the urban matrix (Catterall *et al.* 1989; Green *et al.* 1989), so nectar-producing shrubs are often planted with the aim of encouraging these birds into the urban gardens (Wrigley & Fagg 1990; Hanks 2002). Quantification of these food resources in the urban matrix has demonstrated that nectarivorous species (including those recorded in this study) prefer shrubs that produce greater volumes of more concentrated nectar (French *et al.* 2005). Therefore it could be expected that decisions to cross an edge are based on the quality and quantity of the resource, and the energy expended to acquire the nectar (Wiens 1992). Great tits (*Parus major*) crossing gaps to forage flew at greater speeds to reduce daily energy expenditure (Hinsley 2000). In this study, species tolerant of high-density housing, many of which were medium nectarivores, increased their proportions of crossings as the

distance to shrubs increased, potentially reflecting flight speed and energy considerations.

Small nectarivores were not prominent in this study, with only two species, the eastern spinebill and lewins honeyeater, occurring often enough for individual analysis. Typically small nectarivores share a similar negative response with small insectivores to urbanization (Sewell & Catterall 1998; Parsons *et al.* 2003). In contrast the two small nectarivores in this study were more likely to cross at edges of high-density housing. This is a small but positive indication that urban-sensitive species can be encouraged to cross into the matrix under suitable conditions.

Omnivores had the greatest proportion of crossings of all guilds. The predominant omnivores in this study (Australian magpie and grey butcherbird) forage in open farmlands and urban habitat (Simpson & Day 1996). These species regularly utilize open grassy areas, suggesting their foraging behaviour requires very little adaptation to the open lawns presented in urban environments. Edges of low-density housing had a larger volume of open paddocks than edges of high-density housing, possibly providing greater foraging resources, which would correspond to their greater proportion of crossings at low-density edges.

This study has also demonstrated that the proportion of housing influences the movement of birds between native vegetation and the suburban matrix. However, various measurements of housing are a common variable with which bird community composition, species richness and density are often related. Therefore I agree with other authors in suggesting that housing may be a surrogate variable for several

factors associated with urbanization such as plant and food supplementation, or pets and human disturbance levels (Tilghman 1987; Freisen *et al.* 1995; Jokimaki & Huhta 1996; Yeoman & Mac Nally 2005). Experimental manipulation of suburban matrix characteristics is needed to help determine the identity of these factors and their effect, especially as some potentially influence both daily movements and dispersal movements of sub-populations.

Experimental manipulation may be particularly important as it has the potential to determine whether any barrier effects are physical or behavioural in origin. For example the positive relationship between canopy cover and the proportion of crossings by small insectivores suggest that the barrier was of a physical nature created by diminished native vegetation. However, barriers to dispersal may also be caused by behavioural inhibitions that prevent a species from crossing even though it is physically capable (Harris & Reed 2002). Aggressive competitive interactions are known to occur between medium nectarivores and small insectivores (Davis & Recher 1993; Grey *et al.* 1997). The positive response demonstrated by medium nectarivores at edges of high-density housing potentially induced an inhibitory response among the small insectivores.

The ability to cross the edge potentially gives a species a twofold survival advantage. Species that can maintain a presence in the matrix most likely demonstrate greater behavioural flexibility, which potentially reduces their chances of extinction in the first instance. However, in the event of a sub-population becoming extinct, it also presents opportunities for dispersal and re-colonization to maintain the meta-population. Presence in the matrix has previously been suggestive of the persistence

of bird species in fragmented landscapes, with those that avoided the matrix likely to decline in fragments, and those that tolerated or exploited the matrix likely to remain stable or increase (Gascon *et al.* 1999).

Creating matrix conditions that encourage species sensitive to urbanization into the matrix may be a legitimate option for the maintenance of a high diversity of bird communities in remnants within a fragmented suburban landscape. Initial steps are likely to involve a reduction of the barrier effect. Improving the quality and quantity of matrix vegetation, particularly the canopy level, adjacent to the edge should reduce the contrast between native vegetation and the suburban matrix and provide resources that encourage urban-sensitive species to cross. Reducing the barrier effect may alternately involve the removal of features that discourage urban-sensitive species such as competitive urban-adapted species. Reducing the amount of nectar-producing garden plantings may be an indirect way of reducing aggressive medium-sized nectarivores that appear to out-compete small insectivores.

Currently conditions in the suburban matrix appear to promote several feeding guilds at the expense of others. By creating matrix conditions more suitable for species currently considered sensitive to urbanization, management introduces the potential to simply rearrange which species are promoted at the expense of others. Considering the difference in requirements between the wide range of species, it may be difficult to find a balance that encourages all species in the one area. Sustainable management may need to consider the potential of partitioning and dedicating different areas of the suburban landscape for different species and guilds.

This study has demonstrated that species sensitive to urbanization approached the edge between large tracts of native vegetation and the suburban housing matrix. This response, combined with the relationship between the probability to cross edges and particular habitat features, provides some scope for designing and managing suburban environments to promote dispersal rates required to maintain meta-populations. Furthermore it implies that the value of small remnants can be improved if species dependent on native vegetation can be encouraged to move between remnants. Importantly, the appearance of species sensitive to high-density housing at habitat edges in this study, demonstrates that management strategies in the matrix designed to improve their opportunities for dispersal have the potential to succeed.

Chapter 6

General discussion

Remnants and the matrix: the ecology of urban birds and implications for management

Theory about the effects of fragmentation on bird communities in remnant vegetation is largely derived from research conducted in agricultural and forestry landscapes. The theory of island biogeography has been a prominent research tool (Turner *et al.* 2001) as parallels were often drawn between the oceanic islands on which island biogeography is based, and the remnants of vegetation surrounded by what was considered an inhospitable matrix. Therefore much fragmentation research has focused on the spatial arrangement of remnants and their attributes such as remnant size, isolation distance from other remnants, and internal remnant conditions.

The importance of the surrounding matrix has only more recently been incorporated into landscape models. The corridor-patch-matrix model emphasizes structural connectivity and is based on three components in which patches and corridors are distinguishable from the surrounding matrix (Forman 1995; Lindenmayer & Franklin 2002). The landscape continuum model considers that the structure of patches and corridors may not be readily distinguishable from the matrix. This model emphasizes functional connectivity by describing landscapes within a range of vegetation cover across a spectrum of conditions from intact to relictual (McIntyre 1994; McIntyre & Hobbs 1999; Lindenmayer & Franklin 2002). Accordingly the importance of matrix composition having an influence on communities in remnant vegetation, and the need to manage this composition has only been acknowledged recently.

Research in landscapes fragmented by urbanization has focused on conditions within the matrix. Bird communities of the matrix have been investigated across the gradients of housing density and vegetation cover (Bolger *et al.* 1997; Clergeau *et al.* 1998; Sewell & Catterall 1998; Green & Baker 2003; Crooks *et al.* 2004; Lim & Sodhi 2004; Fraterrigo & Wiens 2005). Recent research has therefore focused on urban remnant vegetation as a continuum of this vegetation gradient (the landscape continuum model), rather than a patch of vegetation distinct from the surrounding matrix. While this continuum approach has many advantages, it does not help distinguish the importance of remnants as a management unit or as a unique unit within highly disturbed surroundings.

This thesis contributes to an assessment of the roles of remnant attributes and the influence of the surrounding matrix in controlling bird community structure. In contrast to the majority of gradient research in urban areas I have taken a corridor-patch-matrix model approach as it enabled suburban remnant vegetation to be considered as a patch of vegetation distinct from the surrounding matrix. Remnant vegetation in the suburban landscape needs to be considered separately from the matrix as it theoretically has the potential to form strongholds for native bird species that might be able to extend their range into the matrix, even though they may be unable to survive in streets and parklands remote from remnants. Therefore remnant attributes similar to those investigated in forestry and agricultural landscapes are theoretically applicable to conservation measures in the suburban landscape and the corridor-patch-matrix model may be a useful tool to understand the ecology of urban birds.

If bird communities in the urban matrix are influenced by characteristics of the matrix then theoretically these characteristics might also influence the communities in nearby remnants through a number of processes. Firstly, as matrix characteristics may influence the quality of the remnant, it is likely to influence bird populations occupying these remnants. Secondly, as remnant area decreases with urbanization, small remnants will become the main source of native vegetation (Porter *et al.* 2001; Stenhouse 2004), and species may need to move between remnants to maintain enough breeding pairs for a genetically viable population (Mortberg 1998). Under this idea, remnants form a habitat network in which the influence of the matrix on species movement could become particularly important to the long-term persistence of the species (Hobbs 2002; Opdam 2002).

In utilizing the corridor-patch-matrix model, I was able to investigate remnant attributes more frequently researched in agricultural landscapes, such as size and internal conditions, in relation to the potential influence of the surrounding housing density on bird communities in remnant vegetation in the suburban matrix. This thesis has helped to establish that the surrounding matrix does have an influence on the bird communities in remnant vegetation in the suburban environment. This influence reflects similar responses to urbanization worldwide in which bird communities in the matrix contain more introduced species, more omnivores and more granivores with respect to bird communities of undisturbed habitats (Marzluff 2001; Chace & Walsh 2006).

Bird movements recorded at the remnant/matrix interface also demonstrated that the influence of the surrounding matrix extended to species movements within the suburban environment. This highlights the need for information on species dispersal and behaviour as currently emphasized in the fragmentation literature. In particular the preference of species to cross into one type of matrix over another adds to the growing collection of research that suggests matrix permeability has an important influence on landscape connectivity and the dynamics between remnants in a habitat network.

Importantly this thesis demonstrates that remnant attributes must be considered in relation to their surrounding matrix if they are to work together to provide effective habitat networks, particularly considering the two are currently managed separately.

Research outcomes

I identified two groups of birds exhibiting opposite responses to urbanization. Species sensitive to urbanization consisted of small insectivores (body size 13-18 cm), while species tolerant of urbanization consisted of medium nectarivores (body size 23-31 cm). Similar species groupings have been identified in other urban areas of Australia (Jones 1983; Sewell & Catterall 1998; Parsons *et al.* 2003; White *et al.* 2005). The loss of small insectivorous species in remnant vegetation reduces the value of remnants for conserving these species and emphasizes the importance of large undisturbed areas for maintaining regional populations of these species. Conservation management will need to focus strongly on improving suburban

conditions (both in and surrounding remnants) to promote small insectivorous species.

Differences amongst remnants in bird community composition seemed largely a response to the surrounding matrix, particularly as remnant size decreased. I demonstrated a difference in bird community composition with types of remnant vegetation. However, when remnants were smaller than 35 ha, these differences were not associated with remnant vegetation nor with remnant size. Furthermore, they were not associated with internal quality of the vegetation structure, which was similar between remnants, or vegetation type. Within a vegetation type, remnants smaller than 35 ha were distinguished from those larger than 80 ha by the presence of bird species associated with the surrounding matrix. These results highlight the importance of conservation planning in the development of suburban areas to improve the quality of the matrix to promote bird communities in remnant vegetation. Bird density and species richness (but not species composition), were influenced by vegetation structure, exhibiting a positive response to high-shrub cover.

The association of urban-sensitive species with remnants surrounded by low-density housing suggests that characteristics of the surrounding low-density matrix maintained remnants and conditions that may be more suited to the requirements of these species. Remnant vegetation surrounded by a low-density housing matrix contained fewer species commonly found in the suburban matrix. In comparison to the high-density housing matrix, the low-density matrix potentially has a lower impact on conditions within remnants by reducing the invasion of species from the matrix into the remnant.

The preference of urban-sensitive species for remnants surrounded by low-density housing may have been a reflection of their dispersal abilities within the matrix. The housing density of less than 4 houses per hectare potentially provided better conditions that may be associated with the movement of these species, such as improved habitat cover or a reduction in factors likely to inhibit movement. As a consequence of this pattern I investigated dispersal abilities at remnant edges that interfaced with high- or low-density housing. I demonstrated that species sensitive to urbanization are more likely to cross into the matrix at edges of low-density housing, and that these species respond to a different set of matrix characteristics than species considered adaptable to urban conditions.

The influence of matrix characteristics on the distribution of urban-sensitive species was indirectly supported through investigations into the foraging behaviour of small insectivores within these remnants. This thesis has determined that species foraged within their normal limits indicating that small remnants in suburban landscapes have potential conservation value through the provision of sufficient foraging habitat. This supports the concept that inter-patch movements, rather than remnant quality, may affect the presence of urban sensitive species in remnants.

Managing the matrix to create and improve habitat networks.

Management options form the remainder of this discussion in an attempt to form useful outcomes for Wyong Shire Council who contributed as an industry partner in this research. At this stage it is necessary to acknowledge that the known biology of the species forming the results of this thesis is incomplete for urbanized landscapes and that detailed research of this biology, along with investigation into source-sink dynamics, ecological traps and predation, would be a necessary component of any management options that were to be implemented.

This thesis suggests that the surrounding matrix influences both the internal remnant quality and the ability of birds to disperse among remnant vegetation. Remnants with suitable habitat quality are the essential basis for habitat networks, while movement between remnants is important for the functionality of the network. Therefore the matrix appears to have a pivotal role if small remnants are to function as part of a habitat network and promote the biodiversity of urbanized landscapes. Importantly, the matrix of low-density housing had several benefits conducive to habitat networks. This matrix appeared to have a lower invasive impact on communities in remnant vegetation, and for urban-sensitive species, may have provided greater functional connectivity between remnants than did a matrix of high-density housing. This matrix may have the potential to provide these benefits while also providing housing, so careful placement of this matrix in relation to remnant vegetation forms one potential management strategy through which both objectives can be met.

To maintain remnant quality, the low-density housing matrix, in conjunction with the matrix of high-density housing, could be configured into a buffer system based on concentric zoning (Freemark *et al.* 2002) in which there is a transition of increasing protection and decreasing intensity of human land-use towards the remnant. This thesis suggests the control of housing density within concentric buffer zones is a practical step that can be incorporated into the planning stages of new developments in the Wyong Shire. These measures are only applicable when establishing housing developments, therefore other management options are also required.

Placement of the low-density housing mixed within high-density housing may be a feasible option to improve connectivity in the suburban landscape, and could potentially be used to create habitat networks at two scales in the suburban landscape. Firstly habitat networks could be formed within a zone of low-density housing if a sufficient collection of remnants were embedded in this matrix. These networks should help improve conditions for urban-sensitive species and promote biodiversity in the suburban landscape. Secondly, large-sized remnants on the outskirts of suburban areas could be buffered against encroaching urbanization by concentric zones of increasing housing density, and connected to other large remnants by the zones of low-density housing matrix that contained a collection of small remnants. Although individual larger remnants are likely to provide a species with all their requirements, the connecting zones of low-density housing might reduce the potential of these remnants to become isolated reserves.

Currently, most low-density housing of the research area is located in a zone between high-density housing and the larger, less disturbed, areas of native vegetation (Anon 2000). While some areas of low-density housing will inevitably be converted to high-density housing, it may be beneficial if, in combination with the less-disturbed native vegetation, sections of the low-density housing are retained as extensions within the high-density housing (Figure 14). This will help to create a multiple-use landscape that provides housing while improving heterogeneity and biodiversity in the suburban landscape. Similar ‘management zoning’ systems have been described to produce multiple-use landscapes within the forestry industry. Three zones with different priorities are established. One zone is designated to the conservation of biodiversity or an endangered species (equivalent to large remnants or continuous vegetation), another zone is designated for wood production (equivalent to high-density housing), and the third zone (equivalent to low-density housing) is designated for joint use to provide some biodiversity conservation and some wood production (Lindenmayer 2003; Perry 2003).

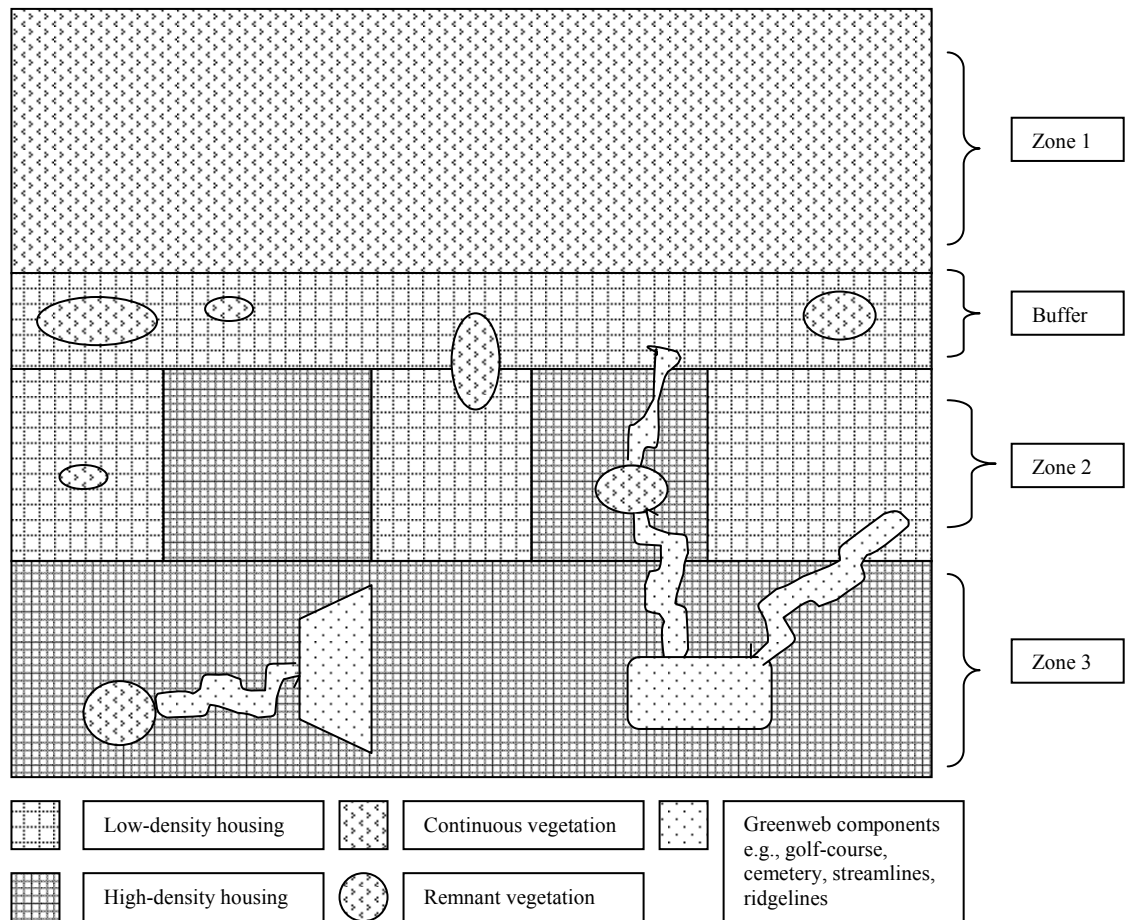


Figure 14: Diagrammatic representation of low-density housing with remnants, and high-density housing with greenwebs to improve matrix permeability and bird diversity of the suburban environment. See text for discussion of zones.

As a matrix that is able to provide connectivity, the low-density housing supports the idea that structural corridors may not be necessary to promote connectivity (With 2002). Structural connectivity occurs when vegetation, usually the same type as the remnant, forms a corridor that provides a physical linkage between remnants (Freemark *et al.* 2002; Opdam 2002; Uezu *et al.* 2005). Functional connectivity occurs when species are able to use characteristics of the matrix in the absence of corridors. In this study region, structural connections were absent between remnants surrounded by the low-density housing matrix, suggesting that this matrix provided functional connectivity.

While this thesis suggests that maintaining and connecting zones of low-density housing is an important step towards creating habitat networks, human population growth creates a demand for housing. This demand ensures that high-density housing will always be a feature of the suburban landscape. Therefore it is important that management strategies attempt to improve conditions for urban-sensitive species within the matrix of high-density housing. This is especially important given that high-density housing utilizes a smaller area than an equivalent number of houses in a low-density setting, and is potentially one method to reduce initial fragmentation caused by urban sprawl (Alberti *et al.* 2001).

Management of the high-density matrix may need a twofold approach. Firstly elements invasive to remnant vegetation should be kept to a minimum to maintain remnant quality. Secondly, in relation to species movement, matrix characteristics that promote the ability of urban-sensitive species to move between remnants should be established and maintained, while those that discourage movement may need to be removed or reduced.

Elements from the matrix that invade remnant vegetation include human disturbance, rubbish dumping, domestic pets and introduced species (Marzluff & Ewing 2001). Those that discourage urban-sensitive species from crossing into the matrix are potentially the same set of factors. This thesis suggests that in Australia, medium nectarivores, especially the noisy miner, are one element that may need regulating if urban-sensitive species are to be encouraged in the suburban matrix. Medium nectarivores demonstrated an increase in the proportion of crossings as the proportion of housing increased, while small insectivores demonstrated a decrease. Aggressive competitive interactions are known to occur between medium nectarivores and small insectivores (Davis & Recher 1993; Grey *et al.* 1997), so the positive response demonstrated by medium nectarivores at edges of high-density housing potentially induced an inhibitory response among the small insectivores. A reduction in nectar-producing shrubs may discourage a predominance of medium nectarivores. These shrubs are commonly recommended as plants that will attract nectarivores into gardens and backyards (Wrigley & Fagg 1990; Hanks 2002) however, they may also be counter-productive by producing habitat that favours aggressive nectarivorous species (Sewell & Catterall 1998). Reducing larger-flowered nectar-producing shrubs, suited to medium nectarivores, might improve the conditions within the

suburban matrix, especially high-density housing, by reducing invasive elements and inhibitory conditions for urban-sensitive species. Planting smaller-flowered nectar-producing shrubs may improve conditions for the smaller more urban-sensitive nectarivores. Similar reductions to the food resources of cowbirds in urban environments have been recommended in an attempt to reduce their abundance and invasive effect on adjacent environments (Chace *et al.* 2003).

Improving the characteristics of the high-density matrix that promote the movement of urban-sensitive species is an alternative management option. This thesis suggests canopy trees are important on a daily basis for urban-sensitive species. Investigations into the foraging behaviour of small insectivores in remnants determined that these species regularly utilized canopy trees. A reduction in canopy plant species and their associated structural elements is likely to result in very significant changes in movement and foraging ability within and between remnants. Urban-sensitive species again highlighted the importance of canopy trees. They demonstrated an increase in edge crossings as the canopy cover in the matrix increased. Other studies similarly highlight the importance of canopy trees in the matrix (Law *et al.* 2000; Grabham & Klomp 2001; Murakami & Nakano 2001) and in remnants, with most bird species being observed in the tree canopy of riparian remnants (Fisher 1997), and along a regeneration gradient (Fisher 2001). Therefore increasing canopy cover e.g., by planting large street trees, to improve functional connectivity throughout the majority of the matrix might be feasible where high-density housing is contained in moderately small areas.

In areas where high-density housing covers a much larger area, improving matrix permeability may be more feasible if urban-sensitive species are provided with pathways. Corridors or linear strips of native vegetation are often recommended for incorporation into planning designs in urban landscapes (Zalewski 1994; Briffett *et al.* 2000; Poague *et al.* 2000). Remnant vegetation could be connected into a network (Noss & Harris 1986) or system of 'greenwebs'. The concept of greenways, currently popular in the northern hemisphere (Jongman *et al.* 2004), may form a starting point towards the establishment of a greenweb. Greenways have a similar function to corridors but are distinguished by being established along natural topographic features, such as river systems or ridgelines (Jongman *et al.* 2004). Therefore greenways are often considered as a regional scale solution however they can also be effective on a more local scale (Bryant 2006).

The basis on which to form greenways may already exist in the high-density matrix as natural water-courses and steep ridges are considered more difficult to develop and not utilized for housing. Consequently they often retain clusters of vegetation that could be improved to form greenways or corridors to promote connectivity. It has been recommended that greenways should be closely linked with suburban programs that manage surface water and erosion control (Bryant 2006). The maintenance of native riparian channels (Green & Baker 2003), and the design of greenspace corridors (Mortberg & Wallentinus 2000) have specifically been mentioned as management options important to maintaining bird diversity in urban areas.

In keeping with utilizing pre-existing vegetation in the suburban matrix, features such as golf courses, cemeteries and managed parklands could be incorporated (Figure 14). Golf courses with their partial forest cover have the potential to provide refuge for fauna in urbanized areas (Yasuda & Koike 2006). These non-linear patches of vegetation would form nodes in the network, as discussed by Noss & Harris (1986), as they are likely to have a higher ecological value than the surrounding matrix, especially if sections are improved to resemble the remnant vegetation also included in the network. Indications are that networks have the potential to improve biodiversity in the suburban landscape as corridor connectivity between remnants had a positive relationship with bird species richness (Drinnan 2005). Networks in agricultural landscapes appear to improve connectivity, as the loss of potential dispersers was lower within ‘well-connected’ neighbourhoods of small ground-foraging birds than in poorly connected neighbourhoods (Brooker & Brooker 2002).

While it is well established that large remnants will provide a better conservation outcomes than small remnants (Renjifo 1999; Cornelius *et al.* 2000; Major *et al.* 2001; Beier *et al.* 2002; Castelletta *et al.* 2005) the management options described here are emphasized as they have more potential to work within the constraints of the suburban landscape where the numbers of large remnants are often limited. Managing the permeability of the matrix by restricting housing density and connecting already established vegetation features to form a greenweb appears more achievable than enlarging small remnants, which are constrained by permanent structures and impermeable surfaces. Furthermore enlargement plans would require the compliance of a multitude of home owners associated with the small block sizes

in suburban landscapes. Even if small remnants could be enlarged they are likely to remain isolated whereas a greenweb is designed to improve movement between remnants thereby reducing isolation. Nevertheless this thesis also suggests that remnants larger than 80 ha are necessary to conserve biodiversity, especially species assemblages specific to different types of vegetation. I agree with other researchers in recommending that, when available, large remnants should be retained (Breininger 1999; Donnelly & Marzluff 2004) and connected into the greenweb system.

Areas of concern for managing the matrix

Currently conditions in the suburban matrix appear to promote several feeding guilds at the expense of others. By altering matrix conditions to improve its suitability for species currently considered sensitive to urbanization, management introduces the potential to simply rearrange which species are promoted at the expense of others. Considering the difference in requirements between the wide-range of bird species, it may be difficult to find a balance that encourages all species in the one area. Sustainable management may need to consider the potential of partitioning and dedicating different areas of the suburban landscape for different species and guilds. Initial trials should segregate species that exhibit aggressive competitive behaviour towards urban-sensitive species. Segregation of landscape functions provided by greenways has recently been suggested (von Haaren & Reich 2006).

Nevertheless, while zones of different housing density may be partitioned for different species or functions, zones of low-density housing are still likely to share edges with zones of high-density housing, as are greenweb systems within the high-

density matrix. In narrow strips of vegetation, edge effects can cause mortality among dispersing individuals and reduce the capacity of a species to function as meta-populations (Soule & Gilpin 1991; Simberloff *et al.* 1992; Hess & Fischer 2001). Therefore design dimensions of the low-density zones and the greenweb corridors should be wide enough to prevent the domination of edge effects that originate from the high-density housing matrix. Remnants embedded in the low-density matrix may also need to be set back a minimum distance from the low-density/high-density interface to reduce the possibility that invasive elements from the high-density matrix may traverse the low-density matrix and reach these remnants. Research determining the appropriate width for such zones will be needed as large areas of low-density of housing and greenwebs may reduce the housing capacity of the study region and be in conflict with the demand for housing in the area. Zones of low-density housing may provide some compensation as they create a multiple use zone that provides some degree of connectivity while partially meeting housing requirements.

Management of the matrix needs to be cautious about creating species population sinks. Providing conditions that encourage species into the matrix to disperse will be ineffective if the dispersers do not survive once in the matrix (Fahrig & Merriam 1985; Yoder *et al.* 2004). Conditions in the matrix will need to ensure a rate of survival within matrix that creates sustainable meta-population dynamics. Management may also need to accommodate within population differences in dispersal. For example among small ground-foraging birds most long-distance dispersal between habitat patches was made by juvenile females, while shorter

movements within habitat patches were made by breeding females and juvenile males (Brooker & Brooker 1997).

Conclusion

This thesis contributes to the growing collection of research that suggests remnant vegetation, even small remnants, have conservation value and play an important role in promoting avian diversity in the suburban landscape. Importantly this value may be dependent on the permeability of the surrounding matrix and the connectivity this provides between remnants. To promote avian diversity, individual remnants need to be managed in conjunction with characteristics of the surrounding matrix to form a functional habitat network. Priority should be given to remnant vegetation according to the permeability of the surrounding matrix for the bird species of concern. Recommendations relating to remnant size, as researched in agricultural landscapes, should be secondary to management of suburban matrix characteristics that will provide connectivity between remnants.

Managing the suburban landscape for high avian diversity is beneficial both for bird species and human suburban residents. In relation to bird species the suburban landscape is a relatively new environment in an evolutionary timeframe. Currently only a few bird species have adapted to, and exploited suburban conditions. For species without adaptations, the longer they can be maintained in the suburban environment, the better the opportunity for humans to understand, adapt and reduce their impact on these species.

In relation to human suburban residents, high avian diversity creates an amenable environment. High avian diversity reduces the opportunity for several species to become dominant and this ensures that many individual bird species can provide ecosystem services without becoming an environmental nuisance to suburban residents. More importantly birds are highly visible in the suburban environment. In combination with high visibility, high avian diversity has the potential to instill humans with a wildlife ethic that can be nurtured towards an awareness and concern for a broader range of environmental issues.

Manuscripts arising from thesis

Chapter 2

Compositional changes in bird communities of remnant bushland in response to suburban housing density and remnant size.

Manuscript in preparation for Wildlife Research

Chapter 3

Compositional changes in bird communities of remnant bushland in response to vegetation type and remnant size in an urbanized landscape.

Manuscript in preparation for Austral Ecology

Chapter 4

A comparison of foraging behaviour by small, urban-sensitive insectivores in continuous woodland and woodland remnants in a suburban landscape.

Accepted with revision to Wildlife Research.

Chapter 5

Avian movement across abrupt ecological edges: differential responses to housing density in a suburban matrix.

Corrected Proof In Press with Landscape and Urban Planning

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