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Holly Maree Parsons
University of Wollongong

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**THE EFFECT OF URBANISATION ON
THE SUPERB FAIRY-WREN
(*Malurus cyaneus*)**

**A thesis submitted in partial fulfilment of the
requirements for the award of the degree**

DOCTOR OF PHILOSOPHY

From

UNIVERSITY OF WOLLONGONG

By

**HOLLY MAREE PARSONS
BACHELOR OF ADVANCED SCIENCE
(BIOLOGY: HONS)**

**SCHOOL OF BIOLOGICAL SCIENCES
2009**

THESIS CERTIFICATION

I, Holly M. Parsons, declare that this thesis, submitted in partial fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualification at any other academic institution.

Holly M. Parsons

Date

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ABSTRACT

The process of urbanisation is altering much of the world's natural habitats, resulting in landscapes vastly different from those they replace. However, the urban matrix is not devoid of wildlife. In fact, its capacity to support a wide diversity of fauna is becoming increasingly valued. Urbanisation changes the patterns of resources and habitat structure, creating mosaics of optimal and sub-optimal patches. Therefore we would expect to see changes in the behaviour and ecology of species living in urban habitats.

The superb fairy-wren (*Malurus cyaneus*) is a small insectivorous bird species whose response to urbanisation is unclear. It has been shown to prefer the edges of remnant habitat, particularly in weed-infested areas, yet is patchy in its distribution in urban landscapes, and thought to be in decline there. In this thesis I have examined how (a) vegetation characteristics, (b) territory size, (c) behaviour, including foraging and (d) food availability differ by living in urban habitats compared to rural/remnant habitats.

Superb fairy-wrens showed a preference for suburban landscapes with shrubs, usually native, and avoided suburban locations without them. In both rural/remnant edge habitat and suburban habitat they were also associated with the introduced weed lantana (*Lantana camara*). It is likely that this shrub provides important shelter, especially in the absence of native vegetation that provides equivalent structure.

Radio-tracking of female superb fairy-wrens revealed that territories in suburban locations were, on average, half the size of territories in rural/remnant habitats when calculated using the minimum convex polygon method. Calculations made with the fixed kernel method indicated that there was no difference in territory size. This difference in size calculated by different methods suggests that superb fairy-

wrens utilise more of the vegetation within suburban territories and avoid larger areas of unsuitable habitat in rural/remnant edge locations. The sizes of both the suburban and rural/remnant habitats were similar to that in higher quality fragmented habitats, as calculated by previous studies.

Regardless of the location of their territories, superb fairy-wrens foraged largely on the ground but spent the most of their time, on average, in shrubs. Males spent significantly longer foraging in suburban locations than rural/remnant habitat, with females showing the same, but non-significant trend. This increase in foraging time was not taken at the expense of other behaviours however and appeared to be due to the size of food items in suburban territories. The biomass of individual arthropods was smaller in suburban locations than rural/remnant territories but the total biomass per site was the same, largely due to the greater abundance of orthopterans in rural/remnant areas. This suggests that superb fairy-wrens foraged for longer in suburban territories to obtain equivalent intake to that in rural/remnant territories. Suburban areas without superb fairy-wrens did not have a lower biomass of arthropods than suburban fairy-wren territories and therefore it is unlikely that birds in suburban habitats were selecting their territories based on food availability.

Superb fairy-wrens instead appear restricted in their distribution in urban habitats due to a shortage of suitable vegetation, primarily comprised of the shrub layer. While there were changes to food resources, the flexible behaviour of this species with urbanisation allows it to modify its foraging behaviour to compensate for this difference. We do not know the long term consequences faced by individuals occupying the urban landscape, but it appears that that these two habitats, with varying degrees of urban impact, provide suitable habitat for this species to persist.

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CHAPTER ONE

Introduction and Literature Review

1.1 Anthropogenic Habitat Modification

The loss and fragmentation of natural habitat for the development of human uses is far reaching and has ramifications for biota around the world (Cincotta *et al.* 2000). This major global trend is undergoing rapid acceleration associated with human population pressures (Marzluff 2001). Natural landscapes are cleared and fragmented to create space for anthropogenic activities such as agriculture, forestry and urban developments. Those areas of natural vegetation that remain within these anthropogenic matrices are usually isolated in small pockets and subjected to altered disturbance regimes and pressures from the surrounding matrix (Fahrig 1999). It is unlikely that these fragmentation and modification processes will diminish in the foreseeable future and therefore ecologists must determine how wildlife populations are affected by these anthropogenic changes as well as how best to mitigate and manage the detrimental impacts.

The types of anthropogenic activities that result in the fragmentation of natural landscapes vary in their effect on wildlife (Marzluff and Ewing 2001). Agricultural developments are currently having the largest impact on flora and fauna, with 32 % of global land cover devoted to these activities (Houghton 1994). In such systems vegetation cover is simplified or removed and often replaced with exotic plantings (Newton 1998). Urban areas, which can be characterised by human dwellings in conjunction with industrial, commercial and residential infrastructure, now comprise more than 4 % of the global land area, or 471 million hectares (UNDP 2000). It is estimated that the human urban population alone will increase from 6 billion to

approximately 8 billion by 2025 (UNFPA 1996). Therefore, the extent of urbanised landscapes is likely to increase dramatically, with urban sprawl spreading over large portions of the planet (Buechner and Sauvajot 1996). As urbanised areas grow in size, some residents relocate to locations outside this urban core, resulting in an increase in this urban sprawl and a decrease in the population within the urban centre (Gobster *et al.* 2000). For the first time, in 2008, more than half of the world's population (3.3 billion), live in these urban areas, with this expected to reach 5 billion by 2030 (UNFPA 2007).

1.2 Urbanised Landscapes as New Habitat

Urban landscapes differ greatly from the agricultural landscapes that are occupying the greatest land cover of any anthropogenic activity currently (Houghton 1994). Concrete and built-up patches of buildings, roads and paved areas are interspersed with vegetation and 'green' space ranging from remnant vegetation through to cultivated and modified parks, gardens and streetscapes of varying sizes, shapes and states (Gilbert 1991; Burgman and Lindenmayer 1998; Pryke and Samways 2003; Angold *et al.* 2006. Whitney (1985) and McKinney (2002) describe urban habitats as belonging to one of four main categories that decrease in vegetation coverage towards the urban core:

1. Built habitat: buildings and sealed surfaces.
2. Managed vegetation: regularly maintained vegetation and green spaces in residential and commercial areas.
3. Ruderal vegetation: cleared, but not regularly managed vegetation including empty lots, margins of transport corridors and abandoned farmland.

4. Natural remnant vegetation: remaining patches of natural vegetation that are usually also subjected to weed invasion.

As a consequence of fragmentation and habitat loss associated with urbanisation, the composition and structure of ecosystems within and surrounding the urban landscape are also altered (Forman 1995; Golley 1996; Rees 1997; Baskin 1998; Wilcove *et al.* 1998; Marzluff and Ewing 2001; Bisonnette 2002; Faulkner 2004; Yeoman and MacNally 2005). The scale at which these habitat modifications occur suggests that if the urbanisation of natural landscapes were halted, and even reversed, it is unlikely that the natural world would fully recover (Marzluff and Ewing 2001; Lugo 2002). Therefore there is a need to understand how flora and fauna are affected by urbanisation in order to correctly manage potentially harmful impacts where possible.

For many species, the loss of natural habitat and fragmentation results in large scale population declines (Kareiva 1987; Saunders *et al.* 1991; Andrén 1994; Simberloff 1995; Fahrig 1999; Cincotta *et al.* 2000; McKinney 2002). However amidst the destruction of habitat and anthropogenic modification, the urban matrix is not devoid of wildlife. In fact, its capacity to support a wide diversity of fauna, including rare and threatened populations, is becoming increasingly recognised (e.g. Niemelä 1999a, b; Koh and Sodhi 2004; Garden *et al.* 2006; Snep *et al.* 2006).

Those faunal populations that can exist within the urban matrix are exposed to a variety of anthropogenic pressures. Urbanisation is generally associated with:

1. The loss of original vegetation and natural habitat.
2. The introduction of flora from outside its natural range that cohabits with the in-situ native biota (McDonnell and Pickett 1990; King and Buckney 2000; Pickett *et al.* 2001).

3. Availability of new food, shelter and nesting resources (Catterall *et al.* 1989; Blair 1996; Case 1996; Marzluff 2001; French *et al.* 2005).
4. Competition from non-native species that have a long history of human cohabitation and are better able to exploit the new resources (Kerpez and Smith 1990; Anglestam 1992; Blair 2001; Marzluff 2001).
5. Exposure to larger populations of non-native predators (Diamond 1989; Robinson and Wilcove 1994; Mankin and Warner 1997; Marzluff and Restani 1999; Jokimäki and Huhta 2000).
6. Alteration of disturbance regimes such as fire (Rapoport 1993).
7. The heat-island effect (Rebele 1994).
8. Increased direct human disturbance (McDonnell *et al.* 1997; Fernández-Juricic 2001a; Blumstein *et al.* 2005).
9. Exposure to pesticides and insecticides (Potter and Braman 1991; Major *et al.* 1996; Boatman *et al.* 2004; Hart *et al.* 2006).

The habitat fragmentation model is often used to describe the layout of urbanised landscapes (Saunders *et al.* 1991; Haila 2002). Under this model, patches of habitat are seen as islands, isolated by a surrounding sea of unsuitable habitats (Saunders *et al.* 1991; Harrison and Bruna 1999; Debinski and Holt 2000; Fernández-Juricic 2001b; Fahrig 2003). Many studies that examine this fragmentation model correlate landscape patterns with species distribution patterns, but such studies do not uncover the ecological processes underpinning the patterns observed (Wiens *et al.* 1993; Hobbs 1994; Fahrig 2003). Fragmentation models also define patches based on human uses, but this is often different from a patch as viewed by fauna (Saunders *et al.* 1991; Fahrig 2003; Fischer and Lindenmayer 2006).

In urbanised landscapes, the fragmentation model is often overly simplistic. Rather than a series of discrete patches that organisms either can or cannot exist in, urbanised landscapes comprise of a heterogenous mosaic of habitats that vary in quality. The variegation model proposed by McIntyre and Barrett (1992) suggests viewing landscapes as habitat gradients rather than discrete patches isolated by an inhospitable matrix. Like the fragmentation model, the variegation model does not examine the underlying ecological processes influencing species distributions and does not consider species-specific differences (Fischer and Lindenmeyer 2006). A third model, the continuum model, takes the understanding of spatial processes from the fragmentation and variegation models and links ecological processes of food, climate, shelter and space with individual species distributions (Fischer and Lindenmeyer 2006). Here, when I refer to the term ‘patch’, I will be referring to the area of habitat occupied by an individual or group of the one species. Patches vary along a gradient of quality for each individual species and are not discrete units. Rather, they form a continuum of habitats, from patches that are unsuited to the species through to habitats that are sub-optimal to optimal patches. An optimal patch is one where all the requirements of individuals are all met such that the population can breed at replacement levels, i.e. it is not a ‘sink’ population *sensu* (Pulliam and Danielson 1991) but acts as a ‘source’ population.

The response of individual species to urbanisation depends largely upon the differential suitability of habitat patches, with life history traits and specialisation of the species governing such suitability (Urban *et al.* 1987; Andrén *et al.* 1997; Newton 1998). The variety of different land use types within the urban environment may fulfil some of the requirements for a species (such as foraging or reproduction), with the quality of each patch, as well as the scale at which the species operates, influencing

the population (Hobbs 1998). Those members of the urban wildlife community that function most successfully within urbanised habitats are those that are not confined to only one habitat type, or patch, but those that can move within and throughout a variety of different patches of varying qualities (Davis and Glick 1978; Hobbs 2005).

1.3 Urban Faunal Communities

Urban fauna can be categorised based upon the level of tolerance a species demonstrates to urbanised habitats. Faunal communities follow the environmental gradient, with the composition closely related to the amount of vegetation of any type within each habitat type. Both Blair (2001) and McKinney (2002) use the terms avoiders, adaptors and exploiters to describe categories of faunal groups whilst Garden *et al.* (2006) uses urban-sensitive, matrix-sensitive and matrix-occupying. All of these terms describe the extent to which fauna will move through, and occupy patches of, habitat within the urban matrix. Blair (2001) and McKinney (2002) does not provide a category for those species that can exist in more urbanised habitats but have some preference for remnant vegetation, whilst Garden *et al.* (2006) does not differentiate between those species that have a total dependence on human-modified habitats (synanthropes) and those that also live successfully within their traditional habitats as well as in the urban matrix. Catterall (2004) uses a classification system specific to the avian community found within urban habitats of the east coast of Australia with these groupings based on the response of species to changes in land cover. There are similarities with the classifications presented by McKinney (2002) and Garden *et al.* (2006), however Catterall (2004) focuses only on Australian bird species. Catterall (2004) characterises birds as:

- *Neglected Foliophiles*: Small insectivores and honeyeaters that feed on or near foliage.
- *Aussie Icons*: Large bodied omnivorous that tend to feed on the ground. These species are found in well-planted suburban habitats and small remnant patches and are amongst the most well known and liked Australian native species.
- *Terrorist*: One species, the noisy miner (*Manorina melanocephala*) is recognised in this separate group. This species has similar requirements to the Aussie Icons.
- *New Arrivals*: These birds are of varying sizes and tend to be ground or aerial feeders. They are characteristic of poorly vegetated suburbs.

While this classification system is well suited to the urban habitat in which this thesis was conducted, I will refer to four types of fauna based on both the terminology used by McKinney (2002) and Garden *et al.* (2006) to provide a more robust description of both the sensitivity of a species to urbanisation and its preferences of habitats within the matrix:

- *Urban Avoiders*: These are native species that are highly sensitive to fragmentation and human disturbance. They are unable to persist in any urban landscape, including small remnant patches of vegetation and are therefore restricted to large natural habitats. They are typically species that have very specialised dietary or habitat requirements, poor dispersal and low reproductive rates. Large mammals such as elk (*Cervus canadensis*) or bison (*Bison bison*), neotropical migrant birds, and foliage foraging insectivorous birds (described as Neglected

Foliophiles by Catterall 2004) are typical examples (Matthiae and Stearns 1981; Beissinger and Osborne 1982; Adams 1994).

- *Urban Tolerators*: These species will occur within the urban landscape but tend to be restricted to remnant patches of vegetation, and while occasionally found in ‘green’ spaces such as suburban gardens, they are generally still reliant on remnants or patches of weedy vegetation and are more common there. Much of the urban matrix is perceived as a barrier for dispersal and associated with increased predation. They therefore have highly fragmented populations and are at risk of localised extinctions. Medium-sized North American and European mammals such as red foxes (*Vulpes vulpes*), racoons (*Procyon lotor*) and opossums (*Didelphis marsupialis*) require forest fragments for shelter but forage for human refuse or on prey throughout the matrix (Dickman 1987). In birds, smaller nectarivores, insectivores and seed-eaters, as well as those reliant on a shrubby understorey or hollows for nesting (a feature generally only found in remnants), are commonly found in this category (Beissinger and Osborne 1982; Parsons *et al.* 2003; Catterall 2004).
- *Urban Adaptors*: These species are able to live within the urban landscape and are not reliant on remnant habitat for survival. They still tend to be found in the more vegetated habitats within the urban landscape, particularly in suburban habitats. Urban Adaptors typically include species that are considered to be ‘edge’ specialists, that is, those adapted to fragmented habitats on the edges of forests and open spaces (Whitcomb *et al.* 1981; Adams 1994). The abundance of

human-provided foods including both cultivated plantings and rubbish allows urban adaptors to often become more abundant in urban habitats than their traditional habitat (Adams 1981; Marzluff 2001; Parsons *et al.* 2003; Catterall 2004). Their natural predators are also often removed from the urban landscape (Gering and Blair 1999). Burrowing mammals such as the European rabbit (*Oryctolagus cuniculus*), eastern mole (*Scalopus aquaticus*) and striped skunk (*Mephitis mephitis*) from North America and Europe are considered Urban Adaptors (Falk 1976; Hadlington and Gerozisis 1985), whilst in Australia, possums, particularly the brushtail (*Trichosurus vulpecula*) and common ringtail (*Pseudocheirus peregrinus*) have become more successful in urban areas (Statham and Statham 1997; Harper 2005). Omnivorous birds, corvid scavengers and aerial sweepers (such as swifts and swallows) are typical urban adapted feeding guilds found throughout the world (Beissinger and Osborne 1982; Adams 1994; Bayly and Blumstein 2001; Parsons *et al.* 2003; Catterall 2004). Catterall's (2004) classification of Aussie Icons and the native New Arrivals fit into this category. In Australia, large nectarivores (such as the noisy miner Terrorist) are also common in urban habitats (Parsons *et al.* 2003; Catterall 2004).

- *Urban Exploiters:* Synanthropous species are totally dependant upon human resources for survival and generally have a long history of human cohabitation (Blair 2001; Johnson 2001). They are often unreliable on the amount or type of vegetation available (Lancaster and Rees 1979; Johnston 2001) and the lack of predators in conjunction

with abundant food resources has allowed them to establish large populations (Lancaster and Rees 1979; Adams 1994). Urban exploiters comprise only of a small subset of species, usually not native to the area, but are able to swiftly colonise and establish in urban landscapes throughout the world (Adams 1994; Blair 2001; Johnson 2001; Marzluff 2001). Mammalian urban exploiters are small and omnivorous, such as the brown rat (*Rattus norvegicus*) or house mouse (*Mus musculus*). They shelter within buildings and forage on human-provided foods. Avian urban exploiters are typically omnivorous ground-foragers that are also able to roost and nest in dwellings due to their history of cavity-nesting (Lancaster and Rees 1979; Adams 1994). They include species such as the rock dove (*Columba livia*), common starling (*Sturnus vulgaris*), common myna (*Acridotheres tristis*) and house sparrow (*Passer domesticus*).

1.4 Avian Urban Bird Communities

Studies of urban ecology have largely focused on the effect of urbanisation on birds with little attention given to other taxonomic groups (e.g. Beissinger and Osborne 1982; Blair 1996; Catterall *et al.* 1998; Clergeau *et al.* 1998; Germaine *et al.* 1998; Fernández-Juricic and Jokimäki 2001; Mazluff *et al.* 2001; Green and Baker 2003; Chace and Walsh 2004; Palomino and Carrascal 2006). In conjunction with being conspicuous and widespread as well as taxonomically and ecologically diverse, they demonstrate sensitivity to environmental change and therefore make good candidates for research on urbanisation (Furness *et al.* 1993).

Early studies of the composition of urban bird communities documented that species richness declines with increased urbanisation (an increase in the amount of built structures) whilst the abundance of birds, or biomass, increases with urbanisation (Emlen 1974; Lancaster and Rees 1979; Beissinger and Osborne 1982; Mills *et al.* 1989; Wood 1993; Clergeau *et al.* 1998). This low richness but high abundance reflects the dominance of the select few Urban Exploiters that are found in highly urbanised habitats, whilst generally Urban Tolerators and Urban Adaptors are found in the more vegetated areas of urban landscapes (Jones and Wieneke 2000; Catterall 2004). Other studies have found that avian diversity tends to peak at moderate levels of disturbance, often located in suburban habitats or at the edge of forest/urban patches as that is the place where Urban Tolerators, Urban Adaptors, as well as Urban Exploiters all coexist (Jokimäki and Suhonen 1993; Blair 1996; Blair 2001; Sandström *et al.* 2006). The importance of these vegetated areas to the conservation of bird species cannot be underestimated as they provide not only refuge for many species but also function as sub-optimal patches of habitat through which individuals may move through to optimal patches or settle in (Tomialojc 1998; Park and Lee 2000; Savard *et al.* 2000; Parsons *et al.* 2006). Still, species display an individual response to habitat characteristics. Some Australian species classified as Urban Tolerators such as the willie wagtail (*Rhipidura leucophrys*), magpie-lark (*Grallina cyanoleuca*) and welcome swallow (*Hirundo neoxena*) favour open and often more highly urbanised habitats rather than those with high densities of shrubs and trees.

Understanding the processes and factors that govern the distribution of species is the ultimate goal of ecologists. It is the cumulative effect of inter-specific interactions and environmental variables that appears to shape the composition of urban bird assemblages, and results in a community vastly different to those found in

natural habitats (Garden *et al.* 2006). While studies of urban avian ecology have largely focussed on bird communities and their response to the ecological gradient (e.g. Beissinger and Osborne 1982; Germaine *et al.* 1989; Blair 1996; Jokimäki and Suhonen 1998; Parsons *et al.* 2006), by not understanding individual species at this fundamental level, we are potentially missing part of the puzzle (Marzluff and Ewing 2001).

1.4.1 Birds in Australian Urban Habitats

While, in general, the urbanisation of the landscape has resulted in similar ecological structures throughout the world, the response of guilds of native species in Australia is different to the pattern observed in Northern Hemisphere urban ecosystems. Just as in the Northern Hemisphere, omnivores and corvids are common Urban Adaptors in Australian urban assemblages (Veerman 2002; Catterall 2004; Chace and Walsh 2004). However while small-bodied granivores, aerial insectivores and ground-foraging insectivores tend to be favoured in urban habitats of the northern hemisphere assemblages (Emlen 1974; Allen and O'Conner 2000; Jones and Wieneke 2000), this is not the case in Australian communities. Instead, medium to large-bodied nectarivores (many of whom display interspecific aggression) and parrots (as well as the omnivores and corvids) dominate the urban matrix (Sewell and Catterall 1998; Jones and Wieneke 2000; Fitzsimmons *et al.* 2003; Jones 2003; Parsons *et al.* 2003; Catterall 2004; Wood and Recher 2004; Parsons *et al.* 2006).

Despite their dominance, these Australian Urban Adaptor species are not found universally throughout all urban habitat patches. Local habitat characteristics play a large role in influencing their distribution (Fitzsimmons *et al.* 2003; Catterall 2004; Wood and Recher 2004; French *et al.* 2005; Tait *et al.* 2005; Daniels and

Kirkpatrick 2006). The popular urban park and garden design of open lawn space and tall trees are most reminiscent of natural woodland habitats and the addition of exotic plants that produce large crops of edible berries have created ideal food sources for some birds (Catterall *et al.* 1989; Munyenyembe *et al.* 1989; Bass 1995; Sewell and Catterall 1998).

While some native birds such as the pied currawong (*Strepera graculina*), Australian magpie (*Gymnorhina tibicens*), rainbow lorikeet (*Trichoglossus haematodus*) and noisy miner (*Manorina melanocephala*) are increasing in number in the urban environment (Blakers *et al.* 1984; Veerman 1991; Barrett and Silcocks 2002; Barrett *et al.* 2002; Barrett *et al.* 2003; Wood and Recher 2004) other birds such as the white-browed scrubwren (*Sericornis frontalis*), brown thornbill (*Acanthiza pusilla*), superb fairy-wren (*Malurus cyaneus*) and new holland honeyeater (*Phylidonyris novaehollandiae*), once more common, appear to be in decline (Green 1984; Hoskin 1991; Sewell and Catterall 1998; Parsons *et al.* 2006). These species are primarily small insectivores and nectarivores (White *et al.* 2005). Vegetation structure (Munyenyembe *et al.* 1989; Catterall *et al.* 1991; Sewell and Catterall 1998; Parsons *et al.* 2006), vegetation composition (Green 1984; Catterall *et al.* 1989; Green *et al.* 1989; Lenz 1989; White *et al.* 2005; Parsons *et al.* 2006), distance to natural vegetation (Catterall *et al.* 1989; Munyenyembe *et al.* 1989) and interactions with other birds (Major *et al.* 1996; Parsons *et al.* 2006) have all previously been shown to influence the composition of the bird communities of urban habitats in Australia and are suggested to be contributing towards the decline of these smaller native species.

In recent years, research has shifted from the composition of urban bird assemblages onto the behavioural adaptations and dietary requirements of urban birds in Australia. However, much of this research has focused on Urban Adaptor and

Urban Exploiter species, those common throughout urban habitats, in an attempt to explain their dominance (Jones and Everding 1991; Smith and Carlile 1993; Major *et al.* 1996; Fulton and Ford 2001; Hasebe and Franklin 2003; Ross 2004; Shukuroglou and McCarthy 2006). Such examinations have rarely been conducted for the less common Urban Tolerators, both in Australia and worldwide. The importance of local habitat features have been shown to influence the presence or absence of some Urban Tolerators (White *et al.* 2005), but we do not know how habitat selection impacts upon those individuals that occupy patches of different qualities.

1.5 Habitat Selection in Urbanised Landscapes

Most species are distributed non-randomly throughout landscapes, influenced by the distribution of resources in both time and space (Clutton-Brock and Harvey 1978; Harvey and Clutton-Brock 1981; Macdonald 1981; Sullivan and Sullivan 1982). Individuals must assess the suitability and quality of a habitat that will maximise their future fitness. This will then impact upon the ecology and evolution of the species (Cody 1985; Rosenzweig 1985; Rosenzweig 1991; Charlesworth 1994; Sutherland 1996). Understanding the driving forces behind an individual's selection of habitats and the impacts of these selections is vital for both evolutionary and conservation understanding (Cody 1985; Sutherland 1996; Pärt and Doligez 2003).

Under the ideal free distribution model (IFD) of habitat selection, it is assumed that individuals have access to ideal habitat patches with full knowledge of these habitats and their relative quality (Fretwell and Lucas 1970; Fretwell 1972; Bernstein *et al.* 1991). Habitat suitability under the IFD model is density-dependant with individuals therefore distributing themselves in proportion to the resource availability within each habitat. However, urbanised systems, and even natural systems, are

usually far from ideal and there are likely to be constraints placed on individuals, with other factors such as inter-specific interactions likely to confound selection (Cody 1985; Danchin *et al.* 1998; Pöysä *et al.* 1998; Jones 2001). Consequently, the habitat choice exhibited by an individual can have ramifications for both the fitness and survival of the individual as well as the population. Differences in behaviours, habitat use within the patch and reproductive success would therefore be expected to be related to the relative quality of a habitat patch selected by individuals.

Under the ideal-free distribution model, individuals are able to choose a territory regardless of the presence of other individuals and are instead selecting habitat purely based upon its relative quality. However, under the ideal-despotic model, the individual's habitat selection is constrained by the territorial behaviour of already settled individuals (Fretwell and Lucas 1970). Subordinate individuals are forced into less suitable habitats and thus individual fitness would be expected to be higher in preferred habitats than in sub-optimal patches. Huhta *et al.* (1998) found that habitat selection of the pied flycatcher (*Ficedula hypoleuca*) followed the ideal-free model at the macro-habitat level. Density of individuals and reproductive success was related to the quality of habitat patches. However, at the micro-habitat scale, the ideal-despotic model was observed. Older males displayed greater dominant behaviour, had greater fledging success of offspring than young males and they excluded young males from optimal habitat through territorial behaviour (Huhta *et al.* 1998).

In a heterogeneous landscape, such as those comprised of urban habitats, individuals are expected to maximise their reproductive output by displaying non-random spatial distribution (Pulliam 1996). There are areas that contain the optimal conditions for the species to be successful, a series of sub-optimal patches and locations that are totally unsuitable for occupation by the species. The ecological

requirements and plasticity of the individual species dictates the relative quality of these patches.

Resource availability is central to the individual's habitat selection, affecting survival as well as reproductive output (Sutherland 1996). Both temporal and spatial changes can affect resource availability and quality, with anthropogenic habitat modification changing the pattern of availability of resources (Hansson *et al.* 1995; Law and Dickman 1998). A reduction in the availability of high quality habitat might, therefore, compel individuals to use sub-optimal patches, which then has consequences for the fitness of the individual (Lambrechts *et al.* 2004).

1.5.1 Consequences of Habitat Selection for Urban Tolerators

In urbanised landscapes, locating patches that provide shelter, food and nesting resources may be difficult for many Urban Tolerator species, forcing them to occupy sub-optimal habitats. We would expect that the qualities of habitat patches as seen by individual species in urban landscapes to be influenced by the vegetation characteristics present as well as food availability. There are also likely to be consequences of occupying these habitat patches that would manifest themselves in the foraging and other behaviours of individuals.

Australian Urban Tolerators (primarily small insectivores and nectarivores) tend to be species which have a high reliance on vegetation cover (Sewell and Catterall 1998). Vegetation cover provides them with almost all the resources they require for survival with many forage and nest in shrubby understorey vegetation (Catterall 2004). Predation pressure in the urban landscape is likely to change in response to predator as well as vegetation distribution (Tomialojic 1982). While the 'safe nesting zone' hypothesis proposed by Gering and Blair (1999) predicts that the

risk of nest predation and abundance of nest predators decreases with urbanisation, many studies have also suggested that nest predation actually increases in urban landscapes (e.g. Major *et al.* 1996; Jokimäki and Huhta 2000; Sorace 2002; Jokimäki *et al.* 2005) resulting in changes to habitat selection patterns and bird community structure (Jokimäki *et al.* 2005). Shrubs are characteristically limited in urban habitats (Sewell and Catterall 1998; Catterall 2004) and therefore subtle variation in shrub distribution and quality in conjunction with the distribution of both adult and nest predators, are likely to explain the distribution of Urban Tolerators.

Understanding how species respond behaviourally to the availability of food can provide important insights into the mechanisms that structure communities (Blendinger 2005). Habitat selection patterns when foraging reflect two different constraints: avoiding predation and obtaining food (Lima and Dill 1990). The optimal behaviour will therefore vary with both the fitness of the individual and the state of the foraging patch (McNamara and Houston 1986; Mangel and Clark 1988). Birds with a lower fitness would be willing to take more risks given foraging resources are scarce or poor, manifesting in an increase in foraging time. However, individuals with higher fitness levels are more protective of their survival potential and do not need to forage for the same duration (Clark 1994). While the predation risk per unit of foraging time is the same for both individuals, the cost of the predation is higher for the bird in higher quality habitat (Olsson *et al.* 2002). Patch use behaviour has been shown to reflect the relative quality of artificial habitats (Olsson *et al.* 2002). Individuals in the poorer habitat work harder to obtain food and are less disturbed by simulated predation risks. However, birds in the better habitat adopt a foraging strategy to increase their chance of survival, even though energy gains are smaller. In urbanised landscapes, with patches of variable quality, we would therefore expect that

changes in foraging behaviour and duration can be used to reflect this relative quality and has consequences for the long-term fitness prospects of the individual.

The floristic origin of plants in urban habitats has previously been related to the presence of native birds and their foraging requirements. Native birds are more selective in their choice of plants, usually sheltering and foraging on native plants more often than exotic ones (Green 1984; Green 1986; Catterall *et al.* 1989; Green *et al.* 1989; Daniels 1991; Day 1995; Germaine *et al.* 1998). Food availability may be driving this pattern for some foraging guilds. The copious nectar produced by native and hybrid native plants popular in Australian gardens is a preferred source of food for the common native honeyeaters and may contribute to their success in urban areas (French *et al.* 2005). However, interspecific competition for these food resources may result in the smaller honeyeaters being unable to obtain sufficient food in urban areas, despite its availability. Conversely, it is conceivable that the availability of arthropods may control the ability of many insectivores to establish populations in urban habitats.

Despite their ubiquitous nature, arthropods are often overlooked in urban ecological studies (McIntyre 2000; McIntyre *et al.* 2001; Niemelä *et al.* 2002). Of the research that has been conducted, the majority of studies have focused on the response of specific taxa, particularly pest species (Ebeling 1978; Dreistadt *et al.* 1990) with few examining the assemblage as a whole and its role as a food source. Just as for birds, fragmentation and urbanisation have been shown to alter the composition of arthropod communities (Jokimäki *et al.* 1998; Zarette *et al.* 2000; Bolger *et al.* 2002). While some species are unable to survive within modified urban habitats, the arthropod community is thought to be considerably diverse, with some species having a global distribution (Zapparoli 1997; McIntyre 2000; Hostetler and McIntyre 2001). Still, urbanisation and habitat fragmentation may potentially be altering interactions

between arthropods and other organisms and therefore interfering with food web dynamics (Didham *et al.* 1996; Gunnarsson and Hake 1999). Indirect effects of the use of pesticides and insecticides have impacted on many urban and farmland bird species worldwide with changes in breeding systems and foraging ecology documented (Major *et al.* 1996; Boatman *et al.* 2004; Hart *et al.* 2006). Such changes may explain the loss of many insectivorous bird species from Australian urban habitats.

1.5.2 Correlates of Habitat Selection for Territorial Species

The consequences of habitat selection are particularly important for territorial species (those that defend an area from a conspecific) with the quality of the matrix and the quality of the territory established likely to have ramifications for the fitness and reproductive potential of the individual (Cody 1985; Pärt 2003). The costs associated with abandoning a territory in search of one of higher quality are likely to be very high. Individuals must therefore maximise their fitness by establishing a territory that is large enough to meet their resource requirements but be manageable enough to be defended from conspecific intruders.

Resource distribution within the matrix plays an important role in the success of territorial species. Where animals are found within an exclusive territory, the availability, distribution and quality of these resources would be expected to be correlated with the body condition and breeding success of the inhabitants. The distribution of resources has been linked to the evolution of territorial behaviour in carnivorous mammals. The availability of resources within a territory is correlated with the number of individuals occupying the territory, with larger group size assisting in bringing down larger prey, territorial defence and vigilance behaviours

(Macdonald 1981; Kruuk and Parish 1982; Macdonald 1983; Atwood 2006; Delahay *et al.* 2006). In birds, territory size is correlated with the survival of nestlings and a decrease in nest predation in monogamous territorial species (Krebs 1971; Harper 1985; Both and Visser 2000; Lopez-Sepulcre and Kokko 2005), while polygamous species show increased numbers of mates with larger territories (Davies and Lundberg 1984; Wimberger 1988; Langen and Vehrerncamp 1998).

The settlement of new territories is often related to the density of individuals within the habitat. Thus intra-specific competition for resources works at a local scale in territorial species. In cooperatively breeding species, having a higher density of individuals may be advantageous for the breeding individuals as there are greater reproductive success rates in larger groups (Valencia *et al.* 2006; Raihani and Ridley 2007). The helpers may be more successful at passing on their genes through assisting their parents, though only when the cost of solitary brooding is high (Pruett-Jones and Lewis 1990; Emlen 1991; Mulder 1995). However in non-cooperatively breeding species, increased densities of individuals within a habitat would put pressure on available resources and result in higher mortality and poorer reproductive output (Brown 1987; Magrath 2001; Clutton-Brock 2002).

If individuals have the ability to assess habitat quality, then we would expect that higher quality habitats would be established before low quality ones (Fretwell and Lucas 1970; Hunt 1996). Once each successive poorer habitat is filled those still without a territory would be forced to occupy habitats in which they have lower reproductive success or are unable to reproduce at all and individuals in these habitats would experience higher mortality (Brown 1969). Therefore in non-saturated urban habitat we would expect to find birds occupying the best quality habitat patches available.

Territory size can also indicate habitat quality, a measure that is generally accepted to reflect the availability of resources (Smith and Shugart 1987). Those territories which contain higher quality or more abundant food resources may not need to be as large to meet the territory-holder's needs, resulting in smaller territories (Hunt 1996). This has been demonstrated in a number of studies of raptor species, with food abundance and other measures of habitat quality negatively correlated with territory size (Village 1982; Bloom *et al.* 1993; Marzluff *et al.* 1997; Leary *et al.* 1998). Conversely, if a territory is poor in resources, individuals may be forced to search larger areas to obtain sufficient food, thereby requiring them to defend a larger territory. Spatial heterogeneity of resources has also been shown to influence territory size, as demonstrated by the northern flicker (*Colaptes auratus*) in which the distribution of foraging patches with home ranges had a large influence on their size (Elchuk and Wiebe 2003).

1.5.3 Assessing the Quality of Habitat Patches for Urban Tolerators

Determining the suite of vegetation characteristics used by a species is the first step in assessing the relative quality of habitat patches. We can then confirm whether these individuals settle non-randomly through the landscape due to some vegetation requirement that may be in limited supply (Wiens 1985; Bisson and Stutchbury 2000). In obtaining information about the vegetation characteristics that individuals seem to prefer across multiple habitats we can begin to understand the flexibility, or otherwise, that a species may have in a heterogenous landscape. Still, such research simply demonstrates that individuals settle non-randomly and that they can tolerate a wide or narrow range of vegetation variables as non-random settlement may result from constraints rather than choices (Wiens and Rotenberry 1981). At a second level

we can then begin to associate the relative quality of different occupied and unoccupied patches of habitat using cues from habitat qualities, such as food availability, and from behaviours of individuals within these patches. Given the importance of habitat selection for territorial species, they make useful models for examining habitat selection in fragmented habitats. The availability of optimal habitat is likely to be limited and therefore competition for such patches would be strong, forcing many individuals into sub-optimal patches. The consequences of such habitat selection can then be assessed.

1.6 Thesis Aim

The aim of this thesis is to investigate food resources, foraging behaviour, habitat selection and territory size in a single species of Urban Tolerator, with the ultimate goal of furthering our understanding of the effect of urbanisation on bird communities. I have selected the superb fairy-wren (*Malurus cyaneus*) as a study species because it is one of only a few species of small insectivore that is still present in urban areas (Parsons *et al.* 2003, Catterall 2004). Its natural history and behaviour in natural areas is relatively well understood, so there is firm reference point against which deviations in behaviour can be assessed.

1.7 Study Species: Superb Fairy-wrens (*Malurus cyaneus*)

1.7.1 Distribution

The superb fairy-wren (*M. cyaneus*) is a small (~ 10 g) insectivorous Australian passerine of the Family Maluridae. It is a resident species that is found along the eastern and south eastern coastline from Brisbane in the north through to Tasmania and west to Adelaide. Its range also extends further west to the inland

slopes and plains of NSW (Rowley and Russell 1997). The most recent *Atlas of Australian Birds* (Barrett *et al.* 2003) shows an increase in recording rates of the superb fairy-wren from 1998-2002 compared to the previous atlas from 1977-1981. However there was much regional variation, with much of this rise in observations recorded in central Queensland, rather than along the urbanised coast where there was no significant change (Barrett *et al.* 2003).

1.7.2 The Life History and Ecology of Superb Fairy-wrens

All Maluridae are sedentary and territorial, breeding either in pairs or groups. Superb fairy-wrens are insectivorous ground foragers that occupy their territory year round with all group members taking part in territorial defence (Rowley 1965; Mulder 1992; Nias and Ford 1992). They have strong legs but short rounded wings and are therefore relatively weak fliers (Rowley 1965; Schodde 1982; Schodde and Mason 1999). Foraging therefore occurs largely on the open ground and amongst leaf litter and fallen logs but also less frequently on shrub and tree branches generally within 2 m of the ground (Schodde 1982; Tidemann 1983; Recher *et al.* 1985; Ford *et al.* 1986; Cale 1994; Rowley and Russell 1997; Paton *et al.* 2002, Tidemann 2004; Schlotfeldt and Kleindorfer 2006). In semi-arid shrubland superb fairy-wrens also foraged at heights of up to 5 m from the ground for 22% of their observed foraging time (Tidemann 2004). Such flexibility in foraging behaviour is likely to reflect levels and locations of food resources available due to vegetation structure at each location and suggests this species is a generalist and opportunistic forager. Differences in vegetation structure have been shown to influence the foraging ecology and morphology of superb fairy-wrens on Kangaroo Island which has resulted in adaptive

divergence and the evolution of a subspecies (*M. c. ashbyi*) (Schlotfeldt and Kleindorfer 2006).

The superb fairy-wren diet consists largely of arthropods, however some small seeds have also been found in stomach contents (Rowley 1965; Barker and Vestjens 1990). Over 40 families of arthropods have been identified in stomach content analysis with ants (Hymenoptera: Formicoidea) in particular considered to be an important dietary component (Rowley 1965; Tidemann *et al.* 1989; Barker and Vestjens 1990; Rowley and Russell 1997). The food fed to nestlings is both larger and of different taxa to that of the adults, with flies (Diptera) and moths, butterflies and their larvae (Lepidoptera) more commonly provided (Rowley 1965). Generally adults eat very small items while nestlings are fed larger items. However, quantification of the range of sizes in each diet has not been made.

Superb fairy-wrens are sexually dichromatic. Each family group usually consists of a dominant male, female and a number of male helpers. The dominant male is usually found year round in breeding plumage (metallic blue cap, mantle and ear tufts with a black bill, loreal stripe, collar and upper body with whitish chest and dark blue tail) while the adult females have a grey-brown back, off-white chest, rufous loreal stripe and eye ring with a red-brown bill and grey-brown tail with a greenish hue. Dominant males in non-breeding plumage appear similar to females but they retain a black eye-ring, loreal stripe and bill with the dark blue tail (Schodde 1982). Immature birds resemble the females except that the greenish tinge in the tail of the female is absent in juveniles (Rowley and Russell 1997).

They are cooperative breeders and so during the breeding season, all group members assist with the raising of young (Rowley 1965; Pruett-Jones and Lewis 1990; Mulder 1992; Nias and Ford 1992). They construct a dome-shaped nest made

from grasses and spiderwebs, with the nest located usually within one metre from the ground in dense shrubs (Rowley and Russell 1997). The breeding season usually ranges from September to January but, in favourable conditions, can extend into March (Rowley and Russell 1997). Cooperative breeding allows the group to produce more clutches and fledge more young successfully (Rowley 1965; Ligon *et al.* 1991). This also liberates females from costs associated with extra-pair paternity (such as abandonment from the paired male), with helpers always available to raise young (Mulder *et al.* 1994). Males from previous clutches generally remain within the family group to act as helpers (and are sexually active) whilst juvenile females emigrate from their natal territory within a year of fledging and either establish a new territory or die (Mulder 1995). The mortality rate for dispersing females is estimated to be at least 65-75% in high quality habitats (Mulder 1995). In habitats where territories are patchy due to a limited availability of suitable habitat, this mortality rate would be expected to be much higher.

Despite appearing monogamous, superb fairy-wrens are sexually promiscuous although they remain paired while both partners are alive (Mulder 1992; Mulder *et al.* 1994; Cockburn *et al.* 2003) and some divorce has been recorded (Cockburn *et al.* 2003). High levels of extra-pair paternity have previously been demonstrated (76% of offspring, Mulder *et al.* 1994) and while males display and attempt to solicit extra-pair copulations by visiting neighbouring females throughout the day, mating takes place before dawn when the female travels to the territory of her preferred mate (Double and Cockburn 2000). Both the male and female return to their individual social partners and helpers to raise each clutch (Dunn and Cockburn 1996). Helper males may also father clutches within their family group (Cockburn *et al.* 2003, Double and Cockburn 2003). Given a high turnover of dominant females (usually through death or

divorce), helper males are sometimes unrelated to the dominant female (Dunn *et al.* 1996). Males related to females will not compete for within group fertilisations therefore avoiding incest (Cockburn *et al.* 2003).

Due to the territorial nature of superb fairy-wrens, it is possible to investigate small-scale habitat selection. Each family group selects and defends a territory that must provide all of their foraging and nesting requirements. Previous studies of superb fairy-wrens conducted in a number of habitats have indicated that the ecology of this species is very flexible, with territory size associated with the quality of the habitat. Birds in low quality habitats would be expected to occupy large territories as they are forced to search larger areas to obtain resources, whilst those found in high quality habitat are expected to have smaller territories as all of their resource requirements can be met in a smaller area. Having a smaller territory also creates a more manageable boundary that can be defended from conspecifics.

The smallest territories previously identified are located at the Australian National Botanic Gardens with territories averaging 0.6 ha (Mulder 1992)(Table 1.1). Whilst the areas surrounding the superb fairy-wren habitat is urban, the habitat itself is a continuous plantation of ironbark woodland with a shrubby understorey. The entire woodland is saturated with superb fairy-wren territories. This habitat most closely reflects the traditional habitat occupied by superb fairy-wrens prior to clearing and fragmentation. The supposed high quality of this habitat has allowed numerous territories to be established and, despite their individual small sizes, territories support large numbers of superb fairy-wrens. The largest territories have been recorded in the Taunton National Park in Central Queensland. Superb fairy-wrens were most commonly found in recently disturbed regrowth areas and their territories averaged 8.7 ha (Chan and Augustyn 2003). Large areas of the habitat were unsuitable for

superb fairy-wrens, particularly where brigalow shrubs (*Acacia harpophylla*) were uncommon or absent, requiring the birds to occupy much larger territories and suggesting that habitat quality is much lower. Finally, territories averaging 1.25 ha and 1 – 2 ha have been recorded in both Armidale and Booligal respectively (Nias 1987; Tidemann 1983) (Table 1.1). Both of these sites were located in fragmented pastoral land where not all of the landscape was suitable for the birds. However when comparing territory size and quality with other studies, these fragmented habitats would appear to be of relatively high quality for this species. We would expect that superb fairy-wrens occupying marginal habitat such as that in rural fringes to have similar territory sizes to these, however, it is unknown how territory size would be affected in suburban habitats.

Table 1.1: Territory and group sizes of superb fairy-wrens previously measured in a variety of different habitats.

Please see print copy for Table 1.1

1.7.3 Habitat Requirements

Much of the superb fairy-wren's traditional habitat of open woodland and forest has been cleared for farming and has therefore been lost (Rowley and Russell 1997). However, fragmentation and habitat modification has not necessarily

disadvantaged this species. It prefers habitat with dense shrub cover interspersed with open ground for foraging (Neave *et al.* 1996). The introduction of dense shrubby weeds, particularly lantana (*Lantana camara*), brambles (*Rubus vulgaris*), rose briars (*Rosa rubiginosa*) and blackberry (*Rubus fruticosus*) have provided substitute vegetation cover, especially along the edges of fragmented remnants (Rowley and Russell 1997; Berry 2001). Superb fairy-wrens have been shown to prefer such edges over the interior of remnants (Berry 2001), therefore I will use these habitats as control sites within this study.

Superb fairy-wrens are also found in suburban locations in cities, particularly throughout Sydney, Melbourne and Canberra. Still, they are not common in suburban locations and are very patchy in their distribution (Rowley and Russell 1997; Parsons *et al.* 2003; Catterall 2004; Davies and Kirkpatrick 2006). While it is generally accepted that the lack of shrubs in urban habitats is limiting their distribution, this has not been thoroughly examined. This species has previously shown a preference for native vegetation over exotic in suburban gardens as well as for gardens with more lawn space for foraging (Davies and Kirkpatrick 2006; Parsons *et al.* 2006). We would expect suburban habitat to be of sub-optimal quality due to resource restrictions (both vegetation and food) and consequently individuals should occupy larger territories and show changes in foraging behaviour.

1.8 This Study

The superb fairy-wren is a species whose response to habitat modification appears complex. Unlike many other small insectivorous birds it is not necessarily disadvantaged by urbanisation. It prefers semi-natural patches (rural/remnant edge) to what remains of its traditional habitat and is also found in some suburban habitat,

though it is very patchy and limited in its distribution there (Berry 2001; Parsons *et al.* 2003; Catterall 2004; Parsons *et al.* 2006). I will determine whether superb fairy-wrens are limited to a patchy distribution in suburban habitats because of vegetation or foraging requirements. By comparing the territory sizes and behaviour of superb fairy-wrens in semi-natural control habitats (rural/remnant edges) with those in suburban habitat I will investigate whether urban habitat patches truly are sub-optimal for this species or if they can live as successfully in these urban territories in which their resource requirements are met.

All research has been conducted within the Wollongong, Shellharbour and Kiama Local Government Areas (LGA's) of the Illawarra region of NSW, Australia (34.26 S, 150.53 E). All LGA's had a combined estimated residential population of 280331 individuals in 2007 and occupies a total of 108919 ha (ABS 2007). In Wollongong, 63.7% of the population occupy separate houses, 82.5% of Shellharbour and 67.3% in Kiama while 15.4% of Wollongong residents, 16.0% of Shellharbour and 12.4% of Kiama residents live in medium density (townhouses, semi-detached houses and villas) and high density housing (flats and apartments) (ABS 2006).

Geographically, the Wollongong region (Wollongong and Kiama LGA's) is a linear corridor located along the coastline approximately 80 km south of Sydney, NSW. To the west, the escarpment rises to 300m above sea level with the human population found on the plains between the escarpment and the ocean. The Illawarra Escarpment Bioregional Assessment (NPWS 2002) details 59 different vegetation communities within the Wollongong LGA (47304.66 ha), however data was not available for vegetation communities of Shellharbour and Kiama LGA's. Urban habitat, cleared or exotic vegetation comprises 41.2% of the Wollongong LGA (19564.59 ha), native vegetation comprises 30.9% of the area (14668.95 ha) and

scattered native trees 2.6% (1211.34 ha). Major native vegetation communities identified include Coachwood Warm Temperate Rainforest (2295.3 ha), Escarpment Blackbutt Forest (1833.51 ha) Exposed Sandstone Scribbly Gum Woodland (1551.49 ha) and Acacia Scrub (1227.95 ha). Aerial photographs indicated that approximately 45% of remaining vegetation within the Wollongong LGA displays some level of disturbance.

In Chapter 2 I will examine the vegetation requirements of superb fairy-wrens in suburban and control (semi-natural) habitats and compare these to suburban locations in which superb fairy-wrens are absent. This will determine whether vegetation structure and/or floristics are limiting the distribution of superb fairy-wrens in suburban habitats.

Chapter 3 will investigate the sizes of superb fairy-wren territories in suburban and control habitats using radio-telemetry. Territory size tends to be inversely related to territory quality. We would expect that birds in higher quality habitats will occupy smaller territories and therefore territories in the suburban sites would be expected to be larger than the controls. Previous measures of territory size conducted in other habitat types will be compared. I will also assess the merits of different analysis techniques for measuring territory size.

The foraging and general behaviour of superb fairy-wrens in suburban and control territories will be investigated in Chapter 4. We would expect that, if there are differences in habitat structure and resource availability, individuals in suburban habitats will behave and forage differently to those in the control sites. Limitations in resources in suburban habitats may also impact upon male and female social behaviour.

Finally, Chapter 5 will examine arthropod availability of suburban and control habitats. If suburban habitats are poorer quality we would expect that there would be fewer arthropods available with lower diversity and biomass. I will also compare abundance and biomass with suburban habitats without superb fairy-wrens. This will determine whether food availability is limiting suburban superb fairy-wren distributions.

One chapter (Chapter 2) has already been accepted for publication and all data chapters are written as separate scientific papers. Therefore there is some repetition of introductions and methods between chapters.

Each chapter represents a single-year study and is written as a scientific paper. While long-term research often provides more robust data than single-year studies given the larger amount of data generated and potential temporal changes, the single-year studies used here were the only way to provide an overview of the impact of urbanisation on the superb fairy-wren for this thesis.

In each of the data chapters, sites are referred to as ‘suburban’ or ‘non-suburban’. Suburban sites were those found within suburban residential zones (photograph 1) classified by low-density housing and being at least 10 years old. These suburban locations contained a mix of planted vegetation (such as parks and gardens) along with weedy disturbed patches. Non-suburban sites were located along rural/remnant habitat edges on the foothills of the Illawarra Escarpment (photograph 2). All locations used here were identified as having moderate to high levels of disturbance (NPWS 2002). Many of the same sites were used in each of the surveys, with further sites located wherever necessary. Suburban sites where superb fairy-wrens were absent were located by using random numbers to locate potential areas on a map and then surveying the site (using call-play back as well as observations) for

superb fairy-wren presence/absence. New suburban sites without superb fairy-wrens were found for each study.



Photograph 1: A garden within a typical suburban site with superb fairy-wrens (Photographer – Holly Parsons).



Photograph 2: A typical 'non-suburban' site with superb fairy-wrens (Photographer - Holly Parsons).

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CHAPTER TWO

The Vegetation Requirements of Superb Fairy-wrens (*Malurus cyaneus*) in Non-Urban Edge and Urbanised Habitats

Parsons, H., French, K., and Major, R. (2008). The vegetation requirements of superb fairy-wrens in non-urban edge and urbanised habitats. Emu 108: 283-291.

2.1 Introduction

The urban environment encompasses a broad spectrum of habitats, from highly developed industrial and commercial zones to fragmented remnants and expansive green spaces (Jokimäki 1999). The composition of the bird communities living within these habitats varies along this urban gradient (Bessinger and Osborne 1982; Catterall *et al.* 1989; Blair 1996; Savard *et al.* 2000) with highly urbanised habitats often supporting exotic birds that have a long history of human cohabitation (Case 1996). Some native birds also exploit urban habitats, becoming more prevalent than in their natural habitats (Parsons *et al.* 2003). Studies from Europe (Huhtalo and Jarvinen 1977; Jokimäki *et al.* 1996; Fernández-Juricic 2001; Fernández-Juricic and Jokimäki 2001; Palomino and Carrascal 2006), North America (Emlen 1974; Guthrie 1974; Walcott 1974; Beissinger and Osborne 1982; Rosenberg *et al.* 1987; Green and Baker 2002), and Australia (Jones 1983; Green 1984, 1986; Munyenyembe *et al.* 1989; Catterall *et al.* 1989, Catterall *et al.* 1991; Parsons *et al.* 2003) have shown that as vegetation becomes more prevalent in urban areas, the ability to support a

wider range of native species also increases, although the bird assemblages remain distinct from that which was historically present prior to human development.

Heterogeneous urban landscapes do not limit all birds to isolated suitable habitat patches within a hostile matrix (Hansson *et al.* 1995; With *et al.* 1997). Within the urban matrix a range of habitats may be tolerated by a species and fulfil different requirements (such as foraging or breeding) (With *et al.* 1997). Local factors play a significant role in the structure of habitat occupied by individuals (Davis and Glick 1978; Jokimäki *et al.* 1996; Fernández-Juricic 2001), however the requirements of a population must be met at a landscape scale in order to sustain the population (Weins 1985; Jokimäki *et al.* 1996; Clergeau *et al.* 2006). Further, under the ideal-despotic model, the quality of the habitat occupied by territorial species will also be influenced by the competitiveness of the individual as well as the availability of resources (Fretwell and Lucas 1970). Therefore, understanding the habitat requirements of individuals at a small scale is a vital first step for managing the landscape and promoting the survival of less common species (Savard *et al.* 2000).

Habitat structure and availability both within and around the site has a large influence on probability of occurrence of individuals at a site (Jokimäki and Huhta 1996; Jokimäki 1999; Mörtberg 2001). The loss of vegetation cover has been associated with a reduction in urban bird diversity (Hooper *et al.* 1975; Hohtola 1978; Lancaster and Rees 1979; Beissinger and Osborne 1982; Mills *et al.* 1989; Munyenyembe *et al.* 1989). In natural forests, a variety of different plants of different ages creates complex structural layers, in contrast to the urban park and garden design of open lawn space and tall trees, which are reminiscent of some natural grassy woodland habitats (Jokimäki, and Huhta 2000). In Australia, urban habitats that replicate grassy woodland are dominated by larger, more aggressive avian species

(Catterall 2004; Parsons *et al.* 2006). The limited availability of habitat suitable for smaller, cover-dependant species such as those that traditionally occupy shrubby woodlands, heaths and forests is thought to be at least partially responsible for the decline of small birds in urban Australia (Catterall *et al.* 1989; Munyenyembe *et al.* 1989; Bass 1995; Sewell and Catterall 1998).

The floristic origin of the remaining urban vegetation is also thought to influence species use. It is generally accepted that native birds prefer native vegetation (Green 1984, 1986; Parsons *et al.* 2006) however studies have indicated that this is not always the case. Catterall *et al.* (1989) and Green *et al.* (1989) suggest that native birds are simply more selective in their use of both native and exotic plants than introduced birds. Differences in both food availability and the structure of exotic vegetation may be responsible for native birds avoiding this vegetation (Green 1984, Bhuller and Majer 2000).

The superb fairy-wren (Maluridae: *Malurus cyaneus*) is a small (9-11g) native insectivorous bird that is considered to be an 'edge' species (Rowley and Russell 1997; Berry 2001). It is also found in urban habitats, resident year round, though is not common (Veerman 2002; Parsons *et al.* 2003; Catterall 2004; Parsons *et al.* 2006). One reason for this may be the dependence of this species on shrubs for shelter and nesting sites (Rowley and Russell 1997; Daniels and Kirkpatrick 2006). Given that this species is both highly territorial and a weak flier (Rowley and Russell 1997), competition for good quality patches would be strong if high quality habitat is limited in availability. The ability to select and occupy the highest quality habitat would have large implications for the future fitness of individuals. For superb fairy-wrens, edge habitat along rural/remnant boundaries is considered high quality habitat. Densities of individuals are higher in this habitat than in the interior of traditional woodland

habitat as foraging opportunities are thought to be increased in the open habitat adjacent to the habitat edges (Berry 2001). Density is not always a good indicator of habitat quality expressed in terms of overall fitness (van Horne 1983) as rural/remnant edge habitat may act as a reproductive sinks. However, for the purposes of this study of foraging habitat, comparisons will be made between this edge habitat (hereafter referred to as non-suburban habitat) and suburban habitat.

As local habitat characteristics play a vital role in the fitness of individuals within territories (Luck 2002), habitat choice may be limited in modified landscapes due to a loss of both dispersal ability and high quality patches (Garshelis 2000; Luck 2002; Maguire 2006). In modified habitat (such as in urban areas), we would expect that a loss of shrubby habitat would lead to fewer territories and restrict cover-dependant species to more vegetated areas. This is likely to impact on the abundance and fitness of the population. The availability of fewer high quality territories due to a lack of suitable habitat would lead to an overall reduction in the fitness of the total population as more individuals are forced into poorer quality territories. Isolation of territories would be predicted to cause dispersal difficulties. Recruitment into available territories, both of high and poorer quality would be slow, leading to an overall lower density of individuals across the landscape.

If the distribution of superb fairy-wrens is limited in suburban areas due to a shortage of suitable vegetation we would expect:

1. The structure or floristic composition, or both, of vegetation of sites within suburban Fairy-wren territories to be different to sites in urban areas without Fairy-wrens.
2. The vegetation of suburban territories to be more similar to the vegetation in non-suburban territories than to suburban sites without

Fairy-wrens. The habitat requirements of the birds would require them to settle in suburban territories that have a similar structure or floristic composition to good quality territories in other habitats.

3. A hierarchy in shrub availability and floristic composition across the habitats to be observed:
 - highest quality habitats that are non-suburban territories will have most shrubs and the greatest proportion of native plants;
 - mid-quality habitats that are suburban territories will have equivalent or a lower density of shrubs and mixed floristic composition; and
 - poorest quality habitats that are suburban areas without Superb Fairy-wrens will have fewest shrubs and most exotic vegetation.
4. Urban territories to be more similar to each other than within other habitat types as the type of habitat they type of habitat they require is specific and limited in suburban landscapes. Conversely there would be more variation in the habitat characteristics of urban areas without Superb Fairy-wrens.

The aim of this study was to test these predictions by measuring habitat characteristics of areas occupied by fairy-wrens and unoccupied habitat in suburban habitats and non-suburban edge habitats.

2.2 Materials and Methods

2.2.1 Habitat Characteristics

Superb fairy-wrens were observed in Wollongong, located in the Illawarra region of New South Wales, Australia (34.26 S, 150.53 E) in September 2005. A total of 17 pairs or groups were located in ‘non-suburban’ habitats which were edges located along rural/woodland boundaries. Despite extensive searches we could find no individuals of this species in the interior of woodlands in this region suggesting that edges were preferred habitat. There were 20 pairs or groups of superb fairy-wrens located in suburban areas. Suburban areas were dominated by residential housing (mainly single or two-storey housing and gardens) and parkland (open recreational park space with lawn, some shrubs and trees in various proportions). Observations of the superb fairy-wrens completed in the week prior to the vegetation assessments were used to create approximate territories in the suburban and non-suburban habitats by mapping points where the birds were seen. Previous radio-tracking data of some superb fairy-wren territories were also used (Chapter 3). The shapes of the suburban territories were then used to randomly allocate 20 suburban sites of the same shape where superb fairy-wrens were absent (habitat without wrens).

To investigate habitat characteristics of these 3 groups, 40 quadrats (2 x 2 m) were randomly set up within each approximate territory. From the intersection of lines drawn between the furthest four corners of the approximate territories, a central point was established. Using random bearings and distances, random quadrats were measured from this central point. The quadrats were not measured outside locations from which fairy-wrens were observed and never exceeded 50m from the central point. The presence of the following habitat variables within each quadrat was recorded:

- *Concrete/Road*. Driveways and paths as well as tarred and untarred roads.
- *House*.
- *Fences*.
- *Grass*. Categorised as either short when shorter than the height of the wren (< 10 cm), or long.
- *Herb*. Herbaceous layer < 1.5 m in height.
- *Native Shrub*. A native plant 1-4 m tall with trunk branched close to the ground.
- *Exotic Shrub*. A plant introduced from outside Australia that measured 1-4 m tall with trunk branched close to the ground. Lantana was not included as an exotic shrub but was put in a category of its own.
- *Lantana*. *Lantana camara*, a dense exotic woody shrub that was prevalent at many sites, particularly the non-suburban sites.
- *Native Tree*. Native plant > 1 m in height with a trunk that did not branch near the ground.
- *Exotic Tree*. A plant introduced from outside Australia that measured > 1 m in height with a trunk that did not branch near the ground.

The composition of each of the above categories at each of the sites was represented as the percentage occurrence (in 40 quadrats) rather than percentage cover per quadrat.

2.2.2 Statistical Analysis

Both univariate and multivariate techniques were used to examine the habitat characteristics of non-suburban territories, suburban territories and habitat without

fairy-wrens. To determine if the overall structure of the vegetation differed or if floristic origin also played a role in superb fairy-wren habitat requirements, analyses compared 'all shrubs' (native + exotic + lantana) and 'all trees' (native + exotic) and also native and exotic categories (with lantana separate from exotic shrubs). Differences between each of the individual variables were determined using one-way ANOVAs with post-hoc Tukey-Kramer tests. Data were not normally distributed in all cases. The habitat variable 'house' was square root transformed while 'fence', 'short grass' and 'exotic shrubs' were $\log(x + 1)$ transformed. Four habitat variables 'long grass', 'herb', 'native shrubs' and 'lantana' were not normally distributed despite any transformation, therefore a Kruskal-Wallis test was conducted for each of these. The Kruskal-Wallis test is the non-parametric equivalent of a one-way ANOVA. Values are transformed into ranks to determine if there is no shift in the centre of the groupings. While non-parametric tests have a greater probability of making a Type 1 error, when data for these four variables were viewed graphically the differences between habitat types were evident. To determine if shrub types (native, lantana or exotic – lantana excluded) were independent, correlations were conducted on these for both suburban and non-suburban data. The significance of correlation coefficients were tested using t-tests.

To determine the differences in overall structure between the three habitat types, non-metric multidimensional scaling using Bray-Curtis similarity indexes and a one-way single factor analysis of similarity (ANOSIM) were performed. Non-metric multidimensional scaling graphically demonstrates the differences between all sites within the three habitat types whilst the ANOSIM tests the hypothesis that differences between sites across habitat types are greater than between sites within habitat types using permutation/randomisation tests on the Bray-Curtis similarity indexes. The

variables that contributed the most to up to 50% of the similarity between the habitats were calculated using the SIMPER function.

The dataset was analysed on two levels using these multivariate techniques. The first looked at broad habitat structure whereby native and exotic shrubs were combined for shrubs (including lantana) and trees. Secondly, to see whether floristics also influenced habitat selection, native and exotic origins were included as separate variables. $\text{Log}(x + 1)$ transformations were also conducted for multivariate analyses with the PRIMER statistical package (version 6) (Clarke and Gorley 2001) used for calculations.

2.3 Results

2.3.1 Difference in Vegetation Between Habitats – Univariate Analyses

Analyses of individual habitat variables identified differences between habitats. Of the three anthropogenic variables (house, road and fence), only the proportion of houses sampled showed a significant effect of habitat type ($F_{2,54} = 128.5$, $p < 0.001$). Suburban sites without fairy-wrens had on average a much higher occurrence of houses than either the suburban sites with fairy-wrens or, as would be expected, the non-suburban fairy-wren sites (Fig 2.1a). Short grass availability was lowest in non-suburban sites but both suburban sites were similar ($F_{2,54} = 10.3$, $p < 0.001$, Fig 2.1b). Long grass was in high abundance in non-suburban sites, lower in suburban sites with fairy-wrens but nearly absent from suburban sites without fairy-wrens (Fig 2.1c). While a Kruskal-Wallis test confirmed a significant difference between sites ($H_2 = 28.5$, $p < 0.001$), multiple comparisons could not identify where differences lay. A similar result was found for the herbaceous layer (Fig 2.1d).

When the overall structure of the shrubs and trees were considered, suburban sites without fairy-wrens had the smallest proportion of both these layers (Fig 1e and 2.1f). The shrub layer was significantly smaller in the suburban sites without fairy-wrens than both the suburban and non-suburban sites with fairy-wrens ($F_{2,54} = 16.9$, $p = 0.000$, Fig 2.1e). There was a smaller percentage occurrence of trees in suburban sites without fairy-wrens compared with non-suburban sites, but no significant difference in occurrence of trees between suburban sites with fairy-wrens and either of the other two habitats ($F_{2,54} = 3.8$, $P = 0.028$, Fig 2.1f).

The floristic origin of shrubs and trees differed between habitats although they did not show the predicted pattern. Despite having the highest proportion of shrubs overall, non-suburban fairy-wren sites had fewer native (Fig 2.1g; $H_2 = 17.8$, $p < 0.001$) and exotic shrubs (excluding lantana) (Fig 2.1h; $F_{2,54} = 13.3$, $p < 0.001$), though the Kruskal-Wallis post-hoc analysis could not detect in which habitats the differences between native shrubs was significant. There was no correlation between the percentage occurrence of any of the three shrub types (native, exotic excluding lantana or lantana) with each other in suburban habitats, non-suburban habitats or suburban locations without wrens (Table 2.1; Fig 2.2a,b,c; Fig 2.3a,b,c; Fig 2.4). The absence of lantana from suburban locations without wrens meant correlations could not be conducted with this variable in this habitat.

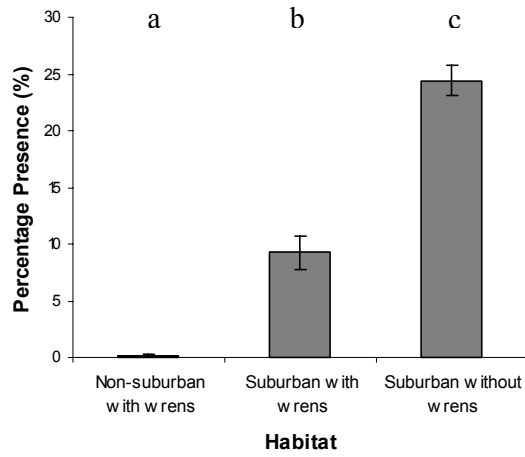
Native shrubs were, however, much more prevalent in suburban habitats with fairy-wrens than in either of the other two habitats. The prevalence of lantana within non-suburban sites was contributing substantially to the overall high proportions of shrubs recorded here (Fig 2.5a). Lantana was therefore substituting for native shrubs in these non-suburban areas. Lantana accounted for an average of 91.9% of the quadrats where shrubs were observed in non-suburban habitat, 41.7% in suburban

sites with fairy-wrens and was totally absent from suburban sites without fairy-wrens. The availability of lantana was therefore significantly different between sites ($H_2 = 37.6$, $p < 0.001$). While the location of the significant difference could not be detected using the Kruskal-Wallis analysis, non-suburban habitats had over twice the amount of lantana recorded than suburban sites with fairy-wrens (Fig 2.1i).

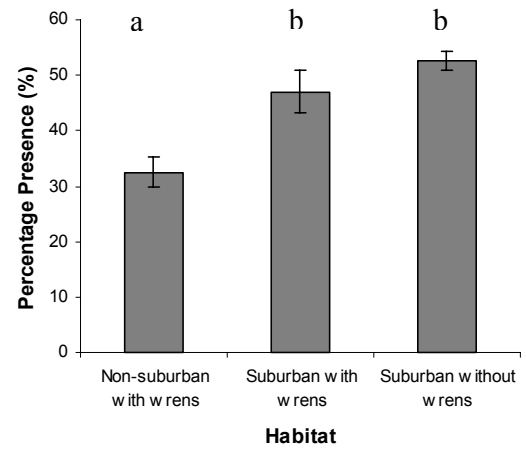
In suburban sites with fairy-wrens, native shrubs were slightly more prevalent in quadrats than other exotic shrubs (not including lantana) (11.3% and 9.5% of total quadrats respectively) while in suburban sites without fairy-wrens, the reverse was seen (6.5% and 12.8% respectively) (Fig 2.5a). Native trees were much more prevalent than exotic trees in fairy-wren habitats (18.4% and 3.3% of total quadrats) (Fig 2.5b). In suburban habitats where fairy-wrens were absent there was a more even mix of native and exotic trees, with native trees present in 8.3% of quadrats and exotic trees in 7.3%. Non-suburban sites had a significantly higher availability of native trees than either suburban habitat with no difference between the two suburban habitats ($F_{2,54} = 8.9$, $p < 0.001$; Fig 2.1j). Exotic trees were more prevalent in the suburban sites without fairy-wrens than the suburban sites with fairy-wrens but non-suburban sites were not significantly different from either ($F_{2,54} = 3.2$, $p = 0.049$; Fig 2.1k).

Table 2.1: Correlation coefficients and t-tests (df = 18) testing correlations between the three shrub variables in suburban and non-suburban fairy-wren habitats as well as suburban habitats without fairy-wrens.

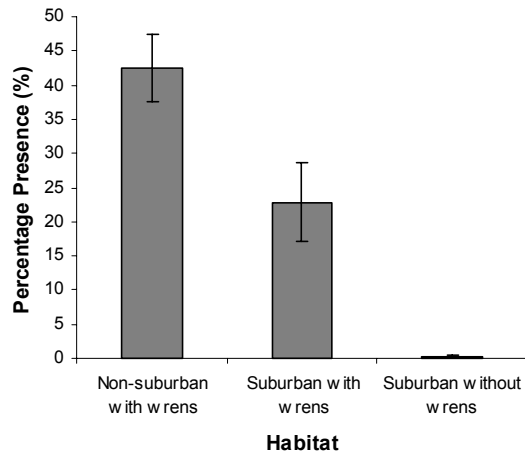
	Suburban	Non-suburban	Suburban no wrens
Native Vs Exotic excluding Lantana	$R = -0.3$, $t = 1.3$, $p = 0.2$	$R = 0.2$, $t = 0.9$, $p = 0.4$	$R = -0.1$, $t = 0.6$, $p = 0.6$
Native Vs Lantana	$R = -0.4$, $t = 1.8$, $p = 0.1$	$R = 0.2$, $t = 0.7$, $p = 0.5$	
Lantana Vs Exotic excluding Lantana	$R = -0.2$, $t = 0.7$, $p = 0.5$	$R = -0.2$, $t = 0.9$, $p = 0.4$	



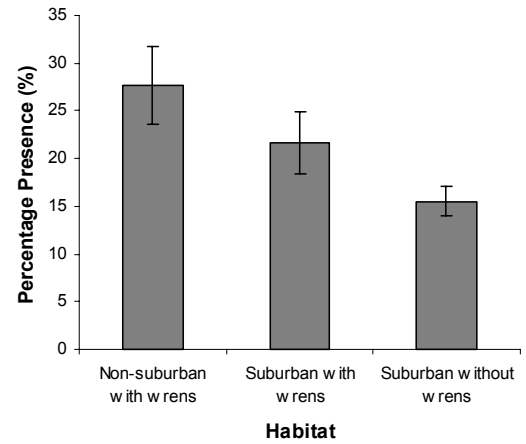
(a) House



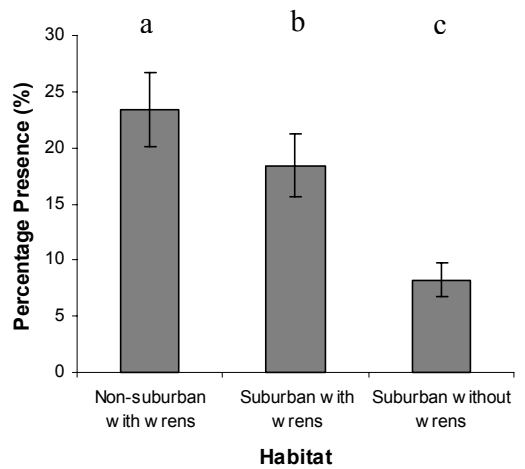
(b) Short Grass



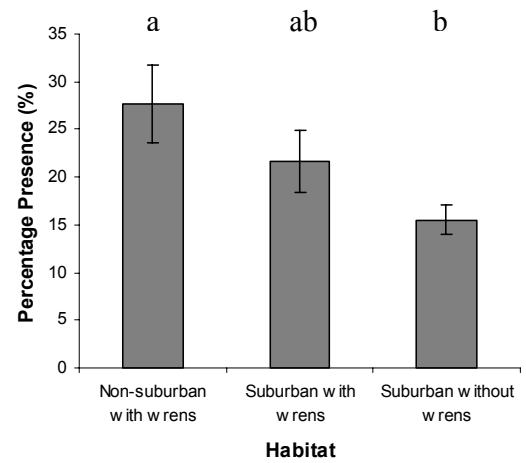
(c) Long Grass



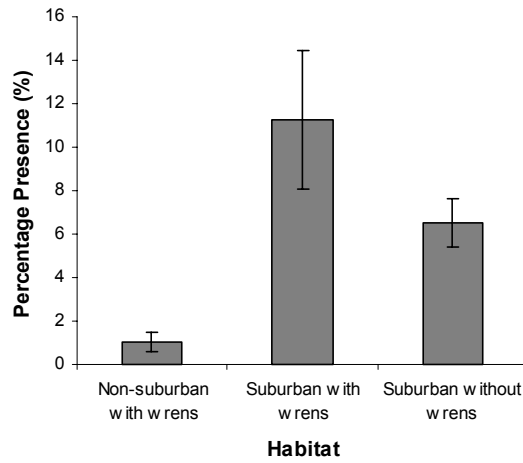
(d) Herbs



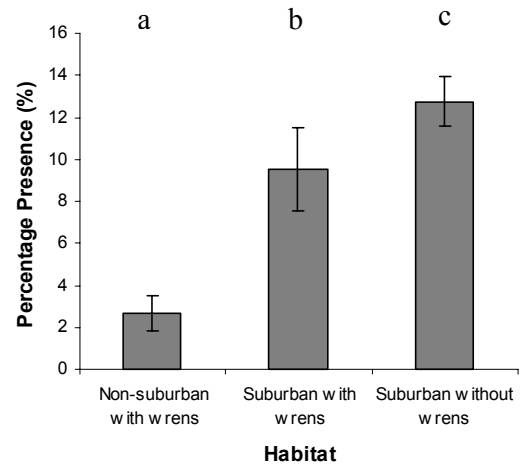
(e) All Shrubs



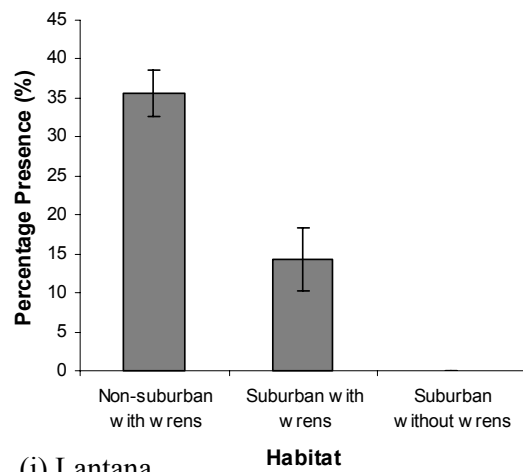
(f) All Trees



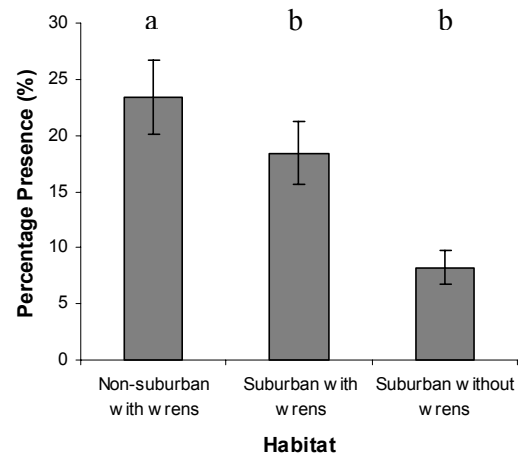
(g) Native Shrubs



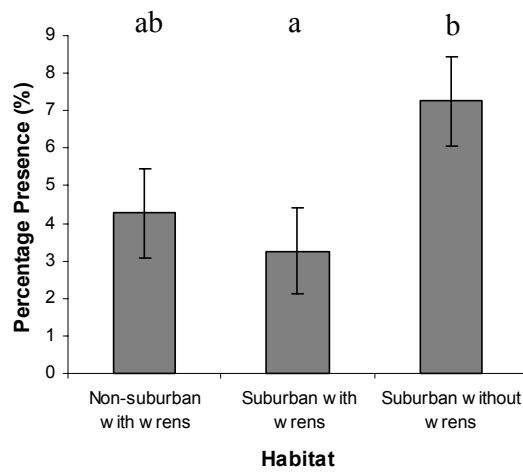
(h) Exotic Shrubs



(i) Lantana



(j) Native Trees



(k) Exotic Trees

Fig 2.1: Percentage presence of variables that displayed statistically significant differences between habitats types included (a) houses, (b) short grass, (c) long grass, (d) herbs, (e) all shrubs, (f) all trees, (g) native shrubs, (h) exotic shrubs, (i) lantana, (j) native trees, (k) exotic trees in 40 quadrats in non-suburban (rural/remnant edge) habitats with superb fairy-wrens, suburban habitats with superb fairy-wrens and suburban habitats without superb fairy-wrens. Letters denote where habitats are statistically different from each other however for long grass, herbs, native shrubs and lantana non-parametric tests meant habitat differences could not be distinguished. Error bars show standard error.

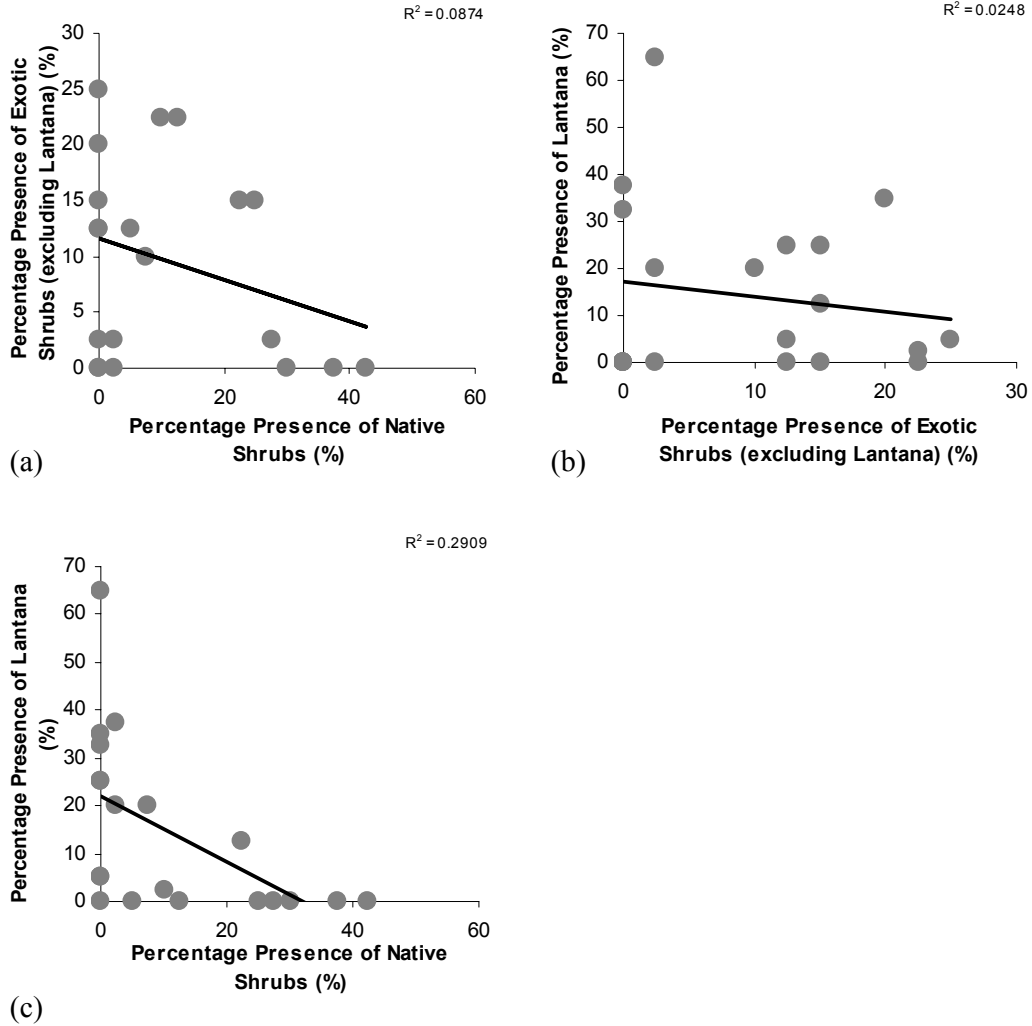


Fig 2.2: Correlations between the percentage presence of (a) native shrubs and exotic shrubs (excluding lantana), (b) exotic shrubs (excluding lantana) and lantana and (c) native shrubs and lantana in suburban habitats. The linear trendline is shown in black.

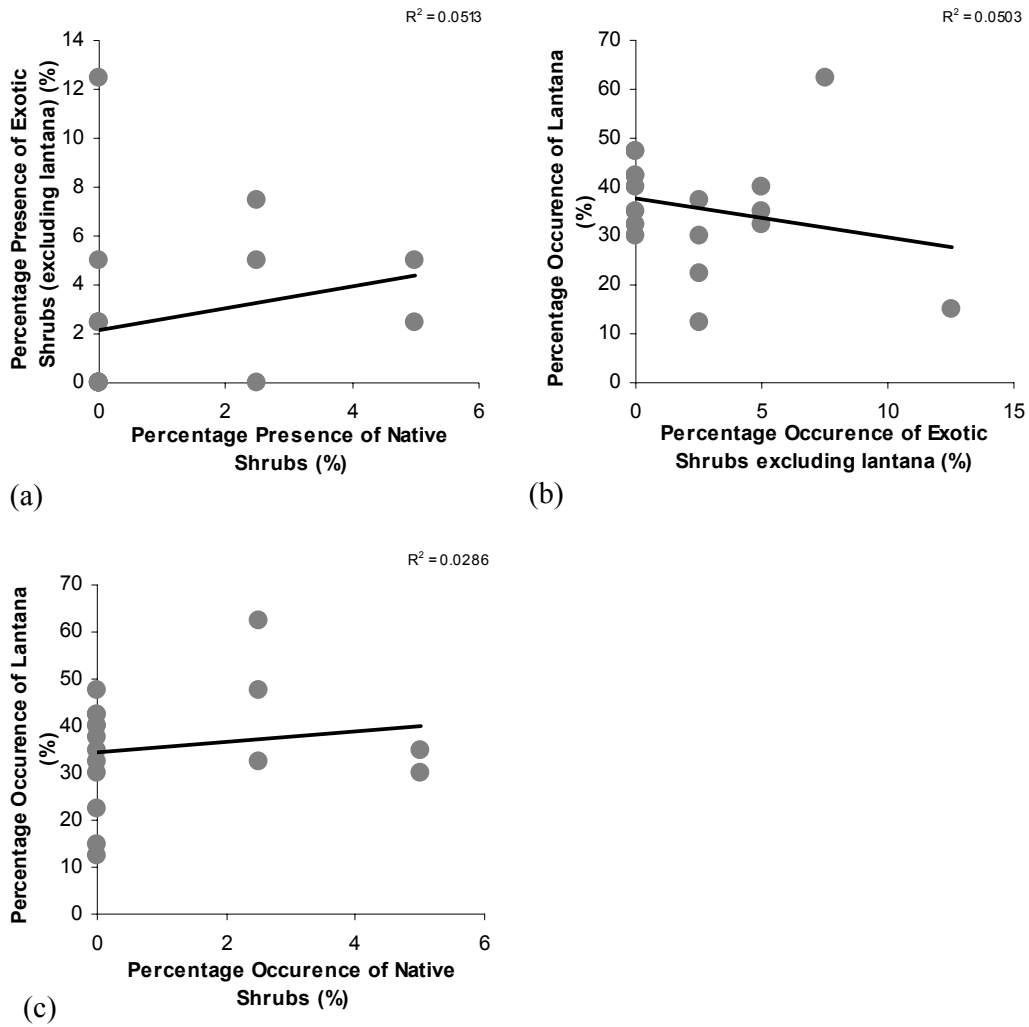


Fig 2.3: Correlations between the percentage presence of (a) native shrubs and exotic shrubs (excluding lantana), (b) exotic shrubs (excluding lantana) and lantana and (c) native shrubs and lantana in non-suburban habitats. The linear trendline is shown in black.

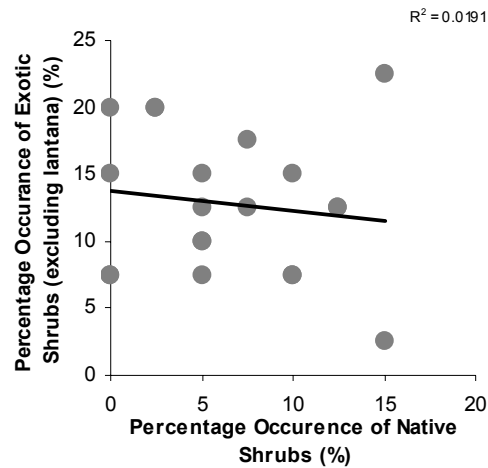


Fig 2.4: Correlations between the percentage presence of native shrubs and exotic shrubs (excluding lantana) in suburban locations where superb fairy-wrens were absent. The linear trendline is shown in black.

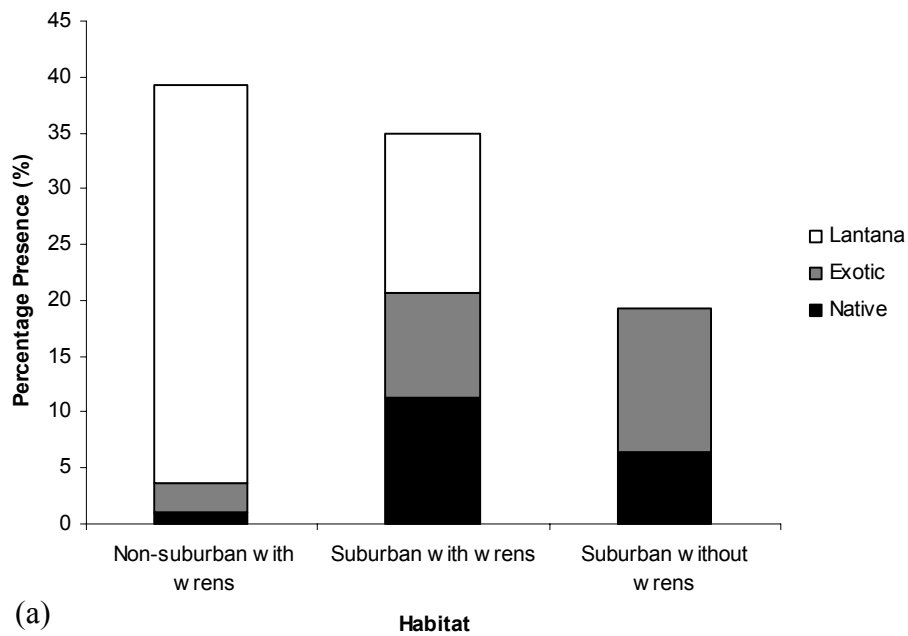
2.3.2 *What Characteristics Distinguish Differences Amongst Habitats? – Multivariate Analyses*

2.3.2.1 Overall Structure

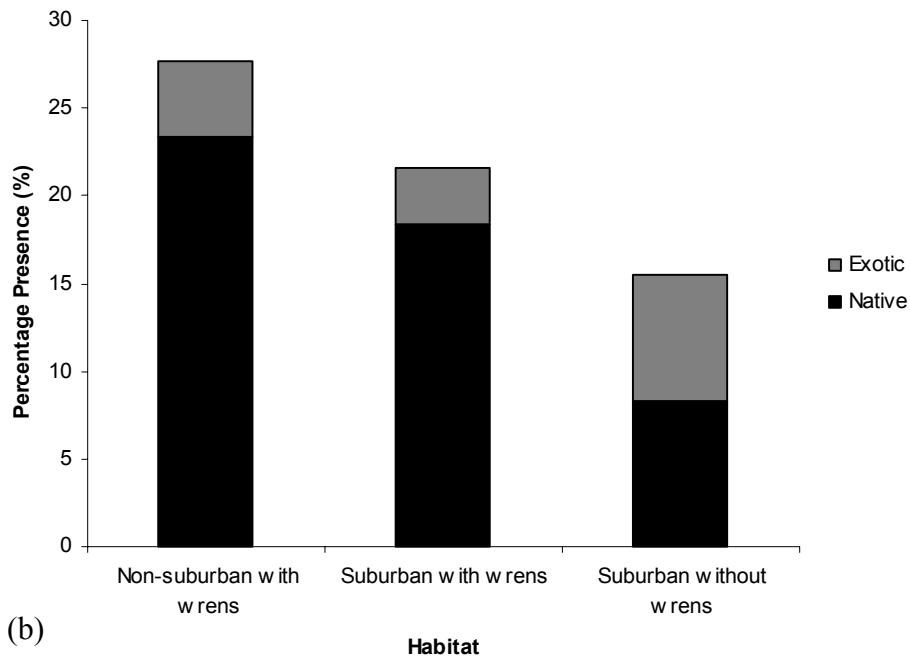
There was a high degree of variation between the non-suburban and suburban habitats, with the overall structure of the vegetation being significantly different between the three habitats (Global $R = 0.26$, $p = 0.001$; Fig 2.6a). All groups of sites showed significant clustering although suburban habitats with fairy-wrens had the most variation between sites (average similarity = 76.7%). This was contrary to our prediction that there would be the least amount of variation in suburban fairy-wren territories. Both the non-suburban fairy-wren sites and the suburban sites without fairy-wrens had a greater amount of similarity within their habitat types (average similarity non-suburban sites = 82.8%; suburban sites without fairy-wrens = 81.4%).

SIMPER analyses revealed that the availability of large amounts of short grass (contributing 23.0% to average similarity) and shrubs (19.9%) as well as the mid-

abundance of trees (15.9%) in suburban fairy-wren territories was most important in characterising suburban fairy-wren habitats. In non-suburban sites, having the greatest amount of shrubs (20.7%), only a small amount of short grass (19.3%) and lots of trees (16.9%) characterised this habitat type by contributing most to the average similarity. Suburban habitats without fairy-wrens were distinguished by a large amount of short grass, road and few trees (contributing 23.0%, 19.9% and 15.9% to the average similarity values).



(a)



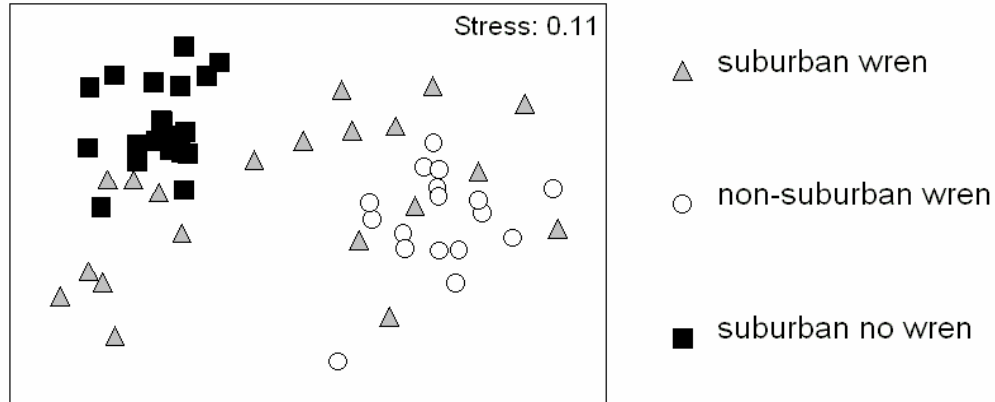
(b)

Fig 2.5: The proportion of introduced and native vegetation in (a) the shrub layer (native, exotic and lantana) and (b) the tree layer (native and exotic) sampled in 40 quadrats in non-suburban (rural/remnant edge) habitats with suburb fairy-wrens, suburban habitats with superb fairy-wrens and suburban habitats without superb fairy-wrens.

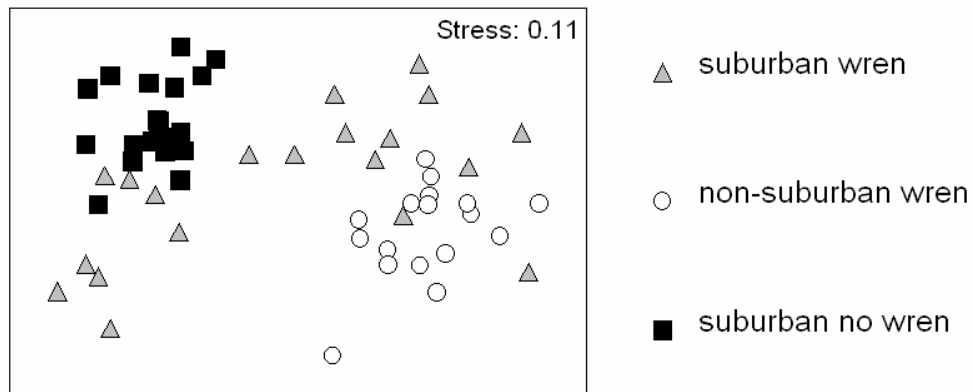
2.3.2.2 Floristic Origin

When floristic origin of plants was included in the models, the clustering pattern remained, suggesting that structure was more important than floristic origin in distinguishing between habitats (Global $R = 0.59$, $p = 0.001$; Fig 2.6b). Variability between suburban sites with fairy-wrens were still high compared to the other two habitat types (average similarity = 66.7%). Suburban sites without fairy-wrens and the non-suburban sites again had less variability (average similarity suburban without fairy-wrens = 84.5%; non-suburban = 82.3%).

Habitats also differed in how the structure of the vegetation available was influenced by floristic origin. The main distinguishing features of suburban sites with fairy-wrens was still short grass (mean % similarity contribution = 23.6%), however, when floristic origin was considered, it was the availability of native trees (15.2%) (as opposed to trees overall) and a low percentage of road (13.5%) that also contributed to the similarity between sites. When floristic origin was considered, shrubs did not become a distinguishing feature of suburban fairy-wren habitats. Non-suburban fairy-wren habitats were characterised by the dominance of lantana (17.5%), rather than shrubs overall, with the lack of short grass (16.9%) and an abundance of long grass (16.0%). The presence of a large percentage of trees did not contribute to the average similarity of non-suburban sites when floristic origin was considered. Floristic origin did not change the features that contributed most to the average similarity of suburban sites without fairy-wrens. These sites were again typified by an abundance of short grass (21.8%) and road (18.2%). Therefore when floristic origin of the shrubs and trees were considered, we see that lantana became an important component in non-suburban sites and native trees became distinctive of suburban sites with fairy-wrens.



(a)



(b)

Fig 2.6: Ordination (nMDS) of habitat variables in suburban fairy-wren, non-suburban fairy-wren and suburban no fairy-wren habitats (stress = 0.11). Habitat variables are based on (a) structure of the vegetation and (b) floristic origin. Points positioned more closely together to each other are more similar in the composition of their habitats.

2.4 Discussion

Determining habitat requirements for a species is vital for effective conservation, especially when the loss of habitat may be causing species decline. While this study

examined only the territories occupied for within a single-year, this species is sedentary, and individuals occupy the same territory over numerous years (Rowley and Russell 1997). Superb fairy-wrens showed clear vegetation preferences in suburban and non-suburban habitats with both structure and floristic origin influencing their occurrence. We found similarities between non-suburban and suburban sites with fairy-wrens. In both habitats they were found in sites with an extensive shrub and tree layer, however there was more short grass available in the suburban fairy-wren habitats and a greater proportion of long grass in the non-suburban habitats. In suburban habitats, fairy-wrens preferred areas with a larger proportion of native shrubs than exotic shrubs however in non-suburban habitats, lantana was the predominant shrub species. The availability of these different shrub types were found to be independent of each other in all habitats, suggesting that the presence of one type of shrub was not related to the presence of another. In both cases, native trees were also a preferred habitat feature.

Superb fairy-wrens were not found in suburban habitats that were poor in vegetation structure, with floristic origin also influencing their avoidance of these habitats. These sites demonstrated a high degree of similarity to each other, suggesting there is a particular characteristic of the habitat that the superb fairy-wrens are avoiding. These sites were dominated by man-made structures, with very few shrubs and trees, and what little vegetation was available was largely exotic. The large proportion of short grass available is a habitat feature that superb fairy-wrens like, however its availability must be in conjunction with a suitable native or lantana shrub layer. The availability of short grass in suburban habitats is due to mowing, which creates a flat surface that superb fairy-wrens use for foraging (Rowley and Russell 1997). It appears that this shrub layer is an important determinant in the presence of superb fairy-wrens in suburban locations, however lantana

has replaced native shrubs in non-suburban locations. Unlike my predictions, the greatest variability was actually seen in their suburban territories, suggesting that suburban habitats have greater structural and floristic diversity than non-suburban habitats and these birds are able to adapt to utilise these different vegetation parameters.

Vegetation structure is important for habitat selection by birds in urban areas (Lancaster and Rees 1979; Green 1984; Mills *et al.* 1989; Sewell and Catterall 1998; Fernández-Juricic 2001; White *et al.* 2005; Sandström *et al.* 2006). A high degree of habitat complexity, which involves a well developed ground, shrub and tree layer, increases the availability of foraging, shelter and nest locations for a range of species (Marzluff and Ewing 2001; White *et al.* 2005). However, it is the understorey layer in particular that is usually less prevalent in suburban locations (Savard and Falls 1981; DeGraaf and Wentworth 1986; Warkentin and James 1988; this study). White *et al.* (2005) found a loss of the insectivorous cover-dependant guild, which includes the superb fairy-wren, in the transition from native streetscapes to exotic and newly developed streetscapes was linked to the loss of suitable shelter locations. Research into the behaviour of superb fairy-wrens in suburban habitats has shown that they utilise a full spectrum of vegetation structures from the ground through to the canopy, however the majority of their time is spent in shrubs, which they also use as a nest site (Russell and Rowley 1997). The loss of shrubs in urban areas could therefore expose these birds to increased nest predation as well as a lack of shelter locations.

In traditional woodland habitats, many fairy-wren species are associated with a high density of shrubs such as brigalow (*Acacia harpophylla*), wandoo (*Eucalyptus wandoo*) and exotic shrubs such as lantana and other brambles (Nias 1984; Ligon *et al.* 1991; Nias and Ford 1992; Brooker and Rowley 1995; Chan and Augusteyn 2003) so it is unsurprising in

an urban setting that a similar habitat element is occupied. Further, a positive association between wrens and native vegetation was found in comparisons within urban areas, similar to studies elsewhere (Jones 1983; Green 1984; Catterall *et al.* 1989; Mills *et al.* 1989; Day 1995; Sewell and Catterall 1998; Parsons *et al.* 2006). Here, native shrubs were more prevalent in suburban wren territories and percentage of shrub occurrence was lower in suburban sites without fairy-wrens, where the proportion of exotic shrubs available was greater. It has previously been suggested that native birds may use exotic vegetation that is structurally similar to natives, in the absence of native vegetation (Emlen 1974; Mills *et al.* 1989), but only lantana appeared to be a favoured exotic in our study.

Structure is not the only aspect of native vegetation that may influence an insectivorous bird's vegetation preference. Native vegetation has been shown to support more invertebrate life than exotic shrubs and trees, and consequently, foraging birds have also shown a preference for native over exotic vegetation, though they will use both (Green 1984; Green *et al.* 1989; Daniels and Kirkpatrick 2006). However the effect of urbanisation on invertebrate communities is relatively unstudied. Urbanisation and habitat fragmentation may be potentially altering interactions between invertebrates and other organisms and therefore interfering with food web dynamics (Didmam *et al.* 1996; Gunnarsson and Hake 1999). This may explain the loss of many insectivorous bird species from Australian urban habitats.

Both suburban and non-suburban superb fairy-wrens showed a high affinity for the noxious weed lantana. It invades the edges of woodland and forest habitat and forms dense thickets, usually replacing the entire understorey. The value of lantana to a range of bird species both as a foraging and shelter location has previously been demonstrated (Crome *et al.* 1994). Here, as superb fairy-wrens forage largely on, or very close to the ground

(Tidemann 1983; Recher *et al.* 1985; Ford *et al.* 1986; Cale 1994), it is likely that lantana is providing the birds with a dense and protective understorey layer rather than a foraging site. The use of lantana by foraging insectivorous birds has not been investigated previously. In suburban locations, the presence of lantana is therefore likely to have a substantial influence on the ability of superb fairy-wrens to occupy a site. Where absent from a site, the availability of native shrubs elsewhere nearby is necessary in order to support this species. Given, its status as a noxious weed, lantana cannot and should not be planted to create habitat for superb fairy-wrens. However its value as habitat has implications for the removal of lantana, with replacement with similarly dense locally native equivalents necessary in order to retain suitable habitat for use by superb fairy-wrens.

Superb fairy-wrens are therefore likely to be limited in their distribution in urban environments due to a lack of suitable habitat. Some variability exists in habitat selection in fairy-wrens in suburban areas, suggesting they can occupy diverse habitat requirements, but superb fairy-wrens were generally utilising sites in suburban areas with a dense shrub layer (of either native plants or lantana) and surrounding grassy areas. If the characteristics of suburban habitats that this species requires are not commonly found throughout the urban matrix then we would expect that the distribution of superb fairy-wrens would be limited.

Increasing isolation of territories in urban areas is likely to have a significant effect on the population structure and breeding biology of this species. High rates of extra-pair paternity in continuous vegetation (Mulder *et al.* 1994), with males displaying to neighbouring females throughout the day and females leaving their territories pre-dawn to copulate with other males (Double and Cockburn 2000), occurs where territories are adjacent. Where territories are isolated, such as in these urban habitats, birds are likely to be restricted in their movements, resulting in an increase in monogamy. In addition, juvenile

females are expelled from their territories to establish new ones once they are no longer reliant on the adult birds. In an urban matrix that is largely unsuitable, these females are likely to be lost from the population and new territories would rarely be founded. In the majority of cases here, searches of the areas surrounding the suburban superb fairy-wren territories (approximately a 1 km radius) failed to locate neighbouring superb fairy-wren territories. There was only one instance in which another territory was located near a surveyed territory and a neighbouring male was observed displaying to the adult female. The enhancement of suburban habitats surrounding territories using native shrubs and trees could therefore increase connectivity between territories and potentially allow the distribution of superb fairy-wrens to proliferate through new territory establishment.

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CHAPTER THREE

The Effect of Urbanisation on the Size and Quality of Superb Fairy-wren (*Malurus cyaneus*) Territories

3.1 Introduction

The selection of suitable habitat is of great importance to an individual as habitat quality can directly impact upon fitness and reproductive potential (Cody 1985, Pärt and Doligez 2003). This is particularly the case for territorial species (those that defend an area from conspecifics), for which competition for good quality habitat is often high and there is potentially a large opportunity cost involved in abandoning a defended space in search of better resources. Individuals maximise their fitness by establishing a territory that is large enough to provide sufficient resources for foraging and breeding, while still manageable to defend from intruders. Increasing territory size has been correlated with greater nestling survival and a decrease in nest predation for monogamous birds (Krebs 1971; Harper 1985; Both and Visser 2000; Lopez-Sepulcre and Kokko 2005), while polygamous species show increased numbers of mates with larger territories (Davies and Lundburg 1984; Wimberger 1988; Langen and Veherncamp 1998).

Territory size can also be used as an indication of habitat quality. If territories are of a high quality, that is, contain high proportions of suitable vegetation and foraging resources, then territories may only need to be comparatively small as all requirements can be met in a smaller area. However, if territory quality is poor due to resources being patchy or widely distributed, territory size would be expected to be larger. This has been

demonstrated for a range of birds. For raptor species both food abundance and habitat quality were negatively correlated with territory size (Village 1982; Bloom *et al.* 1993; Marzluff *et al.* 1997; Leary *et al.* 1998). Similarly, black woodpecker (*Dryocopus martinus*) territories decreased in size with an increase in young plantation vegetation due to the prevalence of a preferred prey (ants) in this vegetation type (Rolestad *et al.* 1998). Spatial heterogeneity of resources has also been shown to influence territory size, as demonstrated by the northern flicker (*Colaptes auratus*) in which the distribution of foraging patches within home ranges had a large influence on their size (Elchuk and Wiebe 2003).

For cooperatively-breeding species where helpers assist in the raising of young, group size has been shown to vary positively with habitat quality (Nias 1984; Nias and Ford 1992; Chan and Augusteyn 2003). The more individuals that occupy a territory, the more resources are required and therefore the area needed to obtain these resources also increases (Nias 1984; Nias and Ford 1992; Brooker and Rowley 1995; Jansen 1999; Chan and Augusteyn 2003). Helper birds have been shown to delay their natal dispersal in higher-quality territories and reproductive potential may be increased as they have the possibility of later inheriting the natal territory. Therefore, a higher-quality territory may be required to support larger numbers of birds and these birds may be better able to defend a larger territory than a smaller group of birds. In poorer territories there is little incentive to remain in a location with lower reproductive success and group size may be expected to be smaller (Ligon *et al.* 1991).

Habitat quality can also have a large influence on the relationship between group size and territory size for cooperatively-breeding species. Groups must find an optimal territory size that maximises the number of individuals but also meets their resource requirements with minimal cost of defence. Larger territories are predicted to occur more

often in resource-poor environments than in higher-quality habitats. However, as the higher-quality habitat can support more individuals per territory, there may be an associated increase in territory size. When the same numbers of individuals are present in each, it might be expected that the optimal territory size would still be smaller in higher-quality habitats.

Understanding the response of populations to the varying quality of urban habitat becomes increasingly more important as urban expansion continues and large areas of native habitat are removed and fragmented. Species from forests and woodlands that are tolerant of urban areas are exposed to a highly fragmented habitat containing a mosaic of patches through which individuals have to disperse and colonise in order to establish new territories. Birds may potentially be restricted in territory size by the amount of suitable vegetation available and may variably respond to changes in structure and floristic characteristics of planted vegetation which are different from the native state (Green 1984; Green *et al.* 1989; Lenz 1990; Sewell and Catterall 1998).

The urbanisation of a landscape results in changes to the patterns of resource availability and influences habitat utilisation, affecting foraging behaviour and breeding success (Hansson *et al.* 1995; Marzluff 2001; Rubin *et al.* 2002; Fleischer Jr *et al.* 2003). Corvids, omnivores and nectarivores have increased in number in some urban areas as their foraging resources are increased by these shifts in vegetation types (Emlen 1974; Bessinger and Osbourne 1982; Rosenburg *et al.* 1987; Blair 1996; Parsons *et al.* 2006). Insectivorous species however are often unable to successfully make the transition into urban areas or are comparatively rare (Emlen 1974; Catterall *et al.* 1991; Sewell and Catterall 1998; Cooper 2002; Parsons *et al.* 2003, 2006). While exotic plants are thought to support fewer invertebrate species than native plants, suburban lawns can provide an abundant and

consistent food source, as well as an easy foraging substrate (Falk 1976; Rosenberg *et al.* 1987) for species that include ground foraging in their behavioural repertoire. Therefore, it might be expected that ground foraging insectivores should be able to live successfully in urban habitats because the quality of the foraging resources available to them would be higher.

Superb fairy-wrens (Maluridae: *Malurus cyaneus*) are small (9 - 11 g) territorial insectivorous passerines whose response to urbanisation is unclear. In their natural range, they occupy patchy forests where they are opportunistic foragers, being flexible in the selection of feeding substrate and habits (Tidemann 2004). In fragmented forest habitats superb fairy-wrens have been shown to prefer the edges as opposed to the interiors of patches (Rowley and Russell 1997; Berry 2001). They are found in gardens and suburban areas, particularly in the major cities of southeastern Australia. However, in the greater Sydney region they are now relatively uncommon (Hoskin *et al.* 1991). It is likely that their foraging flexibility has allowed them to make the transition into some suburban areas, but reasons for their relative rarity are unknown.

Estimates of territory size for the superb fairy-wren have varied with habitat type and quality. The largest measurements of territory size were recorded in Taunton National Park (Central Queensland) (8.6 ± 3.7 ha) in recently disturbed regrowth sites (Chan and Augusteyn 2003). It was thought that the limited availability of resources resulted in large areas of unused habitat and large territories. In fragmented rural and remnant patches of woodland, territories are much smaller (1 – 2 ha) (Tidemann 1983; Nias 1987) but larger than those at the National Botanic Gardens (0.6 ha) (Mulder 1992). Whilst located in an urbanised environment, the National Botanic Gardens consist of approximately 40 ha of

continuous Australian native vegetation (Mulder 1992) and so are very different from habitat usually located within the urban matrix. Territory quality was considered to be high, based on the availability of understorey shrubs and other suitable vegetation, and consequently territories were small and saturated the entire site (Mulder 1992). Understanding variation in the territory size of the superb fairy-wren in urban environments may allow us to gain a better understanding of the relative quality of urban habitat.

3.2 Materials and Methods

3.2.1 Study-sites

This single-year study was conducted during the breeding season for superb fairy-wrens (December – March 2004) in urban and remnant woodland habitats of the Wollongong and Kiama Local Government Areas, NSW Australia (34.26 S, 150.53 E). Urban sites with resident superb fairy-wrens were identified from records reported by local residents following local publicity. Sites with superb fairy-wrens on the rural/remnant edge were selected such that they were near, preferably in the same suburb as, the urban sites.

Because the birds roamed over numerous privately-owned (and fenced) residences, focal birds could not always be followed visually to identify territory boundaries. Instead, each bird was fitted with a small radio-transmitter and the point locations of focal birds were determined by triangulation from moving base-stations operated by two observers.

Due to the labour-intensiveness of this method, only two territories could be monitored simultaneously. Thus each pair of sites (an urban and its paired rural/remnant site) was monitored sequentially for 4 - 6 days over a ten-week period.

3.2.2 *Radio-telemetry*

Adult female superb fairy-wrens (identified by a greenish tinge on the tail) were captured using a combination of call play-back and mist netting. Only females were used, as they were more likely to stay within their own territory during daylight hours than the males, which frequent neighbouring territories to display to other females (Mulder and Magrath 1994). Only those females weighing 9.5 g or more were fitted with radio transmitters to ensure that the transmitters weighed no more than 4% of the total body weight of the individual. A range between 3 – 5% of body weight is less likely to interfere with the behaviour and survival of the birds (Naef-Daenzer 1993).

Single-stage radio transmitters including a mercury battery weighed 350 mg and were set to a unique frequency within the 172-173 MHz range (Titley Electronics). This range ensured that outside electrical interference from a range of sources, particularly in the urban areas, was minimised. Due to its small size, the maximum battery life was 12 days, although in practice, transmitters could not be relied upon to transmit for more than seven days. The radio-transmitter itself had a whip-style transmitting aerial and was fitted with 2 shrink-fit tubes at either end to allow a leg-harness design (or hip-pack) to be used to attach it to the bird. This method has been used successfully in a range of small passerines and is less likely to alter foraging, reproductive and social behaviour than a back-pack harness which can restrict movement (Rappole and Tipton 1991; Bowman and Aborn 2001). Vicryl, dissolving suture material, was threaded through the tubes to create two loops. One loop was threaded over the leg and up as far as possible on the thigh and tightened. The transmitter was then positioned over the synsacrum and the second loop threaded over the other leg to the top of the thigh and tightened till both loops were firm and not liable to

entangle the bird, but also not going to cut into the legs. To test this a matchstick was placed between the bird and the loop until the thread was tied, knotted and secured with super glue and the excess thread cut off. Freedom of movement of each bird's wings and legs was tested before the bird was released. Birds were followed after they were released and all were observed preening around the transmitter for a short time afterwards. Data was not recorded on the day of capture but during surveys on each subsequent day, the focal bird was sighted to ensure that there were no adverse effects of the transmitter attachment. Birds were tracked using hand held collapsible three-element Yagi antennae with Regal 2000 portable receivers (Titley Electronics).

Data were recorded on ten birds located in suburban areas near residential housing and eight in non-suburban habitats located along remnant/rural edges (transmitter failure prevented the inclusion of two non-suburban territories). Triangulation "stations" were marked at distances of 20 m throughout the area occupied by the superb fairy-wrens and the latitude and longitude of each station was recorded using a GPS (later converted to Australian Map Grid reference points - AMGs). Because the transmitters had a short battery life, we attempted to maximise the number of fixes we could obtain on each bird by recording its location every five minutes using bearings taken from the stations on either side of the putative location of the bird. Birds were monitored for an hour at a time (approx 12 fixes) alternating between the birds at each of the two sites, such that there were between three and four hours of data for each bird per day. The birds were detected visually on many occasions during the recording period, and the size of the group with which the female was associated was determined from these observations.

Common methods of analysing territory sizes require the data to be statistically independent. Autocorrelation of data points can be a concern when subsequent positions are

recorded within a short period of time. However the risk of autocorrelation has been found to be acceptable when territory size is relatively small and the animals have the ability to traverse the territory within the sampling interval (Holzenbein and Marchinton 1992; McNay *et al.* 1994). This was the case for superb fairy-wrens. Furthermore, the effect of autocorrelation is strongly related to the number of fixes obtained (Schroder 1979; Anderson 1982; White and Garrott 1990). Here, a minimum of 150 fixes were recorded for each bird, taken over several days. Therefore, any effect of autocorrelation is considered to be minimal. As a further precaution, data obtained from each one-hour recording session were mapped separately, showing that they were scattered and not clustered and isolated from subsequent sample periods.

Upon completion of the radio tracking, the locations of the stations used, the time at which each position was recorded and the bearings from these stations were entered into the Locate II program (Vilis O. Nams, Pacer Computer Software). This program triangulates radio telemetry bearings to give a location of the organism throughout the tracking period. Once the locations of the birds were obtained the outputs from the Locate II program were exported into the ArcView 3.3 GIS program (ESRI, Redlands, CA) and converted to a series of points overlain on a cadastral street map of the entire area. The Animal Movement Analysis Program (Hooge and Eichenlaub 1997) and Spatial Analyst Extensions of Arcview GIS were used to create polygon shapefiles used for territory size analyses.

3.2.3 Territory Size and Shape Estimates

The minimum convex polygon (MCP) (Mohr 1947) is the most commonly used estimate of territory size whereby the outermost locations are simply joined by straight lines

(Mohr 1947). Whilst this method allows comparisons between other studies, it has a tendency to over-estimate territory size as it includes potential outliers and large areas unlikely to be used by the bird (Harris *et al.* 1990). Here the 95% convex polygon is used rather than 100%, to reduce the effect that any outliers might have had (Jansen 1999; Seddon *et al.* 2003; Radford and du Pleiss 2004).

Another non-parametric estimate of territory size is the fixed kernel distribution (with least-squares cross validation ‘LSCV’) (Worton 1987). This method of examining utilisation distributions looks at the frequency distribution of the animal’s locations and produces an isopleth at the area where the designated proportion of time is spent (Worton 1987). It therefore indicates how intensively different areas of the territory are used, something that MCP analysis cannot examine. The fixed kernel analysis (LSCV) is generally considered to be the best territory analysis method currently available (Seaman and Powell 1996; Kernohan *et al.* 2001). It is non-parametric, robust to autocorrelation, works well with small amounts of data (minimum of 50 fixes) and allows multiple areas of core activity (Kernohan *et al.* 2001). The 95% isopleth is used here to represent the location where each bird spent 95% of its time (Worton 1987; Harris *et al.* 1990; Hodder *et al.* 1998; Elchuk and Wiebe 2003).

Using both methods allowed comparisons of their effectiveness in identifying differences in territory size as well as providing more detailed information about territory usage (Van Winkle 1975; Worton 1987). While the MCP calculation represents the outermost boundaries of the birds’ range, the fixed kernel method indicates the actual usage patterns. If the fixed kernel calculation is the same as the MCP calculation then birds are using the entire territory, however, if the fixed kernel calculation is smaller, then the birds

are using only part of their territory with any regularity and the MCP calculation is overestimating territory size by incorporating unvisited habitat within the boundaries.

Whilst the birds may occupy territories of similar size, differences in the two habitats, such as the presence of high-traffic roads in suburban sites might alter or restrict the shape of territories. To examine this possibility the perimeter to area ratio was calculated using the Edge Index (EI): $EI = \text{Perimeter} / 2\sqrt{(\text{Area} \times \pi)}$ (Patton 1975). Territories are more circular in shape as this value approaches 1.

Given that MCP and fixed kernel calculations were not independent as they were conducted on the same territory, analyses of territory size and shape estimates between the suburban and non-suburban habitats were conducted separately using t-tests. Data remained untransformed after testing for normality. In order to test whether there was a difference between the two methods for the suburban and non-suburban sites a t-test was also performed on the data, calculated by subtracting the 95% fixed kernel from the 95% MCP for each site. Regression analysis was used to determine whether group size was related to the size of territories that the birds were occupying. Differences between group sizes in suburban and non-suburban habitats were also tested with a t-test.

3.2.4 Vegetation Assessment

The 95% MCPs and 95% fixed kernel distributions were overlaid on digital aerial photographs of the substrate using Arcview GIS. Broad habitat characteristics were measured by looking at the percentage of each territory occupied by man-made structures (houses, roads and driveways), grass and shrubs/trees. This was calculated by digitizing the boundaries of each characteristic and calculating these as the percentage of total territory.

To determine whether differences in these broad habitat characteristics could predict the presence of superb fairy-wrens, a series of random suburban ‘non-territories’ (i.e. locations where superb fairy-wrens were known not to occur) were also paired with the suburban territories. Thorough searches, incorporating song play-back, were conducted in each non-territory to confirm that superb fairy-wrens did not occupy the ‘territory’ allocated. Each non-territory was simulated from the 95% MCP and 95% fixed kernel distributions of its paired territory, which was within 5 kms. The MCP and fixed kernel distributions were transposed on the same location in the same orientation as the original. The same vegetation assessment was made using the aerial photographs, with the percentage of man-made structures, grass and shrubs/trees measured.

T-tests were used to determine whether the physical structure of the territories (man-made, lawn and shrubs/trees) in suburban habitats was similar to non-suburban territories or to the suburban ‘non-territories’.

3.3 Results

3.3.1 Territory Size and Shape

The 95% MCP method of territory size estimation showed a difference in territories between the two habitats. In suburban habitats, territory sizes based on the 95% MCP method ranged from 0.5 ha to 2.5 ha and averaged 1.4 ha (± 0.3 ha). Non-suburban territories were significantly larger, ranging in size from 1.2 ha to 4.3 ha (mean 2.6 ha ± 0.5 ha) ($t_{17} = 2.3$, $p = 0.042$) (Fig. 3.1).

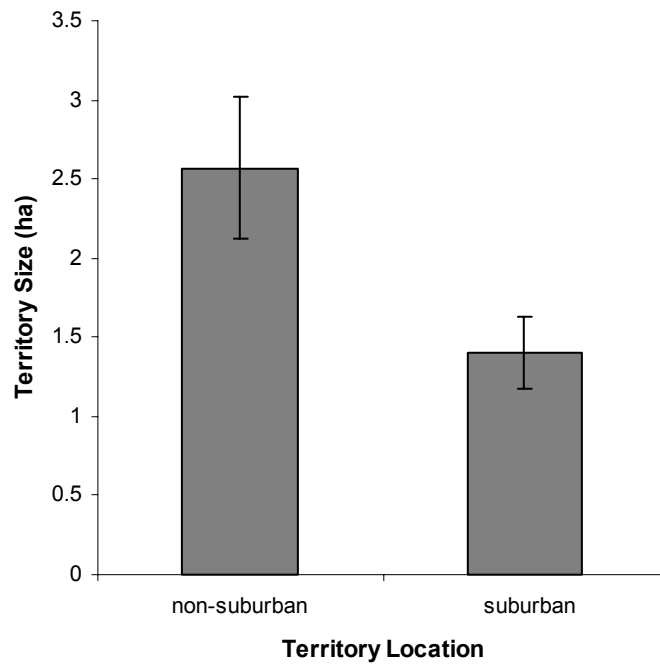


Fig 3.1: The mean size of superb fairy-wren territories in non-suburban and suburban sites calculated using the 95% minimum convex polygon method. Error bars show standard error.

Using the 95% fixed kernel method, territories in suburban habitats were also smaller than those in non-suburban habitats, but these differences were not statistically significant ($t_{17} = 0.9$, $p = 0.43$). Suburban territories had a mean size of $1.4 \text{ ha} \pm 0.3 \text{ ha}$, similar to that calculated using the MCP method, and ranged in size from just 0.07 ha to 2.6 ha. However, territories in non-suburban habitats were smaller than when using the MCP calculation, averaging $1.7 \text{ ha} \pm 0.1 \text{ ha}$ and ranging from 0.9 ha to 3.6 ha. The difference between the MCP and fixed kernel method was significantly larger in non-suburban habitats than in suburban habitats ($t_{16} = 2.5$, $p = 0.03$) (Fig. 3.2).

The shapes of the territories were not significantly different between habitats ($t_{17} = 0.65$, $p = 0.5$). Mean edge index average was 1.1 ± 0.04 in both habitats suggesting that territories were near circular in shape.

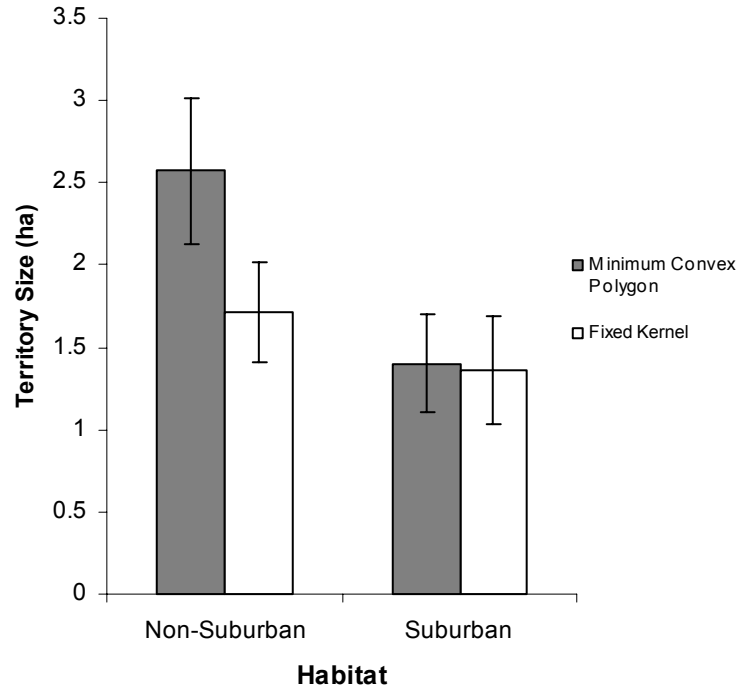


Fig 3.2: The mean sizes of superb fairy-wren territories in suburban and non-suburban habitats calculated using the 95% minimum convex polygon method and the 95% fixed kernel distribution method. Error bars show standard error.

3.3.2 Group Size

Each of the female superb fairy-wrens inhabited a discrete territory that she shared with between 2 and 10 other birds (suburban mean = 4.1 ± 2.2 ; non-suburban mean = 4.6 ± 2.0). There was no statistical difference between the group size in each territory in suburban and non-suburban territories ($t_{17} = 0.51$, $p = 0.61$). Group size was not related to territory

size, regardless of whether it was calculated using MCP or the fixed kernel method (MCP $F_{1,16} = 0.26$, $p = 0.61$; kernel $F_{1,16} = 0.67$, $p = 0.43$). Similarly, when each habitat was analysed separately, group size did not influence territory size (suburban MCP $F_{1,8} = 0.04$, $p = 0.84$; suburban kernel $F_{1,8} = 0.01$, $p = 0.94$; non-suburban MCP $F_{1,6} = 0.03$, $p = 0.86$; non-suburban kernel $F_{1,6} = 2.37$, $p = 0.17$).

3.3.3 *Vegetation Characteristics*

Not surprisingly, the structure of the vegetation in suburban and non-suburban territories was significantly different (Table 3.1). The difference was primarily due to suburban habitats having significantly more man-made structures (MCP $t_{16} = 2.8$, $p = 0.01$; fixed kernel $t_{16} = 2.4$, $p = 0.03$). However the percentages of open grass areas were similar in both habitat types for both the MCP and fixed kernel territories (Table 3.1). While there were significantly more shrubs/trees in non-suburban MCP territories than in suburban MCP territories ($t_{16} = 2.3$, $p = 0.04$), there was no significant difference when analysed using fixed kernel territories (Table 3.1).

There was no significant difference between the suburban territories and suburban non-territories for each of the habitat variables examined in both the MCP and fixed kernel territories (Table 3.2).

Table 3.1: Average percentage cover (\pm standard deviation) of habitat variables in non-suburban and suburban territories of superb fairy-wrens. Probability values (p) of two-tailed t-tests are presented. Significant differences are in bold.

Territory Type	Variable	Non-Suburban Territories	Suburban Territories	P df=16
MCP	Man-made	11.1\pm3.8	33.4\pm22.3	0.013
	Grass	22.0 \pm 18.4	26.9 \pm 10.5	0.490
	Shrubs/Trees	64.3\pm21.6	39.7\pm23.4	0.036
Fixed Kernel	Man-made	13.3\pm6.4	31.7\pm21.2	0.031
	Grass	25.1 \pm 21.4	26.4 \pm 13.0	0.872
	Shrubs/Trees	61.6 \pm 18.4	41.6 \pm 27.5	0.101

Table 3.2: Average percentage cover (\pm standard deviation) of habitat variables in suburban superb fairy-wren territories and suburban territories without superb fairy-wrens. Probability values (p) of two-tailed t-tests are presented. Significant differences are in bold.

Territory Type	Variable	Suburban Territories	Suburban Non-territories	P df=16
MCP	Man-made	33.4 \pm 22.3	42.4 \pm 6.2	0.233
	Grass	26.9 \pm 10.5	23.2 \pm 7.7	0.388
	Shrubs/Trees	39.7 \pm 23.4	34.3 \pm 10.4	0.513
Fixed Kernel	Man-made	31.7 \pm 21.2	34.7 \pm 13.6	0.713
	Grass	26.4 \pm 13.0	17.8 \pm 8.6	0.095
	Shrubs/Trees	41.6 \pm 27.5	47.5 \pm 20.1	0.605

3.4 Discussion

Suburban territories were significantly smaller than non-suburban territories when calculated using the minimum convex polygon (MCP) method of analysis. Inverse relationships between territory size and habitat quality are expected when quality is strongly influencing the area utilised. It is therefore possible that these suburban territories are of

higher quality than the non-suburban fragmented rural habitats. Previous estimates of territory quality, represented by food availability have reflected this negative relationship in raptors (Village 1982; Bloom *et al.* 1993; Marzluff *et al.* 1997; Leary *et al.* 1998), woodpeckers (Rolestad *et al.* 1998; Bonar 2001) and ovenbirds (Smith and Shugart 1987). Changes in territory boundaries that reflect resource fluctuations are more likely to be observed in habitats where territories do not saturate the site. In saturated habitats the costs associated with redefining and defending changing territory borders is likely to be costly for the group (Luck 2002). Here, neither habitat appeared saturated by territories, but in two cases in non-suburban sites and one instance in suburban habitat, there were adjacent territories occupied by other groups of superb fairy-wrens (H. Parsons *pers obs*).

There was no relationship between group size and territory size for either suburban or non-suburban sites. Groups in cooperatively-breeding birds arise because the surviving juveniles from a clutch remain within the family group to assist in raising subsequent young (Brown 1987). Groups monitor and adjust territory sizes to ensure that availability of resources can support the energy requirements of all group members (Armstrong 1965; Simon 1975; Salmonson and Balda 1977; Brown 1982; Jansen 1999; Brouwer *et al.* 2006). In addition, helpers from good quality territories are likely to delay their dispersal from these territories because there are sufficient resources to support them and an opportunity to inherit the territory in the future. Helpers in poor quality territories have little incentive to stay and therefore total numbers of individuals are likely to be lower. In previous studies of cooperatively breeding species, including the superb fairy-wren, there has been a positive relationship between group size and territory size, as larger numbers of individuals require greater resources (Nias 1984; Komdeur 1992; Nias and Ford 1992; Langen and Vehrencamp 1998; Chan and Augusteyn 2003). However this trend was not seen in this

situation (Table 3.3). On average, group size was larger here (between 2 and 10 individuals) than has been recorded previously (between 2 to 6 individuals), but territory sizes are similar to calculations from previous research (Table 3.3). Neither of the two habitats examined were saturated (H. Parsons *pers obs*), so potentially, the territories are simply expanding to a size able to support all the birds. Alternatively, if there were patches of unsuitable habitat surrounding the territories, and as the territories themselves appear to be of good quality, there may be little incentive for juveniles to leave, provided resource requirements are met. By remaining within a territory and assisting to raise other young, the reproductive potential of these birds might actually be improved, especially if there is the opportunity to inherit the territory, regardless of whether they are related to the dominant pair's offspring (Dunn and Cockburn 1996; Cockburn 2007). The extremes in territory size, overly large and very small territories were also not evident in the sites observed (given small standard errors) and the sample size is small ($N = 18$), therefore the relationship between group size and territory size may have been masked.

Table 3.3: Comparisons between mean territory and group sizes recorded for superb fairy-wrens in a range of locations throughout eastern Australia.

Please see print copy for Table 3.3

The accuracy of the calculation of territory size was largely influenced by the method used. The difference in territory size was significantly larger in non-suburban habitats, with MCP territories larger than those calculated by the fixed kernel method. The MCP represents the outermost boundaries of the birds' range whilst the fixed kernel method indicates the actual usage patterns. Therefore it appears that the 95% MCP was overestimating the area used by the superb fairy-wrens by encompassing more unvisited habitat than the fixed kernel method. Previous studies have also examined the relative merits of different territory calculators (Van Winkle 1975; Worton 1987). Estimates of breeding densities of the migratory passerine *Dendroica cerulea* also highlight the more accurate calculation of territory size obtained through the fixed kernel method as opposed to the MCP (Barg *et al.* 2005). This then provides more accurate measures of vegetation utilisation within the territory. However in suburban habitats, territory size was similar regardless of the method used to calculate it, indicating that birds were not making extra forays into largely unused edges of territories. This suggests that suburban habitats were of higher quality as birds were maximising habitat usage within their territories rather than seeking extra areas outside their usual area of usage.

Alternatively, birds may occupy smaller territories in suburban habitats because movement is more difficult. Roads are known to cause high mortality of birds, including the superb fairy-wren, in urban landscapes (Sherwood *et al.* 2002; Ramp *et al.* 2006). In some instances, roads have become a barrier, restricting the permeability of a landscape and leading to resource inaccessibility. Those who avoid roads reduce their access to mates, food and suitable vegetation (Mader 1984; Dunning *et al.* 1992). Similarly, predator-avoidance behaviours may result in birds staying away from areas of high human activity (Fernández-Juricic *et al.* 2003; O'Neal Campbell 2006) or domestic pets (Baker *et al.* 2005;

Langston *et al.* 2007). However, if birds were less likely to move due to physical restrictions, then we would expect to have seen a difference in the shape of territories in suburban habitats compared to non-suburban habitats. Suburban territories would show marked boundaries along roads or other avoided locations, and the shape would be expected to be more linear, following these boundaries. Territories in both habitats were almost round in shape. Therefore it is unlikely that territory size in suburban habitats is smaller due to avoidance of undesirable habitat for this species, instead, birds appear to utilise all habitat within their territories.

Sizes of the territories in both suburban and non-suburban sites were similar to superb fairy-wren territories located in continuous high quality habitats elsewhere (Table 3.3). In the woodlands of the National Botanic Gardens, high quality habitat resulted in the area being saturated with superb fairy-wren territories of just 0.6 ha (Mulder 1992). Territories of 1.25 ha and 1 - 2 ha were also recorded in rural fragmented habitats, where not all available habitat was suitable (Tidemann 1983; Nias 1987). However, limited resources in fragmented acacia woodlands resulted in territory sizes of 8.6 ha (Chan and Augustyn 2003). Given the similarity of territory sizes here (suburban: 1.4 ha both MCP and fixed kernel; non-suburban: 2.6 ha MCP and 1.7 ha fixed kernel) to other comparatively high quality habitats in fragmented environments it appears both these urbanised environments provide good-quality habitat in which this species can successfully live and potentially expand its range.

Broad-scale vegetation characteristics could distinguish suburban territories from non-suburban territories but could not define a suburban superb fairy-wren territory from other suburban habitat. In Chapter 2, more detailed and small-scale vegetation assessments were conducted that were able to characterize suburban superb fairy-wren territories. Here,

vegetation types could not be distinguished and therefore ‘shrubs/trees’ included vegetation of various heights and floristics. With the exception of the presence of man-made structures within suburban territories, superb fairy-wrens appear to be utilizing two habitats with similar vegetation characteristics. Superb fairy-wrens forage predominantly in open spaces on the ground (Recher *et al.* 1985; Ford *et al.* 1986; Cale 1994). In this study grass occupied approximately 25% of each of the territories, regardless of whether the MCP or fixed kernel method was used. There was a greater proportion of shrubs/trees in the MCP non-suburban territories than in the MCP suburban territories. Whilst this was also the case for the fixed kernel method, the difference was not significant. This suggests that there may be vegetated areas that are unused by the non-suburban superb fairy-wrens. Alternatively, the smaller amounts of vegetation within suburban territories may be different in structure or composition and provide ample cover and/or foraging resources to support the wrens in a smaller territory. The importance of suitable shrub cover for superb fairy-wrens has been demonstrated in other studies of this species. The size of territories has been related to the presence of wandoo trees and reproductive success correlated with the availability of bramble cover (Nias 1984; Ligon *et al.* 1991; Nias and Ford 1992; Brooker and Rowley 1995). This study did not examine the type of vegetation, its structure or composition, all variables that may effect superb fairy-wren habitat selection.

The sizes of a superb fairy-wren territory in these fragmented habitats may be determined largely by the density and quality of resources within the habitat rather than simply be a consequence of the number of individuals or demographic factors within the group. This study did not uncover specific habitat characteristics that distinguished a superb fairy-wren territory from other suburban areas. However, our new information on territory size in an urban environment relative to non-urban environments supports the contention

that the urban environment provides high quality habitat for small, ground-feeding insectivores, and may prove valuable in the absence of significant tracts of native vegetation.

3.5 References

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CHAPTER FOUR

Habitat Modification and its Effects of Foraging Behaviour and Habitat Use of Superb Fairy-wrens (*Malurus cyaneus*)

4.1 Introduction

Disturbances in natural habitat result in changes to patterns of resource availability and habitat structure, creating mosaics of optimal and sub-optimal patches (Hansson *et al.* 1995). Only those species with a pre-adaptation to the new replacement habitats are able to exploit the resources within this new environment (Marzluff *et al.* 2001). Urbanised landscapes are an example of such a newly-created habitat. Consequently a sharp decline in the presence of native fauna in urbanised zones has been documented throughout the world (Emlen 1974; Dickman 1994; Rebele 1994; Keast 1995).

Despite this, the contribution of urban habitats to the conservation of biodiversity has also been recognized (Savard *et al.* 2000; Marzluff *et al.* 2001) as urban areas do contain some semi-natural and natural habitats such as parks, remnants of native vegetation, gardens and other green spaces that are able to support a range of species (Lancaster and Rees 1979; Tomialojc 1998; Savard *et al.* 2000; Koenig *et al.* 2001; Cornelis and Hermey 2004; Parsons *et al.* 2006). Garden habitats represent an environmental midpoint between a natural habitat and a highly urbanised one, and so the community it supports can be quite different from the adjacent natural habitat as well as highly urbanised zones (Jones 1981; Beissinger and Osborne 1982; Green 1984; Munyenymbe *et al.* 1989; Blair 1996; Cannon

1999). Thus, while the suburban environment may be considered to be sub-optimal, some species are able to successfully utilise this habitat.

Adaptation to suburban habitats appears linked to some life history characteristics such as foraging and nesting. Granivorous and omnivorous species are characteristic of urban and suburban bird assemblages (Emlen 1974; Case 1996), although a range of nectarivores have also increased in abundance in Australia as a result of nectar-producing plants being planted commonly in gardens (Green 1984; Lenz 1990; Sewell and Catterall 1998; French *et al.* 2005). Insectivores however, are generally underrepresented in urban avifauna (Marzluff 2001; White *et al.* 2005).

Little research has examined underlying mechanisms determining the presence of a species in suburban landscapes although it is suggested that bird interactions (Parsons *et al.* 2006) and resource availability (Emlen 1974; Bolger 2001) may be important. Under changed resource levels in urban habitats there should be a change in behaviour and habitat utilisation by species. Florida scrub –jays (*Aphelcoma coerulescens*) forage more efficiently in suburban areas due to the availability of supplementary food, promoting earlier nesting in suburban habitats (Fleischer Jr *et al.* 2003). However, for insectivorous species, where supplementary food is less often available, birds are instead reliant upon food occurring naturally in the vegetation.

Habitat fragmentation and modification associated with urbanisation has generally been linked to the loss of invertebrate diversity and abundance worldwide as well as shifts in community composition (Pyle *et al.* 1981; Clark and Samways 1997; McIntyre *et al.* 2001). However Jokimäki *et al.* (1998) found a decrease in arthropod abundance, small arthropods, flying arthropods and Coleoptera from the edge of fragmented remnants through to the interior (Jokimäki *et al.* 1998). Insecticide use has previously been linked to the

decline of insectivorous birds due to both the direct effect of consuming insecticide-affected arthropods (Mineau *et al.* 2005; Hart *et al.* 2006) and also the indirect effect of food shortages (Rands 1985; Morris *et al.* 2005). Nest productivity of American robins (*Turdus migratorius*) and the number of lawns surrounding the nest that had used chlorpyrifos previously, have been shown to be correlated with a decline in earthworm numbers and biomass (Decarie *et al.* 1993). The foraging intensity of yellowhammers (*Emberiza citronella*) reflected the reduced abundance of invertebrate food available due to insecticide spraying in farmland habitat in England and also had an impact on nestling body condition (Morris *et al.* 2005). Other regular disturbances such as mowing would also be expected to have an impact upon both the arthropods themselves as well as those dependent on them as a food source. Conversely, watering of lawns and application of fertilizer may increase the productivity of urban gardens and therefore the abundance of arthropods (Falk 1976). However, given the visibility of short grass for foraging, arthropod size would be expected to be small, as larger individuals would be removed from the system. Overall, arthropod biomass on short grass in suburban areas is likely to be impacted by maintenance efforts, either negatively as a result of extensive clearing, insecticide use, the maintenance of short grass and fewer patches of shrubs or positively by watering and fertilisers. These impacts would have a strong influence on the foraging behaviour of ground and shrub foraging insectivores leading to lower densities in suburban areas.

Suburban habitats may also promote changes in behaviour because organisms experience increased disturbances or perceive predation risks. The direct impact of human traffic in suburban areas is likely to affect the ability of some bird species to utilise vegetation, which will affect foraging. Patterns of habitat selection in modified environments have been related to the presence of people (Fernández-Juricic and Schroeder

2003). However the risk of predation for bird species in urban environments has been shown in some instances to be very low (Shochat *et al.* 2004). Low pedestrian presence during the day may allow birds to conduct foraging and nesting behaviours with little impact on their fitness, minimising any perceived risks (Fernández-Juricic and Schroeder 2003). Birds also face real predation risks from cats (Trueman 1990; Barratt 1997, 1998) and other birds such as the pied currawong (*Strepera graculina*), a known predator of small birds, eggs and nestlings, whose numbers have increased substantially as a result of human changes to the environment (Bass 1995; Major *et al.* 1996). Harassment from dominant birds, such as the aggressive noisy miner (*Manorina melanocephala*) may also change habitat use and behaviour in urban areas, as this species now occurs in unnaturally high numbers.

The aim of this study is to investigate behavioural and foraging differences between birds inhabiting urban and more “natural” habitats, to determine the relative quality of the suburban environment for insectivorous bird species. This will improve our understanding of bird responses to urbanisation, providing guidance to instigate appropriate remediation measures. For this study I chose to investigate an insectivorous species, the superb fairy-wren (Maluridae: *Malurus cyaneus*).

The response to urbanisation of the superb fairy-wren is unclear. Its distribution extends throughout eastern and southeastern Australia from the coastline to the western plains (Rowley and Russell 1997). While most of the traditional superb fairy-wren habitat of open woodlands has been replaced by agricultural and suburban developments, this species has been shown to prefer the edges of fragmented habitats rather than the interior of remnants (Rowley and Russell 1997, Berry 2001). Therefore, in some instances, this species

has shown a positive response to strong habitat modification, with an increase in recording rates noted between the 1977-1981 and 1998-2002 survey periods in the most recent *Atlas of Australian Birds* (Barrett *et al.* 2003). Superb fairy-wrens are found in gardens and suburban areas, particularly in the major cities of southeastern Australia, but Barrett *et al.* (2003) found the increases in recording rates were due to observations in regional central Queensland rather than along the urbanised coastline, where no significant population change was observed.

Superb fairy-wrens are highly territorial and sedentary. Occupants of a territory generally consist of a pair of adults or social groups consisting of a breeding female, primary adult male and up to 5 younger males, usually from previous clutches (Rowley 1965). These males act as helpers to raise subsequent broods and all members take part in territorial defence, usually in the form of song battles. Most singing occurs throughout the early morning and evening, though some singing can be heard throughout the day (Rowley and Russell 1997). Further, males are the only members of the species that give a Type II call, a call triggered by the call or presence of potential predators (Langmore and Mulder 1992). This vigilance behaviour announces the presence of the male and may serve to demonstrate fitness or lure potential threats away from the rest of the family group (Rowley and Russell 1997). Both sexes take part in territorial defence but despite being socially monogamous, superb fairy-wrens have one of the highest rates of extra-pair fertilizations of any bird species (76% in Mulder *et al.* 1994). Males display to neighbouring females throughout the day and females choose their mate by traveling to neighbouring males predawn to solicit copulations (Double and Cockburn 2000). If the availability of food resources in suburban habitats are limited, I would expect that general non-foraging behaviours would be less-frequently observed in favour of foraging.

In more traditional habitat, the superb fairy-wren has been described as an opportunistic forager, being flexible in its selection of feeding substrate and foraging techniques (Tidemann 2004). It is likely that this flexibility has allowed the species to make the transition into some suburban areas, but reasons for its limited distribution in these areas is unknown, particularly given that other fragmented habitats are considered optimal in quality for this species. By comparing the foraging (attempted prey capture) behaviour and habitat use of superb fairy-wrens in areas where they are more abundant (optimal habitat: rural/remnant edges) and areas where they are rare (apparently sub-optimal habitats: suburban), we aim to determine if the effects of habitat modification are reflected in changed behaviour. We test two predictions based on changes in predation risk and food availability. If suburban habitats truly are sub-optimal I would expect to see support for one or both of these hypotheses:

(1) *Food Limitation Hypothesis*: If attempted prey capture duration is different between the two habitats then this suggests that there are changes in resource availability that are important. Under a scenario of low food availability we would also expect birds to perform other behaviors less frequently due to the need to search for food and male and female differences in attempted prey capture to be less defined as the emphasis would be on finding adequate resources rather than gender specific behaviours such as territorial defence (calling)

(2) *Predator Disturbance Hypothesis*: Under this hypothesis we would predict that there would be less attempted prey capture in open areas by both males and females due to increased disturbances and a greater reliance on protection from a shrub layer. Attempted prey capture within shrubs would

be more evident with gleaning, snatching and hawking becoming important prey capture behaviours.

4.2 Materials and Methods

4.2.1 Study Area

Superb fairy-wrens were observed in the coastal Illawarra region of New South Wales, Australia (34.26 S, 150.53 E). Twenty family groups of superb fairy-wrens were located in a zone dominated by residential housing and parkland (referred to as suburban sites), and 17 family groups were located in rural/remnant habitats (referred to as non-suburban sites). The latter sites were located on the outskirts of the suburban zone and bounded by a continuous patch of native vegetation, comprising the footslopes of the Illawarra escarpment.

4.2.2 Behavioural Sampling and Habitat Utilisation

The adult female (distinguished from helpers by the greenish tinge on the tail) and dominant male (in nuptial plumage) of each group were observed between December 2004 and February 2005, during the later half of the breeding season. Each bird was followed for 10 to 15 minutes (male and female sequentially) at three different time periods; morning (6am till 9am), midday (11am till 2pm) and afternoon (4pm till 6pm) and birds were followed for only one time period on any day. During the observation period, the substrate that each bird utilised was recorded. Each time a bird changed substrates or a new behaviour was observed, the time, behaviour, new location and approximate height was recorded.

Five different prey capturing acts were identified. These were modified from Recher *et al.* (1985), Rowley and Russell (1997) and Tibbetts and Pruett-Jones (1999) and were identified as separate activities to simply moving around on or through the substrate:

- *Glean*: The bird takes prey from a nearby substrate while remaining perched in a tree or shrub.
- *Hop-search*: The bird hops on the ground or through low vegetation in search of food. The bird pecks to grab prey.
- *Pounce*: The bird flies a short distance from a perch or the ground to take prey from the ground.
- *Hawk*: The bird flies from a perch to take flying prey in the air.
- *Snatch*: The bird flies from a perch to take prey from another perch.

In addition to attempted prey capturing acts, other behaviours were also recorded. *Perching* was recorded when the bird stayed in the one spot for more than one minute without feeding or preening. *Preening* was recorded when the bird preened either itself or another bird. *Calling* was recorded when the bird sang either the Type I or Type II songs described in Rowley and Russell (1997). These songs are used to discriminate between members of the social group, neighbours and unknown intruders, and for territorial defence (Cooney and Cockburn 1995).

In conjunction with behavioural observations, habitat use was recorded throughout the observation period. The plant or man-made structures utilised were divided into the following categories;

- *Concrete/Road*: Driveways and paths as well as bitumen and unsealed roads.
- *Bare Ground*.

- *House*.
- *Grass*: Categorised as either *short* when shorter than the height of the bird, or *long*, when the grass was taller than the bird.
- *Herb*: Herbaceous layer < 1 m in height.
- *Shrub*: Categorised as *native* or *introduced* in origin. Plant 1–4 m tall with trunk branched close to the ground.
- *Lantana*: *Lantana camara*, a dense introduced woody shrub that was prevalent at many sites, particularly the non-suburban sites.
- *Tree*: Categorised as either *native* or *introduced*. Plant > 1 m in height with a trunk that did not branch near the ground.

Observations and habitat usage were recorded on a Sony Memory Stick IC Recorder and began after the first change in behaviour/location after it was initially located. Recording was concluded once the maximum time of 15 minutes was reached or the bird was out of sight for more than 2 minutes. If the minimum 10 minutes of visual recorded time was not achieved then the data was erased and observations conducted on another day. This minimized the risk of missing attempted prey capturing in dense vegetation when the bird was out of view and only happened on one occasion. Therefore the chances of underestimating prey capturing attempts and biases towards open lawn observations were only small. Recording was conducted from a distance (usually a minimum of 10 m) so as not to interfere with the activities of the birds. In no instance did my presence appear to alter bird behaviour either by resulting in them retreating into vegetation (and giving an alarm call) or causing them to be hesitant to move into open space. The amount of time spent on each

substrate as well as performing each behaviour or foraging act was tallied and expressed as a proportion of the total time recorded.

4.2.3 Habitat Characteristics

To determine preferences for particular habitat components, it is necessary to know the relative occurrence of each component as well as the use of that component by the birds. Therefore both these variables were recorded for each territory. Throughout the observation period (3 surveys per bird), movements of the birds were noted on a map. This was used to make a minimum convex polygon (MCP) of the habitat that both the male and female within each site occupied during the survey period. Because birds often moved from sight, these polygons should not be considered as home ranges. From the intersection of lines drawn between the furthest four corners of the MCP, a central point was established. Using random bearings and distances, 40 quadrats (2 x 2 m) were measured from this central point. Man-made structures and any vegetation present within each of the quadrats were recorded, and the compositions of the sites were represented as percentage present in the 40 quadrats. Quantitative description of habitat characteristics is provided in Chapter 2 and is not reported again here. Indices of occurrence of these characteristics are used as covariates in the analyses that follow.

4.2.4 Statistical Analysis

Changes in the duration of substrate usage between suburban and non-suburban habitats as well as throughout the three time periods were statistically tested by 2-way blocked, nested ANOVA (SYSTAT). The amount of time spent on each substrate (substrate

usage) was the dependant variable with time of day and habitat type (with sites nested) being the independent variables. Males and females were analysed separately and in order to determine whether the availability of vegetation cover was influencing fairy-wren use in either habitat, the percentage indices of occurrence (vegetation availability) for each variable were included as a covariate in the model. As availability of each vegetation covariable was the same within each site regardless of time of day, interaction terms involving these indices could not be examined. However the slope of the line indicated the associations between the availability of vegetation and the time spent in the vegetation for each habitat type. All vegetation variables, with the exception of introduced shrubs (excluding lantana), all shrubs (native and introduced shrubs combined), all trees (native and introduced shrubs combined) and road were transformed using the $\log(x + 1)$ transformation.

Differences in habitat use between males and females throughout the three time periods were also examined using the 2-way blocked, nested ANOVA, by also including gender as an independent variable along with habitat type and time period but excluding the covariate of habitat availability. Significant differences in habitat use with time of day were distinguished using Student Newman-Keuls multiple comparisons.

The 2-way blocked and nested ANOVAs were also used to examine differences in specific behaviour of both male and female superb fairy-wrens in suburban and non-suburban habitats, as well as any changes in behaviour associated with the time of day. All prey capture data was not normal and was therefore $\log(x + 1)$ transformed.

4.3 Results

4.3.1 Habitat Use

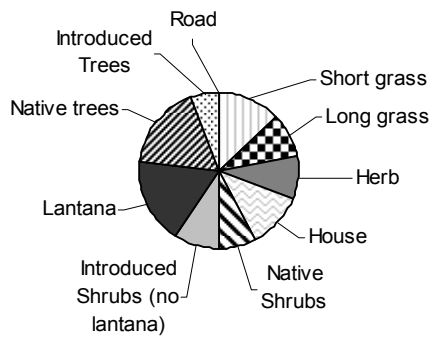
4.3.1.1 Females

A total of 25 hr 41 mins of observation were obtained for female superb fairy-wrens, with 51.6% conducted in suburban habitats and 48.4% in non-suburban habitats. Females' use of the variety of different structures available in suburban habitats was much more evenly distributed than in non-suburban habitats (Fig 4.1a and b). In both suburban and non-suburban habitats, female superb fairy-wrens were observed most frequently in shrubs (mean \pm std error = 38.4% \pm 3.1 and 48.8% \pm 4.0 respectively). After the influence of availability was included in the model as a covariate, there was no significant difference between non-suburban and suburban habitats in the amount of time female superb fairy-wrens spent in all shrubs combined ($F_{1,28} = 4.1$, $p = 0.052$) though there was a clear trend, native shrubs ($F_{1,28} = 0.5$, $p = 0.506$), lantana ($F_{1,28} = 2.3$, $p = 0.143$) or other introduced shrubs ($F_{1,28} = 0.02$, $p = 0.891$). For both habitats, the amount of time spent in all shrubs was proportional to availability in each habitat, indicated by a significant covariate of shrub availability in the model ($F_{1,20} = 8.7$, $p = 0.008$; Fig 4.2a). While this relationship was evident for both habitats, it was the relationship in non-suburban habitats that appeared to be governing the trend (non-suburban $r^2 = 0.51$; suburban $r^2 = 0.14$). This suggests that there may have been an interaction between shrub availability, habitat and time spent in shrubs though the nature of the model meant that this could not be tested. It appears likely that the pattern seen in all shrubs is generated by lantana and to a lesser extent, other introduced shrubs. The amount of time spent in lantana was also proportional to availability ($F_{1,20} = 13.9$, $p = 0.001$; Fig 4.2b). However the linear relationship was more evident in

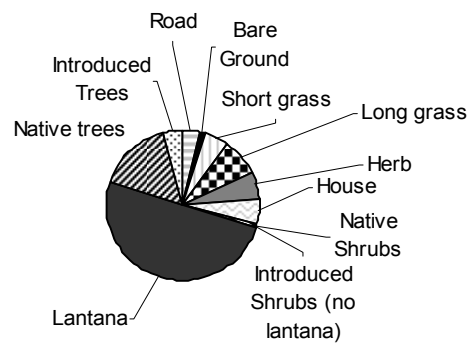
suburban habitats ($r^2 = 0.7$) than non-suburban habitats ($r^2 = 0.13$). The relationship between availability and the time spent in introduced shrubs (not including lantana) was limited to the suburban habitat because there were few introduced shrubs (not including lantana) available in non-suburban habitats and hence their use of them was restricted ($F_{1,20} = 8.2$, $p = 0.01$; Fig 4.2c). Still, a linear relationship was not strong in either habitat (suburban $r^2 = 0.23$; non-suburban $r^2 = 0.04$).

Female suburban superb fairy-wrens used the ‘all trees’ category equally in both habitats spending an average of $23.3\% \pm 2.7$ of the observed time in trees in suburban areas and $19.1\% \pm 2.4$ of time in trees in non-suburban habitats. However their use of native trees varied with time of day in a different way in each habitat (interaction term, $F_{2,56} = 3.3$, $p = 0.046$; Fig 4.3a).

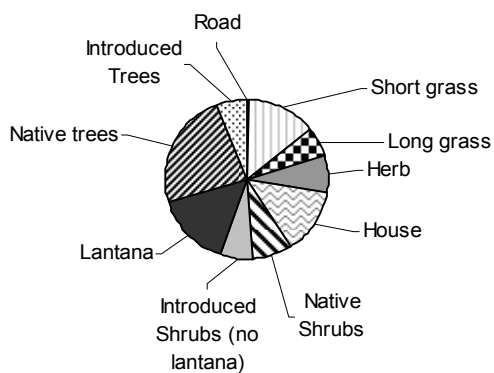
A significant effect of the availability of herbs in the model (covariate) suggests that the female superb fairy-wrens were using the herbs in proportion to the amount available in each habitat ($F_{1,20} = 8.9$, $p = 0.007$; Fig 4.2d). However, there is additional usage on top of this in suburban habitats that explains some of the variation. It appears that the use of herbs was more strongly related to availability in suburban areas ($r^2 = 0.62$) than non-suburban habitats ($r^2 = 0.39$). Furthermore, while female superb fairy-wrens spent, on average, less than 10 % of time in herbs, they were more commonly in herbs in suburban habitats than in non-suburban habitats (mean = $8.1\% \pm 1.8$ and $5.4\% \pm 1.7$ respectively) ($F_{1,28} = 9.935$, $p = 0.004$).



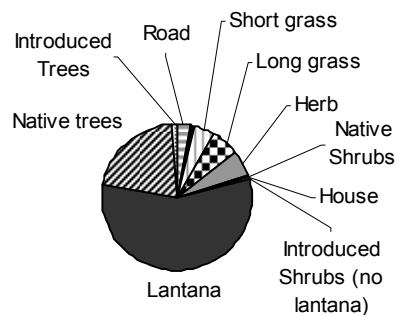
(a) Female suburban



(b) Female non-suburban



(c) Male suburban



(d) Male non-suburban

Fig 4.1: Mean percentage of time spent by female (a and b) and male (c and d) superb fairy-wrens on substrates in suburban and non-suburban habitats.

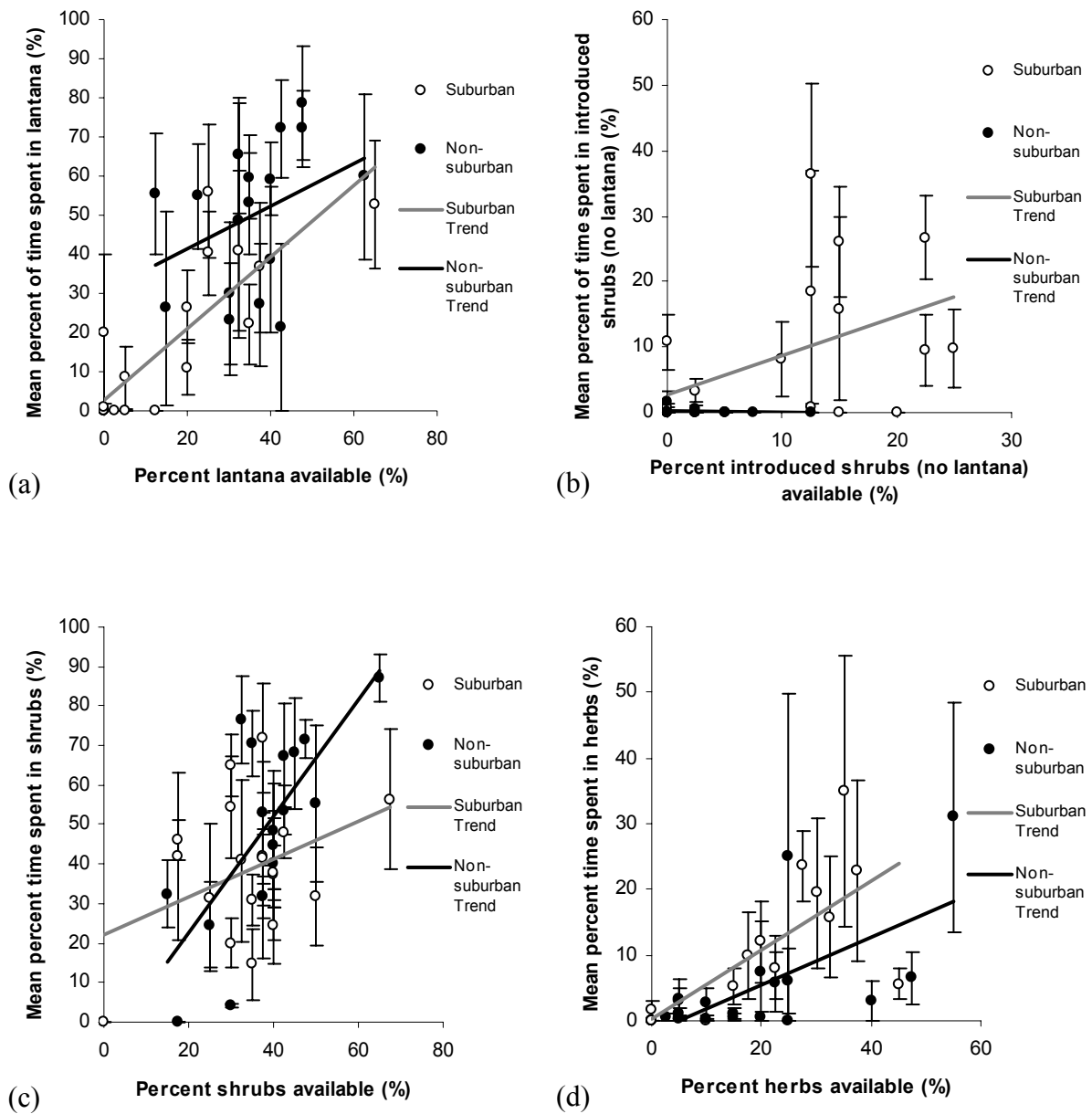


Fig 4.2: Relationships between habitat availability and the average percentage of total observation time (morning, midday and afternoon) that female superb fairy-wrens spent in (a) lantana (b) introduced shrubs (not including lantana) (c) all shrubs combined and (d) herbs. Error bars show standard error, with grey lines representing the linear fit to the model in suburban habitats and the black line in non-suburban habitats.

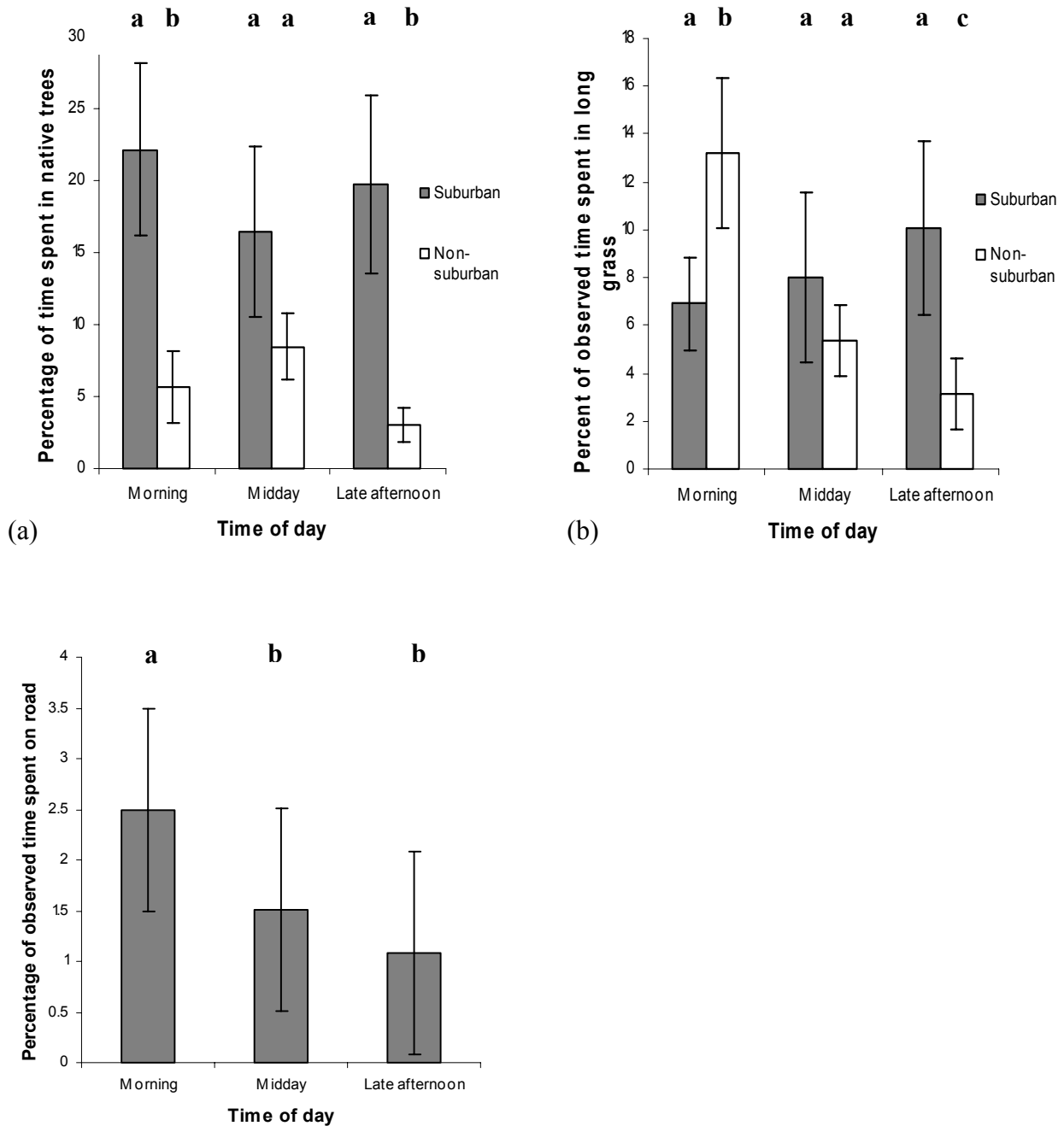


Fig 4.3: Mean percentage of total observed time that female superb fairy-wrens spent in (a) native trees (b) long grass and (c) concrete/road at three time periods; morning (6am to 9am), midday (11am to 2pm) and late afternoon (4pm to 6pm). Error bars show standard error. Letters denote time of day that is statistically different from others.

There was no significant difference in the mean amount of time female superb fairy-wrens spent on the ground (short grass, long grass, ground and road/driveways/paths - each analysed separately) in either suburban or non-suburban habitats (mean time spent on the ground in total = $18.4\% \pm 1.8$). However the time of day in which the individuals were observed influenced their microhabitat use of the ground. Female superb fairy-wrens in non-suburban habitats were more likely to be observed in long grass in the morning and observed less frequently in the late afternoon than at midday ($F_{2,56} = 7.6$, $p = 0.001$). The same variation did not occur in suburban sites, and there was therefore an interaction between time of day and habitat for the amount of time observed in long grass ($F_{2,56} = 4.1$, $p = 0.022$; Fig 4.3b) that was independent of the amount of long grass available ($F_{1,20} = 0.38$, $p = 0.547$). Females also spent more time on road/driveways/paths in the mornings than in either midday or late afternoon irrespective of habitat type ($F_{2,56} = 3.5$, $p = 0.036$; Fig 4.3c). This was independent of the amount road available ($F_{1,20} = 0.137$, $p = 0.715$).

4.3.2.1 Males

Males were observed for 21 hrs 29 mins with 54.2% of this observed time in suburban habitats and 45.8% in non-suburban. While much of their use of the variety of structures was similar to females, their dependence on lantana in non-suburban habitats and native trees in suburban habitat was more evident (Fig 4.1c and d). In non-suburban habitats, an average of $50.3\% \pm 4.3$ of time was spent in shrubs, similar to females. However they spent much less time in shrubs than both males in non-suburban habitats, and than females overall in shrubs in suburban habitats ($29.7\% \pm 2.9$). This difference in usage between habitats for males was significant for all shrubs combined ($F_{1,28} = 7.2$, $p = 0.012$).

and for lantana only ($F_{1,28} = 5.6$, $p = 0.028$). However both shrubs and lantana were both used by males in proportion to availability ($F_{1,20} = 19.1$, $p < 0.001$ and $F_{1,20} = 28.8$, $p < 0.001$ respectively)(Fig 4.4a and 4.4b).

As was the case for females, male suburban fairy-wrens spent equal time in trees in suburban ($27.3\% \pm 3.0$) compared to non-suburban habitats ($20.0\% \pm 2.9$; $F_{1,28} = 1.0$, $p = 0.328$). Exotic trees were utilised significantly more often in suburban habitats than non-suburban habitats ($F_{1,28} = 4.9$, $p = 0.035$; Fig 4.5a), irrespective of the amount of introduced trees present ($F_{1,20} = 1.4$, $p = 0.253$). Males spent more time in native trees in suburban habitats and this was in proportion to availability ($F_{1,20} = 5.4$, $p = 0.03$; Fig 4.4c). In non-suburban habitats there was a decrease in use with an increase in availability, this relationship did not appear to be linear (suburban $r^2 = 0.2$; non-suburban $r^2 = 0.03$).

Male superb fairy-wrens did not spend much time in herbs (suburban $6.2\% \pm 1.3$, non-suburban; $5.1\% \pm 1.3$) however, the difference was significant ($F_{1,28} = 9.7$, $p = 0.004$). Again, the amount of time spent in herbs was in proportion to availability ($F_{1,20} = 8.6$, $p = 0.008$; suburban $r^2 = 0.5$; non-suburban $r^2 = 0.3$; Fig 4.4d).

Males spent an equal time on the ground overall ($14.3\% \pm 1.4$) in both habitats. However males used short grass significantly more in suburban habitats than non-suburban habitats ($F_{1,28} = 7.8$, $p = 0.009$; Fig 4.5b). This was not in proportion to what was available at each habitat ($F_{1,20} = 0.4$, $p = 0.513$). Therefore, male superb fairy-wrens were showing a clear preference for short grass in suburban habitats.

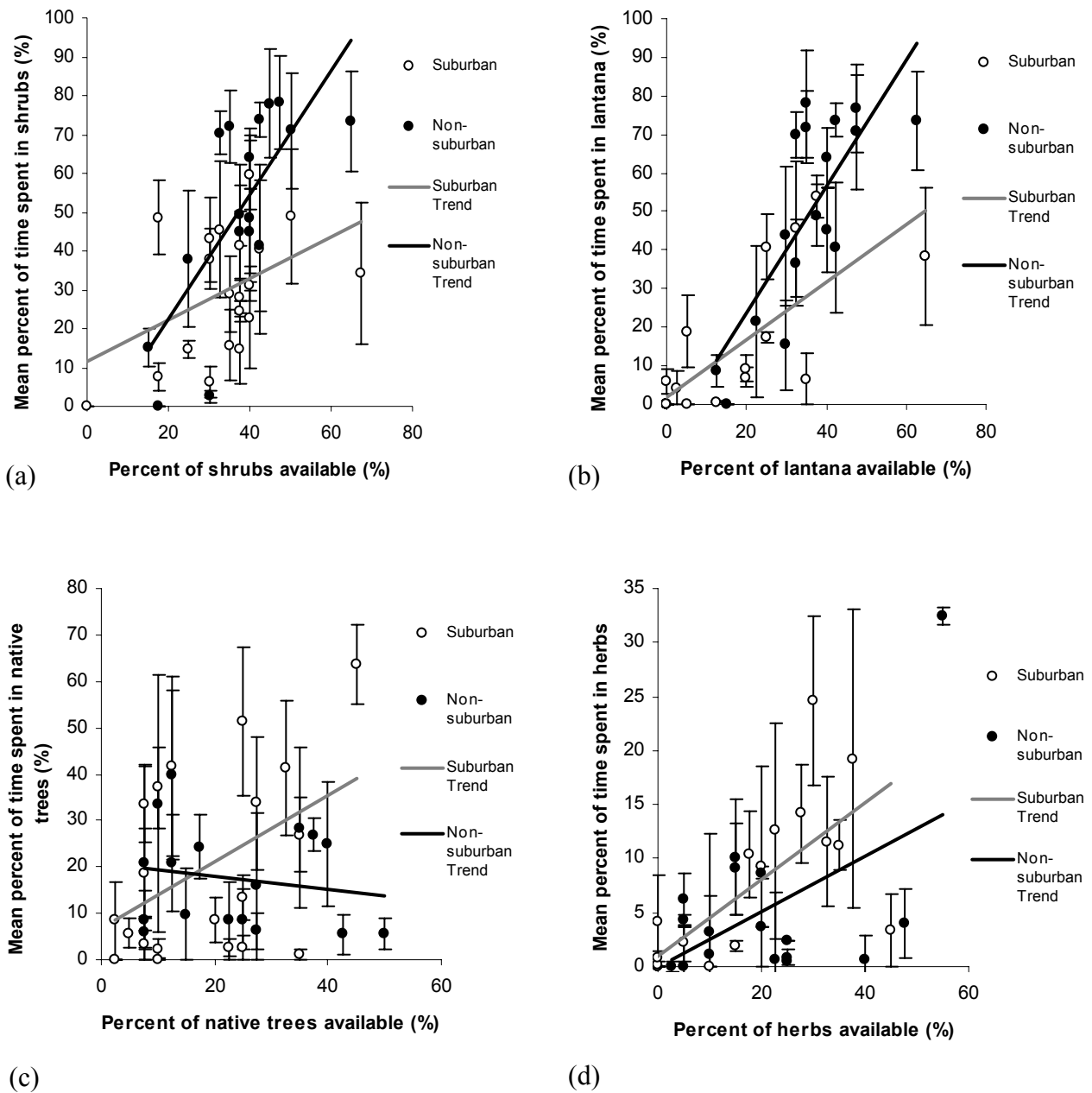


Fig 4.4: Relationships between habitat availability and the mean percentage of total observation time that male superb fairy-wrens spent in (a) all shrubs (b) lantana (c) native trees and (d) herbs. Error bars show standard errors, with grey lines representing the linear fit to the model in suburban habitats and the black line in non-suburban habitats.

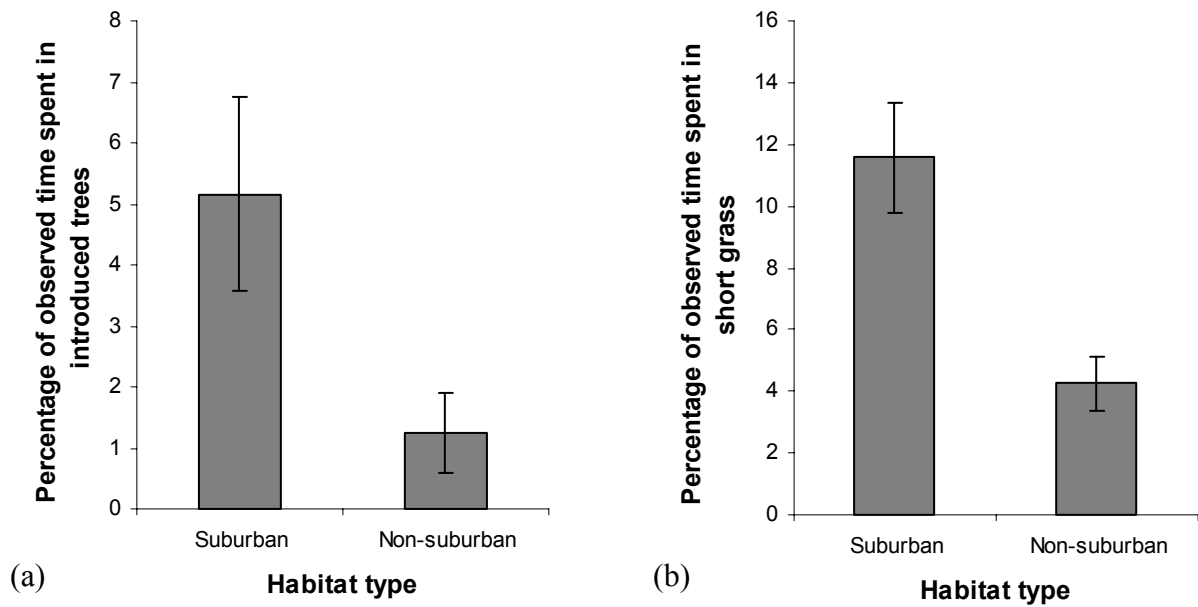


Fig 4.5: Percentage of total observation time that male superb fairy-wrens spent in (a) introduced trees and (b) short grass in suburban and non-suburban habitats.

Error bars show standard error.

4.3.3 *Non-foraging Behaviour*

4.3.3.1 Females

Other behaviours (calling, perching and preening) accounted for, on average $7.3\% \pm 1.4$ in total of the time observed in suburban habitats and $9.1\% \pm 1.8$ in non-suburban habitats (Table 4.1). Neither habitat nor time of day affected the occurrence of any of these three behaviours. Perching was most commonly observed (mean both habitats = $4.4\% \pm 0.2$), preening was performed on average $2.9\% \pm 0.1$ of the observed time and calling was very infrequently observed (mean $0.9\% \pm 0.1$).

Table 4.1: Proportion of total observed time that female superb fairy-wrens spent attempting prey capture and performing other behaviours in suburban and non-suburban habitats. Data represent mean \pm standard error. F-ratios and p values from ANOVA's are also represented.

		Suburban	Non-suburban	F _{1,21}	p
Other					
Behaviours	Perching	4.1 \pm 1.1	4.8 \pm 1.4	0.1	0.8
	Preening	2.2 \pm 0.8	3.6 \pm 1.0	0.6	0.4
	Calling	1.0 \pm 0.3	0.7 \pm 0.2	0.3	0.6
Foraging	Glean	0.2 \pm 0.1	0.1 \pm 0.02	2.8	0.1
	Hop-search	6.8 \pm 1.1	3.9 \pm 1.2	3.9	0.06
	Pounce	0	0		
	Hawk	0.04 \pm 0.02	0.14 \pm 0.1	1.0	0.3
	Snatch	0.1 \pm 0.1	0.1 \pm 0.02	0.01	0.9
	Total	7.2 \pm 1.1	4.2 \pm 1.1	4.3	0.051

4.3.3.2 Males

Males undertook perching, preening and calling, on average, nearly twice as often as females in suburban habitats (14.2 % \pm 1.9) and in similar proportions to females in non-suburban habitats (13.0% \pm 1.8) (Table 4.2). Males perched for much longer than females (9.9% \pm 1.0) however preening and calling were performed at a similar rate to females (preening = 2.5% \pm 0.1, calling = 1.2% \pm 0.02). Habitat type did not affect the performance of any of these three behaviours by males, however the time of day influenced the occurrence of both preening and calling. Preening was undertaken more commonly in the mornings than at midday or in the late afternoon ($F_{2,56} = 4.0$, $p = 0.024$; Fig 4.6a). However the calling was more often performed either at midday or late afternoon than in the morning ($F_{2,56} = 3.2$, $p = 0.047$; Fig 4.6b).

Table 4.2: Proportion of total observed time that male superb fairy-wrens spent attempting prey capture and performing other behaviours in suburban and non-suburban habitats. Data represent mean \pm standard error. F-ratios and p values from ANOVA's are also represented. Statistically significant results are shown in bold.

		Suburban	Non-suburban	F _{1,21}	p
Other					
Behaviours	Perching	9.9 \pm 1.7	9.7 \pm 1.6	0.002	1.0
	Preening	3.0 \pm 0.8	2.0 \pm 0.6	0.2	0.7
	Calling	1.2 \pm 0.2	1.3 \pm 0.3	0.08	0.9
Foraging	Glean	0.1 \pm 0.03	0.1 \pm 0.01	3.8	0.06
	Hop-search	8.3 \pm 1.4	3.8 \pm 1.2	10.1	0.004
	Pounce	0	0		
	Hawk	0.04 \pm 0.02	0.02 \pm 0.01	1.2	0.3
	Snatch	0.1 \pm 0.03	0.2 \pm 0.1	1.1	0.3
	Total	8.6 \pm 1.4	4.1 \pm 1.2	10.3	0.003

4.3.4 Foraging Behaviour

4.3.4.1 Females

The amount of time females were observed performing prey capturing techniques was not significantly different between habitats although there was a trend to suggest that birds foraged for longer in suburban areas (mean suburban 7.2% \pm 1.3, non-suburban 4.2% \pm 1.2; F_{1,21} = 4.3, p = 0.051; Table 4.2). There was no significant difference in the time that female superb fairy-wrens spent in short grass (from section 4.3.1.1)(mean = 8.0% \pm 1.5)) however most of the attempted prey captures performed by female superb fairy-wrens were performed here (61.2% \pm 5.8 and 81.5% \pm 6.5 of the total attempted

prey capture time respectively). No specific attempted prey capture behaviour (hop-search, glean, pounce, snatch or hawk) was influenced by habitat or time of day.

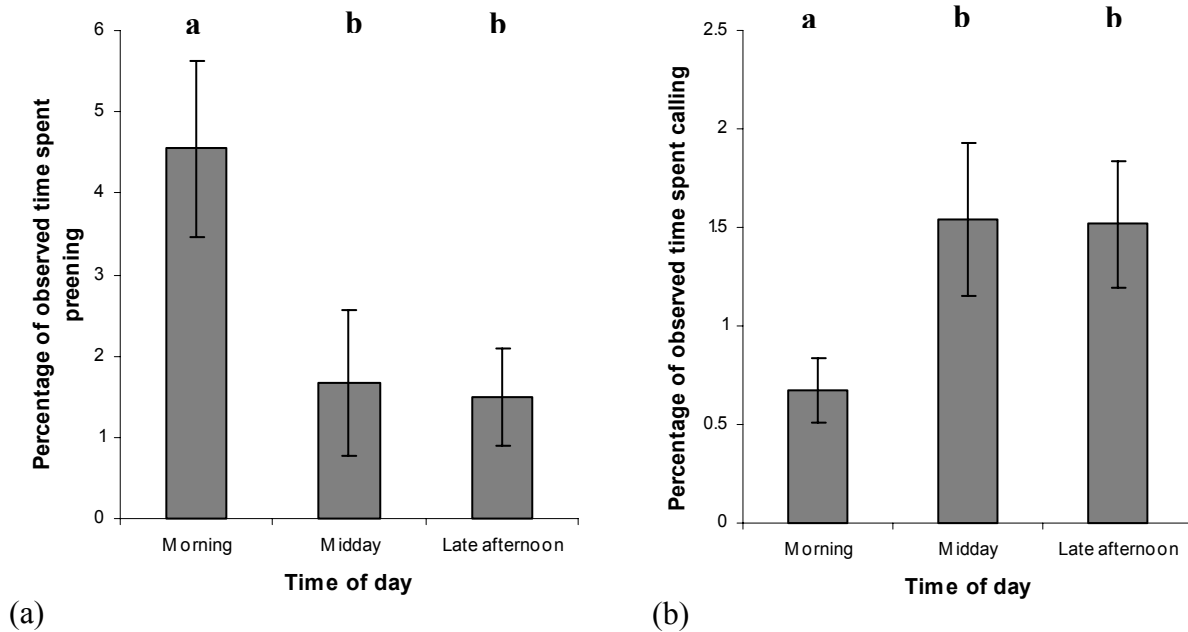


Fig 4.6: Percentage of total observed time that male superb fairy-wrens spent (a) preening and (b) calling at three time periods; morning (6am to 9am), midday (11am to 2pm) and late afternoon (4pm to 6pm) regardless of habitat type. Error bars show standard error. Means sharing the same letter (a, b, or c) are not significantly different.

4.3.4.2 Males

Twice as much prey capturing time was spent by the males foraging in suburban sites ($8.6\% \pm 1.4$) compared to non-suburban sites ($4.1\% \pm 1.2$) ($F_{1,21} = 10.3$, $p = 0.003$; Fig 4.7a; Table 4.2). The hop-search was the only individual attempted prey capture activity that was significantly more common in suburban habitats ($F_{1,21} = 10.1$, $p = 0.004$; Fig 4.7b). They spent twice as much time in suburban habitats ($8.3\% \pm 1.4$) performing

this behaviour compared to non-suburban habitats ($3.8\% \pm 1.2$). Male suburban fairy-wrens were observed on short grass more frequently than non-suburban fairy-wrens (from 4.3.1.2) (mean suburban = $11.4\% \pm 1.8$; mean non-suburban = $4.0\% \pm 0.9$). As for females, in both habitats, most prey capturing acts were performed on short grass (suburban $74.5\% \pm 5.2$ and non-suburban $92.6\% \pm 6.6$ of the total attempted prey capture time).

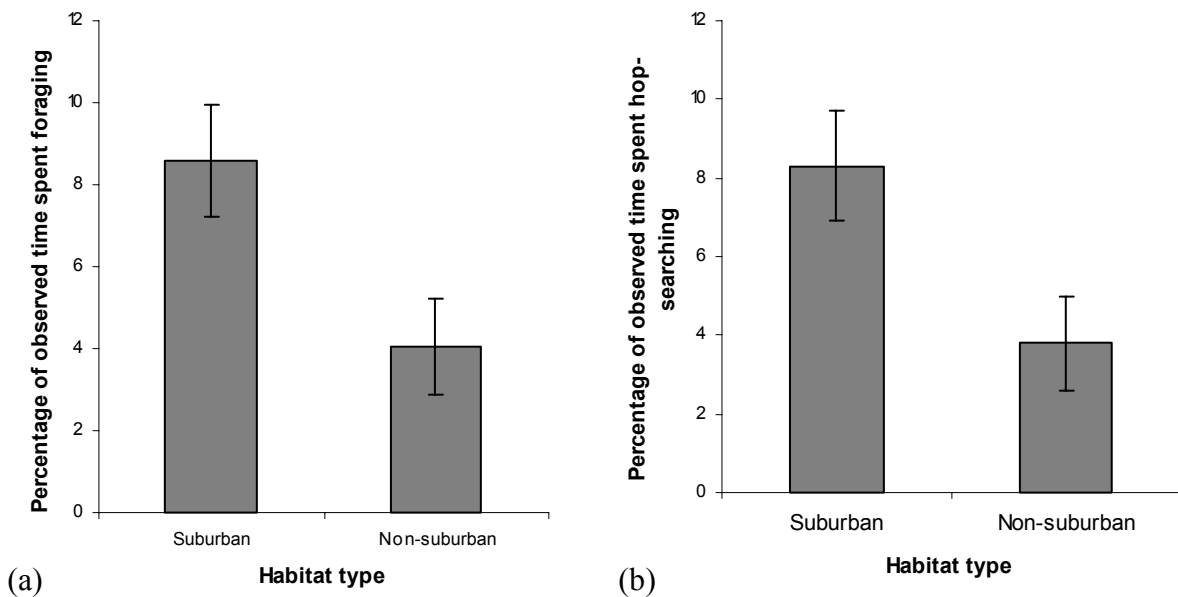


Fig 4.7: Mean percentage of total observation time that male superb fairy-wrens (a) spent attempting to capture prey in total and (b) hop-searched in suburban and non-suburban habitats. Error bars show standard error.

4.4 Discussion

The loss of insectivorous birds from suburbia has previously been linked to changes in vegetation, particularly, a reduction in the availability of dense understorey vegetation (Sewell and Catterall 1998; Parsons *et al.* 2003; White *et al.* 2005). Suburbs with primarily non-native vegetation, and recently-developed suburbs generally have a poor representation of small insectivores that may result from the direct loss of feeding and nesting sites (DeGraaf and Wentworth 1986; Yahner and Scott 1988). The urban environment has previously been assumed to be of poorer quality for superb fairy-wrens than the remnant/rural interface. Their preference for edge habitat coupled with an apparent decline in urban areas has supported this belief (Rowley and Russell 1997; Berry 2001).

The urban and rural/remnant habitats have previously been shown to be very different in floristics as well as structural composition (Chapter 2), and accordingly, the use of these habitats by superb fairy-wrens reflected these differences but there was little difference in male and female habitat use. The need for shrubs was evident at both habitats, but the ground, especially short grass, was the primary foraging location for both the male and female superb fairy-wrens. Males performed attempted prey captures for significantly longer in suburban than non-suburban habitats, with female prey capturing behaviour also following this trend. It is likely that increasing sample size would find this trend would also be significant for females.

4.4.1 Food Limitation Hypothesis

If a shortage of food is limiting superb fairy-wrens in suburban habitats we would expect this to be reflected in a number of changes in behaviour. Firstly, birds would be expected to forage for a longer period of time, secondly, other behaviours associated with reproduction and defence would be less commonly observed and thirdly, there would be less definition in behaviour between males and females as the need to obtain sufficient food would override these differences. There is partial support for this food-limitation hypothesis. While males spent longer attempting prey capturing behaviour in suburban locations (with females only just non-significant), there was no difference in behaviours between habitats and males and females performed gender-specific tasks to the same extent in both habitat types.

In suburban habitats we observed an increase in the duration of prey capturing attempts by males, and this trend was also seen in females though it was just non-significant. The performance of the hop-search behaviour more commonly in suburban habitats for males is largely driving this difference. The ground, in particular, short grass, was the preferred attempted prey capturing location for both the male and female superb fairy-wrens. While it is possible that this apparent preference for open lawn searching and prey capturing was due to ease of visibility of this location, as stated in the Methods, birds were rarely out of sight, even in dense vegetation. Previous examinations of the foraging behaviour of superb fairy-wrens have also recorded foraging activities occurring largely on the open ground and amongst leaf litter and fallen logs and less frequently on shrub and tree branches within 2 m of the ground, supporting the findings made here (Schodde 1982; Tidemann 1983; Recher *et al.* 1985; Ford *et al.* 1986; Cale 1994; Rowley

and Russell 1997; Paton *et al.* 2002, Tidemann 2004; Schlotfeldt and Kleindorfer 2006). The creation of open lawn space is therefore not necessarily detrimental for ground foraging species, and superb fairy-wrens appear to have adapted successfully to prey searching on this substrate, and using the ground in general, in suburban sites.

Some birds forage more efficiently in suburban habitats. Supplementary feeding from feeding stations has resulted in the Florida scrub-jay (*A. coerulescens*) decreasing time spent searching for food. (Fleischer Jr *et al.* 2003). Consequently this food availability in suburban habitats has resulted in earlier breeding and increased reproductive output for this species in suburban habitats (Bowman *et al.* 1998; Fleischer Jr *et al.* 2003; Schoech *et al.* 2004). Urban habitats provide many birds with a greater variety of food resources than natural habitats, with refuse sites, feeders, and exotic vegetation all adding to the natural resources available (Brittingham and Temple 1989; Marzluff *et al.* 2001; Shochat *et al.* 2004).

For insectivorous birds not exploiting these types of food sources, the urban landscape has been shown to be poorer in resources. Whilst shrub and canopy-foraging insectivores inhabiting remnants within the urban matrix have been shown to forage in similar ways to insectivores foraging in continuous habitats, increased prey attacks in these remnants are thought to reflect decreased arthropod availability (Hodgson *et al.* 2006). In the same way as for birds, arthropod communities are affected by fragmentation and urbanisation (Zapparoli 1997; McIntyre 2000; Zarette *et al.* 2001; Hostetler and McIntyre 2001). Changes to food web dynamics could therefore be impacting on the ability of insectivorous birds to forage in urban landscapes (Didmam *et al.* 1996; Gunnarsson and Hake 1999).

4.4.2 *Predator Disturbance Hypothesis*

If human disturbances and predation risk are significant factors limiting the distribution of superb fairy-wrens (Trueman 1990; Bass 1995, Major *et al.* 1996; Barratt 1997, 1998; Fernández-Juricic and Schroeder 2003) we would expect suburban birds to spend more time than non-suburban birds in the protective shrub layer than foraging on open lawn and consequently observe an increase in shrub foraging behaviours such as gleaning, hawking and snatching rather than hop-search or pecking behaviours. Defence strategies, such as calling, and keeping vigilant by perching would also be more frequently observed as all members of the group watch for potential threats. This, however, was not observed.

Open grass was the preferred foraging location for superb fairy-wrens in both suburban and non-suburban habitats. In suburban habitats, male superb fairy-wrens showed a preference for using short grass greater than that expected from its proportional availability. Consequently they performed the hop-search foraging behaviour significantly more than in non-suburban habitats. Shrub-associated foraging behaviours such as gleaning, hawking and snatching were much less commonly observed than ground foraging (hop-searching) in both suburban and non-suburban habitats for both male and female superb fairy-wrens. In suburban sites, over 60% of foraging acts performed by both males and females occurred on short grass, despite spending only around 11% of their time on this substrate. The perceived risks of human disturbance have previously been suggested to be low in suburban locations (Fernandez-Juricic and Schroeder 2003), but actual predation risks by cats and other birds in urban locations are high (Trueman 1990; Bass 1995; Major *et al.* 1996; Barratt 1997, 1998). Foraging in the

open requires individuals to be alert for approaching predators and it is a more risky foraging location than within a dense shrub. In poorer quality habitats, individuals are predicted to perform more risky behaviour, given foraging resources are scarce or poor, manifesting in increased foraging duration (Clark 1994). Conversely, those occupying higher quality habitats have a higher cost of predation because of their higher overall fitness and therefore would not be predicted to forage in riskier locations (Clark 1994, Olsson *et al.* 2002). This suggests that potentially a shortage of arthropod resources (indicative of poorer habitat quality) in suburban locations may be resulting in superb fairy-wrens performing more risky foraging acts. Alternatively, if the abundance of prey arthropods was differentially larger between shrubs and grass in suburban habitats, then the relative benefit gained by engaging in risky behaviour would be greater.

The comparatively more frequent usage of trees in suburban habitats by male superb fairy-wrens may be linked to the higher disturbance levels in suburban areas. While not directly measured, disturbances caused by human traffic are undoubtedly higher in more residential suburban habitats than along remnant/rural edges. Such disturbances may be perceived by organisms as a predation risk and therefore are likely to result in superb fairy-wrens retreating to either shrubs or trees for shelter (Frid and Dill 2002; Fernández-Juricic and Schroeder 2003). However given the role of the dominant male as well as helpers in superb fairy-wren groups in maintaining vigilance against potential predators or intruders (Rowley and Russell 1997), it is logical that moving to a high point such as a tree, when there is a perceived risk, is likely. Therefore, where disturbances are more common this behaviour may be more likely to be observed as was found in this study.

4.4.3 Conclusions

Species that are versatile are more likely to persist in an environment that is unpredictable or subject to frequent disturbances such as those experienced in suburban areas (Craig and Beal 2001). The identification of the superb fairy-wren as an 'edge-species' is not a sufficient description of the capabilities of this species given its adaptation to some suburban environments and ability to exist in an environment much more directly modified and impacted on a daily basis by people. Behaviours exhibited by the birds in both habitats were not strikingly different from each other, but increased attempted prey capture duration in suburban habitat suggests some changes to food resources, giving some support for the food limitation hypothesis. While suburban superb fairy-wrens foraged for longer periods of time, indicative of a poorer quality habitat, they still displayed a full range of other behaviours that were also observed in semi-natural habitats. This suggests suburban and non-suburban habitats are similar in habitat quality.

Despite the superb fairy-wrens ability to occupy a variety of habitats, there is still some limit to the suitability of suburban areas for superb fairy-wren territories (Chapter 2). Determining these necessary vegetation criteria and closer examination of the foraging resources provided by suburban habitats is paramount to uncovering why their distribution in urban areas is limited.

4.5 References

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CHAPTER FIVE

The Ground Arthropod Community of Suburban Areas: Are Foraging Resources Limiting the Distribution of Insectivorous Birds?

5.1 Introduction

The rapid urbanisation of native habitat has been linked to a loss of biodiversity and a shift in the community composition of species able to survive within the urban matrix. Conservation within urban environments has now become a major focus of international research and they are being recognised as important refuges for many organisms (Clergeau *et al.* 1998; Savard *et al.* 2000).

Birds are often used as a model for examining the effects of urbanisation as they are readily observable in sufficient numbers for statistical analysis and the availability of comprehensive field guides makes them easily identifiable. As a result there have been numerous studies from throughout the world examining urban avifauna in a variety of urban habitats (e.g. DeGraaf and Wentworth 1986; Sewell and Catterall 1998; Fernández-Juricic 2000; Parsons *et al.* 2003; Yeoman and McNally 2005; Parsons *et al.* 2006). Most studies have focused on Northern Hemisphere communities, but the types of birds that make up the urban communities of Australia are different. Rather than smaller granivorous species as well as carnivorous and omnivorous species being the most abundant avifauna as in the Northern Hemisphere (Emlen 1974; Beissenger and Osborne

1982; Savard *et al.* 2000; Cooper 2002), Australian urban bird communities consist largely of larger nectarivores, large granivores and omnivorous introduced species (Green 1984; Mason 1985; Green *et al.* 1989). Conspicuously rare or absent are the small insectivores (Parsons *et al.* 2003; Catterall 2004; Parsons *et al.* 2006).

The presence of avifauna is often linked to the structure and floristic origin of urban vegetation (Day 1995; Clergeau *et al.* 1998). Many native birds show a preference for native vegetation, though will, to a lesser extent, also use some exotic plants as well. (Green 1984 and 1986; Catterall *et al.* 1989; Green *et al.* 1989; Daniels 1991; Day 1995; Germaine *et al.* 1998). In birds with specific foraging requirements, such as nectarivores or insectivores, if these resources are linked to a particular floristic type, then the availability of this vegetation may drive distribution patterns (French *et al.* 2005).

Arthropods are a comparatively understudied aspect of the urban landscape, however their role in creating and maintaining urban ecosystems is invaluable (McIntyre 2000; McIntyre *et al.* 2001). Just as for birds, fragmentation and urbanisation have been shown to alter the composition of arthropod communities (Zanette *et al.* 2000). Some arthropods live successfully within urban habitats and are found worldwide while others are unable to adapt to the urban landscape (Zapparoli 1997; McIntyre 2000; Hostetler and McIntyre 2001). Given the importance of arthropods to ecosystem functioning and as a food resource it is likely that such changes to community composition is also affecting the other members of the urban landscape (Didmam *et al.* 1996; Jokimäki *et al.* 1998; Gunnarsson and Hake 1999; Niemelä *et al.* 2002). This may therefore explain the loss of many insectivorous bird species from Australian urban habitats.

The superb fairy-wren (Maluridae: *Malurus cyaneus*) is a small Australian insectivorous passerine that displays an unusual response to fragmentation and urbanisation. While actually preferring to inhabit the edges of fragmented remnants rather than the interior (Berry 2001), this species is also found in suburban gardens in eastern Australia, though it is very patchy in its distribution (Rowley and Russell: Parsons *et al.* 2003; Catterall 2004). However, just what restricts the superb fairy-wren to these patches is unknown. This species is highly territorial, occupying areas that are on average 1.1 ha in size in suburban locations and larger in rural edges, a location where they are commonly reported (Rowley 1965; Rowley and Russell 1997; Chapter 3).

Superb fairy-wrens are generalist insectivores, foraging on a whole variety of arthropods from many orders. Barker and Vestjens (1990) report over 40 families of arthropods being consumed by superb fairy-wrens. Smaller arthropods form much of the diet of the adult birds however the diet fed to nestlings consists of much larger prey such as the Lepidoptera order (both larvae and adults) (Tidemann *et al.* 1989; Rowley and Russell 1997). Previous studies have shown that superb fairy-wrens spend the majority of foraging time on the ground or at a height of 2 m or less in the vegetation (Tidemann 1983; Recher *et al.* 1985; Ford *et al.* 1986; Cale 1994; Chapter 4). Within the Wollongong region despite spending, on average, just 10% of their time on the ground, superb fairy-wrens conducted 60 - 90% of their prey searching there (Chapter 4). Furthermore, superb fairy-wrens spent significantly longer attempting prey capture in suburban habitats than they did in non-suburban habitats (Chapter 4). Why this duration is different between these two habitats is unknown but could reflect that:

1. There are fewer arthropods available in suburban habitats, resulting in superb fairy-wrens needing to forage for longer to obtain sufficient energy requirements.
2. The total biomass of arthropods available in suburban and non-suburban areas is similar but arthropods in suburban habitats are smaller, resulting in birds having to forage for longer periods of time to obtain equivalent energy gains.

This study aims to determine whether the foraging resources available to superb fairy-wrens may be restricting their distribution in suburban habitats by comparing the arthropod resource available to superb fairy-wrens in suburban areas with locations in rural edges and suburban locations where the species is absent.

5.2 Materials and Methods

5.2.1 Site Characteristics

All sites were located in the Illawarra region of New South Wales, Australia (34.26 S, 150.53 E), 80 km south of Sydney. Arthropod sampling was conducted in December 2005 and January 2006 at a total of 40 sites. These sites were established based on habitat characteristics and the presence or absence of superb fairy-wrens (*Malurus cyaneus*). The time period for sampling also coincided with part of the breeding season for the superb fairy-wren, a time when birds are constrained by a requirement to provide large food items to nestlings, as well as catering for their own metabolic needs.

Ten sites were classified as ‘*non-suburban*’. These sites were located along rural/remnant edges and had both short grass and long grass (un-mown grass taller than

20 cm) within a superb fairy-wren territory. The presence or absence of superb fairy-wrens was determined by extensive call playback throughout the area. The remaining thirty sites were located in suburban residential areas. Ten were suburban ‘*wild*’ sites; they were within a superb fairy-wren territory and, like the non-suburban sites, contained short and long grass. Ten were suburban ‘*tame*’ sites. Again, superb fairy-wrens were present but there were no patches of long grass. Instead, the sites were typically suburban with well-maintained lawns containing short grass only. The final ten sites were also located in suburban areas but they were in locations that did not have superb fairy-wrens and contained only short grass. Each of these ‘*suburban non-territories*’ were a minimum of 1 km from the suburban sites in fairy-wren territories. They were found by using random numbers to locate potential areas on a map (residential areas that were > 1 km from actual superb fairy-wren territories) and then surveying each site (using call-play back as well as observations) for superb fairy-wren presence/absence. They did not differ from suburban tame sites other than the presence of superb fairy-wrens. They were selected by

5.2.2 *Arthropod Collection*

Arthropods were sampled by extracting them from the substrate using a vacuum cleaner (650 watt), modified by the inclusion of a stocking within the hose. A total of four, 1 m x 1 m quadrats were randomly distributed within each of the grass types (short or long) at each site. Short grass was categorized as grass that was shorter than the height of a fairy-wren, long grass was grass that was taller than the height of a fairy-wren. The quadrat was delineated by timber walls 50 cm high to trap all arthropods within it. While

a few flying insects did escape, the presence of numerous winged insects within the samples suggests that they were sampled, and any losses were consistent between treatments. Each quadrat was vacuumed thoroughly for two minutes until all visible arthropods were captured. Short grass and long grass samples were kept separate, but each of the four quadrats belonging to each grass length was pooled.

Each sample (consisting of four short or long grass quadrats) was stored in 70% ethanol. They were then sorted to order and lengths measured using digital calipers. As the arthropods were being examined as a food source for a generalist insectivore, further identification was deemed unnecessary. Biomass was calculated using the models from Gowing and Recher's (1984) length-weight equations for invertebrates in south-eastern New South Wales. Such conversions are easier and more efficient than the process involved in measuring dry weight and their accuracy has been previously demonstrated (Schoener 1980, Ganihar 1997). The weight of each individual was added to give an overall biomass per site (mg/dry weight/4 m²). To determine whether biomass was due to a few large individuals or many smaller individuals, the average biomass of individuals per site was calculated by dividing the total biomass per site by the abundance.

5.2.3 Statistical Analysis

Two-factor ANOVAs were used to examine the effects of habitat (suburban or non-suburban) and grass length (short or long) on non-suburban and suburban wild sites. This allowed us to determine whether suburban wild habitat has an equivalent arthropod resource to non-suburban habitat. We investigated the diversity of orders, the number of individuals, total biomass and the average biomass of each individual (total

biomass/abundance) for arthropods overall. For those arthropods for which there were sufficient samples for a statistically viable analysis (Hymenoptera, Hemiptera, Aranea, Acarina, Coleoptera and Orthoptera), abundance, total biomass and average biomass were also analysed separately.

To determine whether suburban non-territories (those without superb fairy-wrens) were different from other suburban sites with fairy-wrens (suburban wild and suburban tame), single-factor ANOVAs were also calculated (with short grass being the independent variable) for order diversity, abundance, total biomass and average biomass as well as for individual orders (with the exception of the Orthoptera as there were insufficient individuals obtained in short grass samples). Order diversity and abundance data was normally distributed and therefore not transformed. Total and average biomass were $\log(x + 1)$ transformed.

5.3 Results

5.3.1 Are Non-Suburban Habitats Different from Suburban Habitats?

A total of 1494 individuals belonging to 16 different orders of arthropods were captured and identified. Of the 16 orders, 9 were represented by less than 15 individuals, with five of these orders represented by only a single individual. Hymenoptera (33.3%), Hemiptera (22.4%), Acarina (13.5%), Diptera (9.2%), Aranaea (7.0%), Coleoptera (6.02%) and Orthoptera (5.9%) were the most abundant orders collected and accounted for 97% of the total number of individuals sampled.

On average non-suburban sites (5.1 ± 0.4) contained the same number of orders of arthropods as suburban wild sites (5.2 ± 0.4) ($F_{1,36} = 0$, $p = 1$; Table 5.1). There was also

no difference in overall abundance of arthropods (21.9 ± 3.2 ; $F_{1,36} = 0.05$, $p = 0.83$). Total biomass was smaller in suburban wild sites (36.4 ± 10.9 mg/dry weight) than non-suburban sites (48.7 ± 9.6 mg/dry weight) though this difference was only just non-significant ($F_{1,36} = 4.05$, $p = 0.052$), however, the average biomass of individuals at each site in non-suburban habitats (2.9 ± 0.6 mg/dry weight) was more than twice that in suburban wild sites (1.3 ± 0.3 mg/dry weight) ($F_{1,36} = 5.92$, $p = 0.02$; Fig 5.1).

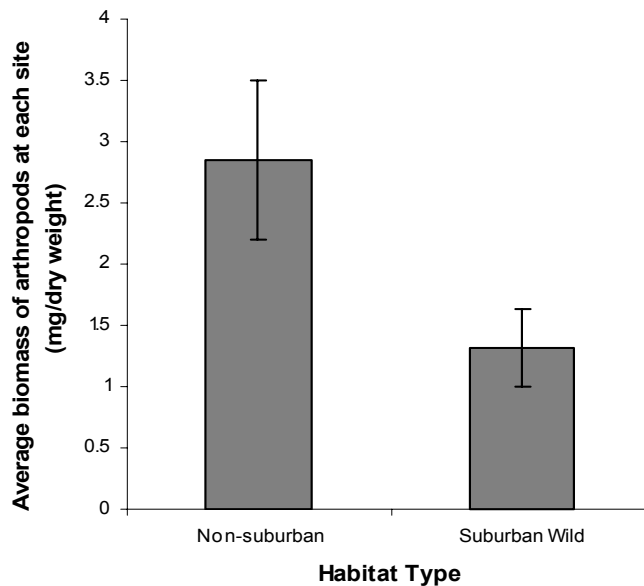


Fig 5.1: Average biomass (mg/dry weight) of arthropods at each site sampled in both long and short grass combined in non-suburban and suburban wild habitats. Error bars represent standard errors.

Table 5.1: Differences between non-suburban and suburban wild habitats in the number of orders, abundance, total biomass and average biomass per site of individual orders and all arthropods combined. Data represent means \pm standard errors. F-ratios and p values from ANOVAs are also presented. Statistically significant results are shown in bold. * denotes a statistically significant result in which there was also a significant interaction term.

Order		Non-Suburban	Suburban Wild	F _{1,36}	p
All	Order Diversity	5.1 \pm 0.4	5.2 \pm 0.4	0.001	1.0
	Abundance	21.4 \pm 2.9	22.4 \pm 3.6	0.05	0.8
	Total Biomass	48.7 \pm 9.6	36.4 \pm 10.9	4.1	0.052
	Av Biomass	2.9 \pm 0.6	1.3 \pm 0.3	5.9	0.02
Hymenoptera	Abundance	5.9 \pm 0.9	4.2 \pm 0.9	0.8	0.38
	Total Biomass	1.0 \pm 0.3	4.8 \pm 4.2	0.02	0.9
	Av Biomass	0.2 \pm 0.02	0.4 \pm 0.2	0.7	0.41
Hemiptera	Abundance	5.4 \pm 0.9	6.4 \pm 1.8	0.3	0.62
	Total Biomass	2.4 \pm 0.4	7.4 \pm 5.3	0.005	0.95
	Av Biomass	0.5 \pm 0.06	0.7 \pm 0.3	0.002	0.97
Orthoptera	Abundance	3.3 \pm 0.7	1.0 \pm 0.4	9.9	0.003
	Total Biomass	36.4 \pm 8.9	3.5 \pm 1.7	28.5	<0.001
	Av Biomass	13.6 \pm 4.2	1.4 \pm 0.7	23.8*	<0.001*
Diptera	Abundance	1.6 \pm 0.6	4.0 \pm 2.5	1.3	0.32
	Total Biomass	1.3 \pm 0.7	0.4 \pm 0.3	0.9	0.35
	Av Biomass	0.2 \pm 0.1	0.06 \pm 0.2	2.0	0.16
Coleoptera	Abundance	1.2 \pm 0.4	1.9 \pm 0.5	1.3	0.25
	Total Biomass	1.1 \pm 0.5	3.1 \pm 1.6	2.2	0.15
	Av Biomass	0.7 \pm 0.5	1.0 \pm 0.3	1.5	0.24
Aranea	Abundance	1.8 \pm 0.3	1.6 \pm 0.3	0.3	0.61
	Total Biomass	2.9 \pm 1.2	1.9 \pm 0.7	0.3	0.6
	Av Biomass	0.9 \pm 0.3	1.2 \pm 0.5	0.002	1.0
Acarina	Abundance	1.7 \pm 0.7	2.2 \pm 0.7	0.2	0.7
	Total Biomass	0.05 \pm 0.03	0.02 \pm 0.007	0.9	0.35
	Av Biomass	0.005 \pm 0.002	0.008 \pm 0.003	1.1	0.3

Grass length also had an impact on the arthropod communities irrespective of habitat type. Order diversity was significantly lower in short grass than in long grass

($F_{1,36} = 12.2$, $p = 0.001$; Fig 5.2; Table 5.2). However, the abundance of individuals, total biomass or average biomass of arthropods did not differ between long and short grass samples ($F_{1,36} = 3.7$, $p = 0.06$; $F_{1,36} = 0.868$, $p = 0.358$; $F_{1,36} = 0.241$, $p = 0.627$). There was no interaction between habitat type and grass length for the diversity, abundance, total biomass and average biomass of arthropods.

In long grass, 57.7% of arthropods sampled from suburban wild sites weighed less than 0.2 mg/dry weight compared to 42.0% of the arthropods in non-suburban sites (Fig 5.3a). The majority of arthropods in long grass in non-suburban sites were therefore larger than 0.2 mg/dry weight, with another 27.2% weighing between 0.21 - 0.5 mg/dry weight compared to 15.5% in suburban wild sites within the same weight range. In short grass a similar trend was observed (Fig. 5.3b). Slightly more arthropods in suburban wild short grass sites weighed less than 0.2 mg/dry weight (60.5%) than in non-suburban sites (55.7%).

The hymenopterans (wasps, ants and bees) were the most commonly collected order in non-suburban sites with an average of $5.9 (\pm 1.7)$ individuals sampled per site. Hemipterans (5.4 ± 0.9) and orthopterans (3.3 ± 0.7) were also abundant in non-suburban samples. At suburban wild sites, hemipterans, hymenopterans and dipterans were the most abundant orders collected (6.4 ± 1.8 , 4.2 ± 0.9 and 4.1 ± 2.5 respectively). However, the abundance of each order did not necessarily equate to the greatest contributors to overall biomass in each habitat. Orthopterans contributed to 75.0% of the total biomass of arthropods available in non-suburban sites, with other abundant orders, the hemiptera and hymenoptera, contributing 5.0% and 4.2% respectively. In suburban wild sites, the hymenopteran order had the greatest individual biomass, comprising 27.4% of the weight

of arthropods and hemipterans contributed 21.7%. All other orders contributed less than 10% to the total biomass of arthropods at the suburban wild sites.

Table 5.2: Differences between short grass and long grass in non-suburban and suburban wild habitats in the number of orders, abundance, total biomass and average biomass per site of individual orders and all arthropods combined. Data represent means \pm standard errors. F-ratios and p values from ANOVAs are also presented. Statistically significant results are shown in bold. * denotes a statistically significant result in which there was also a significant interaction term.

Order		Long Grass	Short Grass	F _{1,36}	p
All	Order Diversity	6.0 \pm 0.4	4.3 \pm 0.4	12.2	0.001
	Abundance	27.2 \pm 4.1	16.0 \pm 3.3	3.7	0.06
	Total Biomass	43.5 \pm 9.9	53.7 \pm 16.8	8.7	0.4
	Av Biomass	1.9 \pm 0.4	3.8 \pm 1.2	0.2	0.6
Hymenoptera	Abundance	5.4 \pm 2.2	6.3 \pm 2.7	0.006	0.94
	Total Biomass	0.9 \pm 0.5	1.1 \pm 0.4	0.007	0.93
	Av Biomass	0.2 \pm 0.02	1.1 \pm 0.5	0.06	0.81
Hemiptera	Abundance	7.2 \pm 1.5	3.5 \pm 0.9	0.002	0.96
	Total Biomass	3.6 \pm 0.7	1.2 \pm 0.2	1.1	0.31
	Av Biomass	0.6 \pm 0.1	0.4 \pm 0.1	0.6	0.46
Orthoptera	Abundance	4.4 \pm 1.0	2.1 \pm 0.7	9.1	0.005
	Total Biomass	32.4 \pm 8.3	40.7 \pm 16.3	3.8	0.06
	Av Biomass	6.9 \pm 1.7	20.3 \pm 7.8	0.6	0.43
Diptera	Abundance	1.8 \pm 0.9	1.2 \pm 0.8	2.2	0.14
	Total Biomass	1.4 \pm 1.3	1.3 \pm 0.9	0.001	1.0
	Av Biomass	0.2 \pm 0.2	0.2 \pm 0.1	0.9	0.35
Coleoptera	Abundance	1.9 \pm 0.6	0.5 \pm 0.3	3.2	0.08
	Total Biomass	1.0 \pm 0.4	1.1 \pm 1.0	0.6	0.45
	Av Biomass	0.4 \pm 0.1	1.1 \pm 1.0	0.02	0.89
Aranea	Abundance	2.3 \pm 0.3	1.3 \pm 0.4	5.4	0.03
	Total Biomass	3.3 \pm 2.2	2.3 \pm 1.1	2.5	0.1
	Av Biomass	1.1 \pm 0.5	0.7 \pm 0.3	0.13	0.7
Acarina	Abundance	2.2 \pm 1.4	1.0 \pm 0.6	0.003	1.0
	Total Biomass	0.08 \pm 0.05	0.01 \pm 0.01	1.6	0.2
	Av Biomass	0.006 \pm 0.004	0.003 \pm 0.001	0.1	0.72

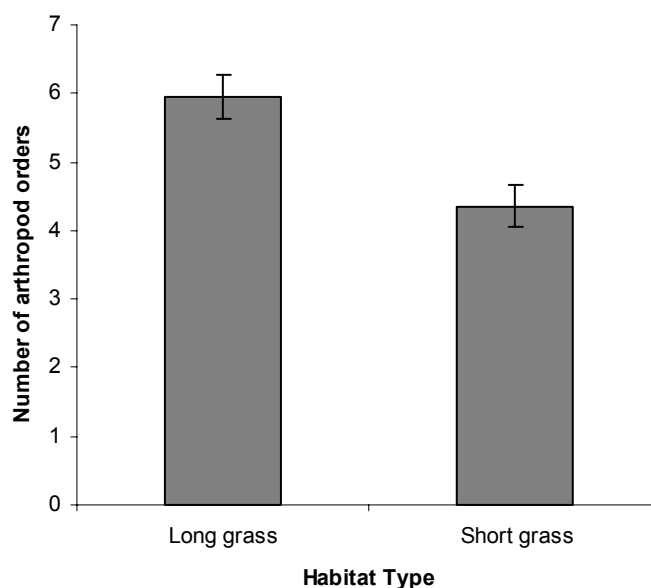
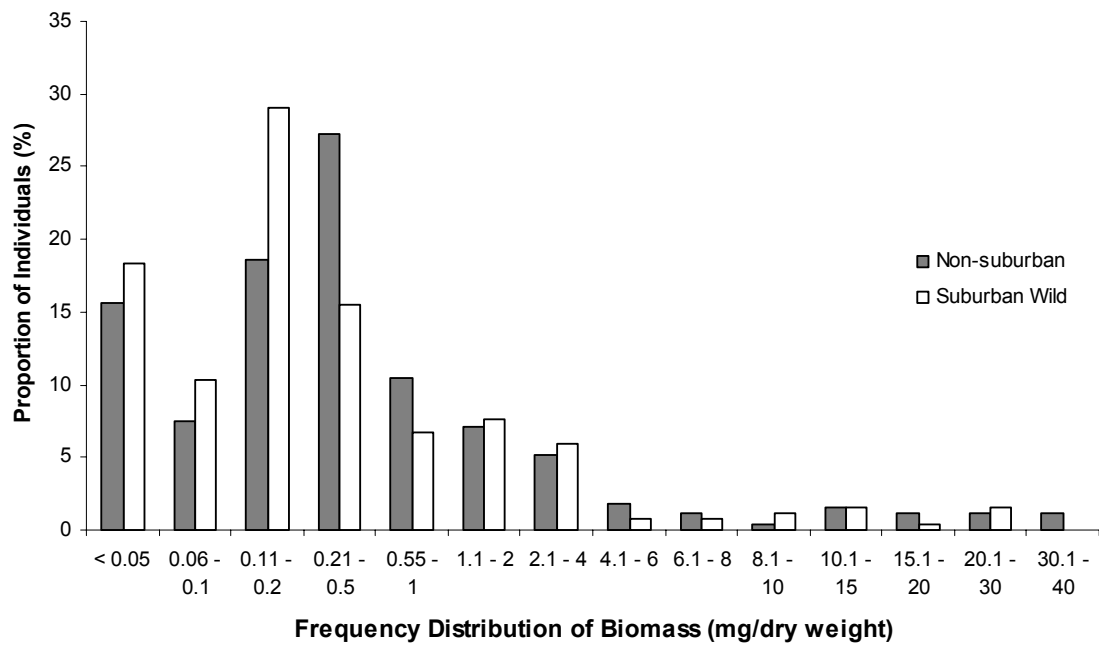
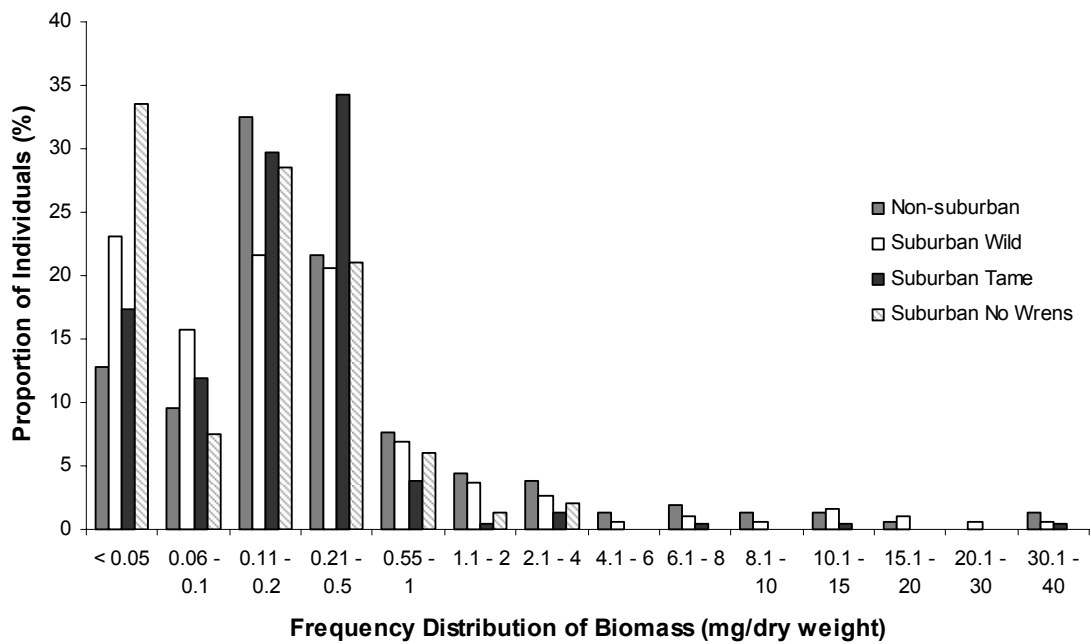


Fig 5.2: Mean number of arthropod orders recorded in long and short grass at both non-suburban and suburban wild habitats. Error bars represent standard errors.

The orthopterans were the only order that showed a significant effect of habitat type on their abundance, biomass and average biomass. They were, on average, three times more abundant in non-suburban habitat than suburban wild habitat ($F_{1,36} = 9.95$, $p = 0.003$) and had a much greater overall total biomass in non-suburban habitats ($F_{1,36} = 28.52$, $p < 0.001$; Fig 5.4a). Orthopterans in non-suburban habitats were significantly larger than those in suburban wild habitats ($F_{1,36} = 23.80$, $p < 0.001$; Fig 5.4b), with non-suburban orthopterans weighing approximately ten times more than suburban wild habitat orthopterans. They were also significantly more abundant in long grass than short grass irrespective of habitat type ($F_{1,36} = 9.103$, $p = 0.005$; Fig 5.4c), however their total or average biomass did not differ between the two grass lengths ($F_{1,36} = 3.84$, $p = 0.058$; $F_{1,36} = 0.642$, $p = 0.428$). There was a an interaction between habitat type and grass length for the average biomass of orthopterans per site ($F_{1,36} = 4.54$, $p = 0.04$).



(a)



(b)

Fig 5.3: The frequency distribution of arthropods (mg/dry weight) in 4 m² quadrats expressed as a proportion of the total number of individuals per habitat in (a) long grass and (b) short grass samples.

5.3.2 *Are Suburban Habitats with Superb Fairy-wrens Different From Suburban Habitats Without Superb Fairy-wrens?*

The short grass habitats in suburban sites were all very similar to each other in terms of order diversity, abundance, total biomass and average biomass. There was no difference in the diversity of orders between each of the three habitats, suburban wild sites, suburban tame sites (both with superb fairy-wrens) and suburban sites without wrens ($F_{2,27} = 0.089$, $p = 0.915$). Similarly, the abundance of arthropods, total or average biomass did not differ between suburban habitats ($F_{2,27} = 2.56$, $p = 0.096$; $F_{2,27} = 0.369$, $p = 0.695$; $F_{2,27} = 2.08$, $p = 0.143$; Table 5.3).

There were some differences seen in the frequency distribution of arthropods in short grass samples (Fig 5.3b). In the suburban habitats without wrens 70% of individuals weighed less than 0.2 mg/dry weight. Within the same weight range, suburban wild and tame sites had 60.5% and 60% of individuals respectively. Each of these three sites had a larger proportion of these very small arthropods than short grass sites in non-suburban habitat (54.8%). Larger arthropods (> 1 mg/dry weight) were more common in short grass samples from non-suburban and suburban wild sites (23.6% and 18.9%) than either the suburban tame sites (6.8%) or suburban sites without wrens (9.4%).

The hymenopterans were the only order to show a significant effect of habitat type. The abundance of hymenopterans in both suburban non-territories and suburban tame sites were significantly greater than in the suburban wild sites ($F_{2,27} = 6.63$, $p = 0.005$; Fig 5.5a; Table 5.3). Total hymenopteran biomass was over three times heavier in suburban non-territories than in suburban wild habitat ($F_{2,27} = 8.31$, $p = 0.002$; Fig 5.5b). However the total biomass of hymenopterans in suburban tame sites was not statistically

different from that of either of the other two habitats. The average biomass of hymenopterans per site did not differ between the three habitats ($F_{2,27} = 0.548$, $p = 0.584$; Table 5.3).

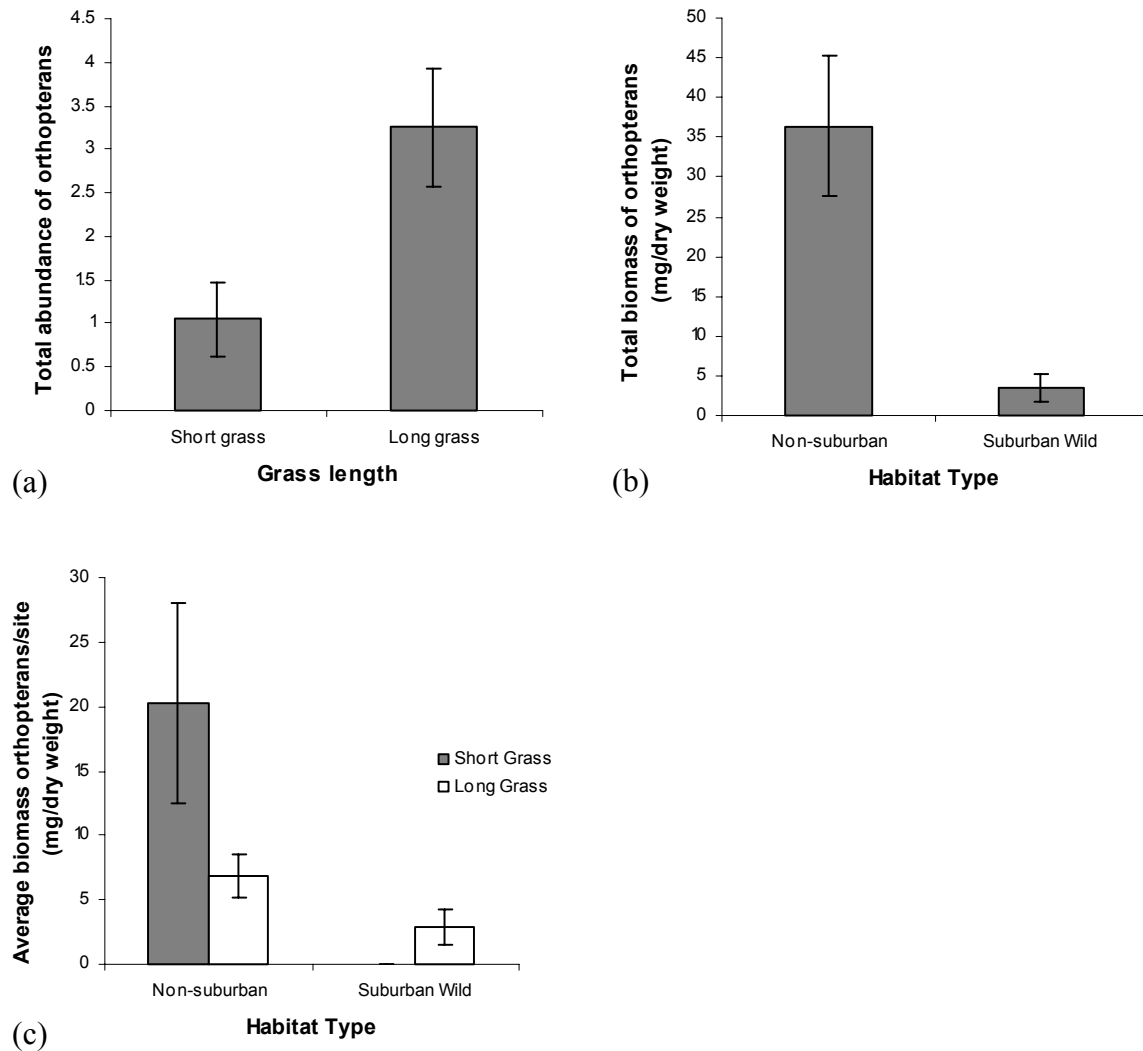


Fig 5.4: The effect of habitat type on the (a) total abundance, (b) total biomass and (c) average biomass of orthopterans sampled in 4 m² quadrats in both long and short grass. Error bars represent standard errors.

Table 5.3: Differences between short grass samples from suburban wild, suburban tame and suburban sites without wrens in the number of orders, abundance, total biomass and average biomass per site of individual orders and all arthropods combined. Data represent means \pm standard errors. F-ratios and p values from ANOVAs are also presented. Statistically significant results are shown in bold.

Order		Suburban Wild	Suburban Tame	Suburban No Wrens	F_{2,27}	p
All	Order					
	Diversity	4.4 \pm 0.5	4.6 \pm 1.3	4.3 \pm 0.62	0.09	0.92
	Abundance	19.1 \pm 3.4	23.5 \pm 4.4	39.1 \pm 10.0	2.6	0.09
	Total					
	Biomass	30.1 \pm 13.9	10.4 \pm 4.0	13.9 \pm 5.6	0.4	0.7
Hymenoptera	Av Biomass	1.2 \pm 0.5	0.4 \pm 0.1	0.4 \pm 0.1	2.1	0.14
	Abundance	3.9 \pm 0.6	11.8 \pm 3.2	13.9 \pm 3.4	6.6	0.05
	Total					
	Biomass	1.0 \pm 0.4	2.4 \pm 0.6	3.9 \pm 0.6	8.3	0.002
	Av Biomass	0.2 \pm 0.06	0.2 \pm 0.03	0.2 \pm 0.03	0.5	0.58
Hemiptera	Abundance	8.4 \pm 3.3	4.5 \pm 1.5	5.4 \pm 1.7	0.8	0.47
	Total					
	Biomass	11.9 \pm 10.6	0.7 \pm 0.3	1.7 \pm 0.7	1.3	0.28
	Av Biomass	0.6 \pm 0.3	0.1 \pm 0.03	0.2 \pm 0.1	2.1	0.14
Orthoptera	Abundance	0	0.1 \pm 0.1	0.1 \pm 0.1	0.5	0.61
	Total					
	Biomass	0	0.2 \pm 0.2	0.3 \pm 0.3	0.5	0.59
	Av Biomass	0	0.2 \pm 0.2	0.3 \pm 0.3	0.5	0.59
Diptera	Abundance	0.7 \pm 0.3	1.3 \pm 0.4	1.2 \pm 0.5	0.5	0.6
	Total					
	Biomass	0.1 \pm 0.05	0.2 \pm 0.07	0.1 \pm 0.06	0.4	0.66
	Av Biomass	0.07 \pm 0.04	0.07 \pm 0.02	0.04 \pm 0.02	0.4	0.69
Coleoptera	Abundance	1.5 \pm 0.6	1.9 \pm 0.7	1.8 \pm 0.7	0.1	0.93
	Total					
	Biomass	4.5 \pm 3.2	1.5 \pm 0.7	0.8 \pm 0.3	1.0	0.38
	Av Biomass	1.5 \pm 0.6	0.9 \pm 0.6	0.2 \pm 0.1	2.0	0.16
Aranea	Abundance	1.2 \pm 0.4	1.3 \pm 0.3	1.9 \pm 0.6	0.8	0.48
	Total					
	Biomass	1.1 \pm 0.8	1.6 \pm 1.0	1.9 \pm 0.9	0.2	0.84
	Av Biomass	0.9 \pm 0.7	0.9 \pm 0.6	0.9 \pm 0.3	0.1	0.89
Acarina	Abundance	2.9 \pm 1.8	2.3 \pm 1.4	10.1 \pm 8.9	0.7	0.51
	Total					
	Biomass	0.03 \pm 0.01	0.04 \pm 0.02	0.1 \pm 0.1	0.4	0.7
	Av Biomass	0.009 \pm 0.005	0.01 \pm 0.005	0.003 \pm 0.001	1.0	0.38

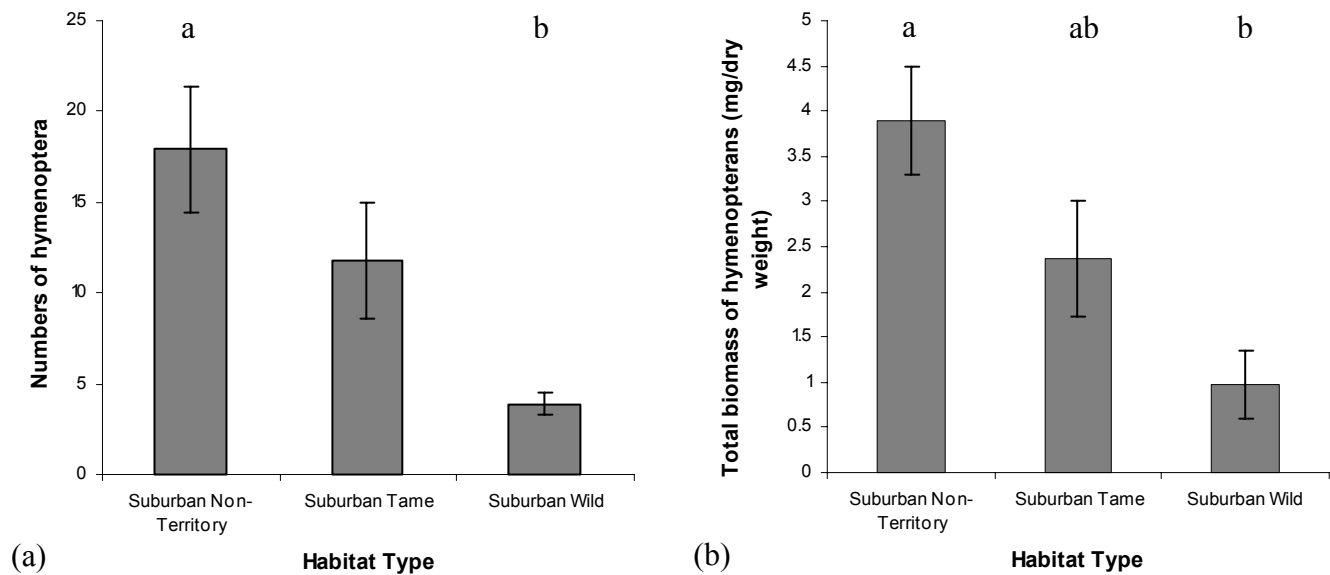


Fig 5.5: The effect of suburban habitat type on the mean (a) total abundance and (b) total biomass of hymenopterans in 4 m² quadrats in short grass. Error bars represent standard errors. Means sharing the same letter (a or b) are not significantly different.

5.4 Discussion

Both arthropods and insectivorous birds are often found to be negatively affected by fragmentation and urbanisation (Majer and Brown 1986; Sewell and Catterall 1998; McIntyre *et al.* 2001; Gibb and Hochuli 2002; Parsons *et al.* 2003; Christie and Hochuli 2005). However here, the availability of arthropods in suburban habitats is unlikely to be limiting the distribution of superb fairy-wrens. The total diversity of orders available, the numbers of individuals sampled and the total biomass did not differ between suburban habitat and non-suburban habitats found along rural/remnant edges. The average biomass of individuals at each site was smaller in suburban wild habitat, suggesting that, overall,

suburban sites tend to be characterised by smaller individuals. Individual arthropods tended to be smaller in suburban habitats, both in long and short grass than in non-suburban habitats. Suburban tame sites and sites without superb fairy-wrens also had fewer larger arthropods.

There were also differences in the numbers of orders supported by long grass compared with short grass irrespective of habitat type. Given the greater structural heterogeneity of longer grass this is unsurprising. However, this is not an artifact of a greater volume of grass sampled as the abundance of arthropods did not differ between short and long grass. Short grass is the preferred foraging location for superb fairy-wrens: despite spending, on average, around 10% of their total observed time on the ground, over 60% of foraging occurs there (Chapter 4). The simple, flat structure provided by short grass is best suited to the hop-search behaviour commonly used by foraging superb fairy-wrens (Rowley and Russell 1997).

Suburban wrens have been shown to attempt prey capture for significantly longer than those occupying non-suburban territories (Chapter 4). We predicted that this difference in duration would be explained by either fewer arthropods in total in suburban habitats forcing superb fairy-wrens to forage for longer, or smaller arthropods in suburban habitats resulting in superb fairy-wrens in suburbia foraging for longer to obtain equivalent biomass. It appears that there is some support for this second hypothesis: superb fairy-wrens are foraging for longer in suburban habitats as the individual food items are smaller, requiring them to extend foraging periods to obtain the same biomass of food. This difference in prey size was largely due to the presence of more, larger-bodied Orthoptera within non-suburban habitats. Suburban habitats could therefore be

considered to be poorer quality given that larger food items are less common, resulting in them modifying their foraging behaviour. While equivalent total biomass of arthropods can be obtained in suburban habitats, foraging for a longer period of time exposes individuals to a greater predation risk.

Superb fairy-wrens are generalist insectivores, previously shown to feed upon a wide array of arthropods (Rowley 1965; Tidemann *et al.* 1989; Barker and Vestjens 1990). In fact, each of the major arthropod groups identified here as being available in both suburban and non-suburban habitats, with the exception of the acari, made up nearly 100% of the diets of superb fairy-wrens reported in these past studies. However, the diet of the superb fairy-wren is more diverse than indicated simply by order, with over 40 families identified (Barker and Vestjens 1990). Therefore it is highly probable that the arthropods available in both the suburban and non-suburban habitats here, with the exception of mites, would be considered a food source for the superb fairy-wren.

In general, superb fairy-wren adults feed upon smaller arthropods, whilst nestlings are fed much larger items (Rowley and Russell 1997). However details on the actual sizes of these arthropods have not been previously recorded. While some of the arthropods sampled here, particularly the acari, were likely to be too small to be actively sought by superb fairy-wrens, the majority of the arthropods were expected to be within a size range to be included in the diet of adult birds. In addition, the larger individuals recorded, which consisted principally of orthopterans as well as lepidopterans, and some of the araneans, hemipterans and hymenopterans, may be a food source for nestlings, having previously been identified as such (Rowley 1965). During the breeding season, Tidemann *et al.* (1989) suggest that both adults in a pair of superb fairy-wrens (without helpers)

require an average of 13.2 g of food per day (Tidemann *et al.* 1989). Of this, 7.6 g is required for each adult and 6.6 g for the brood. Here, where each site also had at least one helper, daily intake is likely to be smaller. The average biomass of arthropods per site in non-suburban habitats here was more than double that of suburban wild sites, suggesting that there is likely to be a much reduced search effort required in non-suburban habitats, as individual items are generally larger and therefore contain more energy.

This difference in average biomass per site was largely governed by the presence of Orthopterans in non-suburban superb fairy-wren territories. Orthopterans have only been found in the diet of nestling superb fairy-wrens (Rowley 1965; Tidemann *et al.* 1989). However in this study, the orthopterans were the only order that showed a negative association with suburban habitats. This order contributed to 75% of the total biomass available in non-suburban habitat, yet were virtually absent from most suburban sites. It was the presence of these larger arthropods that appears responsible for the total biomass of individuals in non-suburban habitats than suburban habitats. During the breeding season, the presence of orthopterans within a non-suburban superb fairy-wren territory may result in adults being able to feed chicks more efficiently than in suburban sites where such larger items are less common. There is a need for greater understanding of the role that orthopterans play in the diet of insectivores and the impact that their relative shortage in urban habitats might have.

It is unlikely that arthropod availability in suburban locations is limiting the distribution of superb fairy-wrens in suburban habitats. All three habitat types had the same overall biomass of arthropods, order diversity, abundance and average biomass of individuals/site. At an order level, hymenopterans were most abundant in suburban

locations without superb fairy-wrens. Ants (which comprised the vast majority of the hymenopterans recorded here), are an extremely important part of the diet of many Australian ground foraging insectivores (Barker and Vestjens 1990; Rowley and Russell 1997). However, arthropod availability is influencing the behaviour of superb fairy-wrens in suburban habitat.

To determine how to best utilise the urban environment's potential for conservation, understanding the factors that limit bird distribution is paramount. The availability of food resources is often overlooked, and in this study there was an association between urbanisation and smaller arthropods. While this does not appear to be limiting bird distribution, it is likely to be having an impact on the foraging behaviour of this species and may have consequences where larger prey items are absent. If birds are forced to spend more foraging because arthropods are smaller, they will be spending more time in exposed locations (on the ground), may be less efficient at feeding young and this would have consequences for the predation risk faced by individuals.

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CHAPTER SIX

Discussion

With urban development progressing rapidly throughout the world, it is becoming increasingly important to understand how living in an urban environment impacts upon wildlife. While many species are adversely affected and avoid urban habitats, others have successfully colonised this landscape and may be as common, if not more so, than in their traditional habitats (e.g. Munyenyembe *et al.* 1989; Jones and Wieneke 2000; Jones 2003; Parsons *et al.* 2003; Catterall 2004). Given the vast differences between urban and natural habitats, we would expect that differences in resource distribution and availability would have implications for the behaviour of individuals that are able to inhabit this landscape (Hansson *et al.* 1995; Law and Dickman 1998).

The superb fairy-wren (*Malurus cyaneus*) is a species that, unlike most other small Australian insectivores, is found in areas fragmented and modified by urbanisation. Given this species' preference for weedy remnant edge vegetation and its limited urban distribution, it is classified as an Urban Tolerator (Chapter 1). That is, superb fairy-wrens tend to be restricted in their occupancy of urban habitats. This thesis found that suburban habitats in which superb fairy-wren territories are found are of similar quality to this weedy remnant edge habitat and I have provided insights into how and why the superb fairy-wren is able to persist in landscapes that have varying degrees of urbanisation.

6.1 Habitat Requirements of the Superb Fairy-wren

There is no single aspect of this species' ecology that explains its continued existence. I found that urbanised sites (suburban habitats) in which superb fairy-wrens were present were characterised by native rather than introduced plants, with shrubs particularly important. In the habitat thought to be more optimal for this species, remnant edge habitat (Rowley and Russell 1997; Berry 2001), lantana (*Lantana camara*) has replaced much of the native shrub layer and provides important protection and shelter for this species, and other small native birds (Crome *et al.* 1994).

Despite shrubs being an important habitat feature for superb fairy-wrens and many small birds, as they provide sheltering, foraging and/or nesting locations, many urban areas worldwide are characterised by a lack of this shrubby understorey (Savard and Falls 1981; DeGraaf and Wentworth 1986; Warkentin and James 1988). In Australia, the loss of this shrub layer is thought to be partially responsible for the decline in small bird abundance witnessed in urban areas (Catterall *et al.* 1989; Munyembe *et al.* 1989; Bass 1995; Sewell and Catterall 1998). White *et al.* (2005) found that the loss of the insectivorous, cover-dependant guild, which includes the superb fairy-wren, occurred in the transition from native streetscapes to exotic and newly developed streetscapes and was linked to the loss of suitable shelter locations. Limitation in the availability of this layer has also been implicated in lower nesting success of insectivores (Boal and Mannan 1999; Matthews *et al.* 1999), with the lack of cover making predation by corvids and other nest predators more likely (Danielson *et al.* 1997; Matthews *et al.* 1999; Jokimäki and Huhta 2000; Marzluff *et al.* 2001; Kristan *et al.* 2003), though relationships demonstrated are generally correlative rather than causal (Chace and Walsh 2006).

The floristic characteristics of urban habitats also influence urban bird communities to a lesser extent than structure. In this study superb fairy-wrens responded positively to both the presence of native shrubs as well as the presence of the introduced weed, lantana. Native species, including the superb fairy-wren have been shown to be more selecting in their choice of plants, usually utilising native vegetation in both more traditional (Nias 1984; Ligon *et al.* 1991; Nias and Ford 1992; Brooker and Rowley 1995; Chan and Augusteyn 2003) and urban habitats (Jones 1981; Green 1984; Catterall *et al.* 1989; Mills *et al.* 1989; Day 1995; Sewell and Catterall 1998; Parsons *et al.* 2006). However, the value of dense, exotic vegetation such as brambles, blackberry and other weeds has also been indicated (Nias 1984; Ligon *et al.* 1991; Nias and Ford 1992; Brooker and Rowley 1995; Chan and Augusteyn 2003). Given that superb fairy-wrens largely forage on open grass rather than in shrubs (Tidemann 1983; Recher *et al.* 1985; Ford *et al.* 1986; Cale 1994; Chapter 4), it is likely that the dense, protective coverage offered by lantana is driving the preference for this weed rather than its potential to harbor a food source, and its value as a food source is unknown. In suburban locations, given that the foraging habitat, open grass, is likely to be abundant in most areas, the presence of shrubs is likely to have a substantial influence on the ability of superb fairy-wrens to occupy a site. Where lantana is absent from a site, the availability of native shrubs is necessary in order to support this species.

Native birds are generally associated with native vegetation (Green 1984, 1986; Parsons *et al.* 2006). However, this is generally thought to be due to native birds being more selective in their use of native or exotic vegetation than introduced species, rather than an overall preference for the origin of the plants (Catterall *et al.* 1989; Green *et al.*

1989). Differences in the structure of the vegetation and food availability are thought to be responsible for the general preference of most birds for native vegetation (Green 1984; Bhuller and Majer 2000).

6.2 What Effect Does the Urban Landscape have on the Superb Fairy-wren?

Suburban superb fairy-wrens modified their behaviour, habitat usage and foraging abilities to cope with different resource availability in the urban landscape. Individuals utilised their territory more efficiently, occupying a smaller area than in non-suburban (rural/remnant habitats). However, the quality of the arthropod food available was poorer, with individual items being smaller in size, though there was equivalent biomass in non-suburban locations. To account for this, urban superb fairy-wrens have modified their behaviour and devote more of their time to obtaining food. Flexibility in habitat utilisation and behaviour has allowed this species to successfully colonise some locations.

Territory size has also been shown to have an inverse relationship to habitat quality in other urban landscapes worldwide. As habitat quality decreases, individuals or groups must search greater distances in order to obtain sufficient resources. Conversely, when habitat quality is high, individuals or groups are able to obtain all resources in a smaller area and do not need to defend larger boundaries from conspecifics. Raptors are a group in which this relationship is particularly well studied (Village 1982; Sodhi and Oliphant 1992; Bloom *et al.* 1993; Marzluff *et al.* 1997; Leary *et al.* 1998). However, raptors often have large territory boundaries which extend beyond the urban landscape and therefore do not always meet all of their ecological requirements within these urban areas (Chace and Walsh 2006). There have been only a few studies which have

demonstrated this territory size and quality relationship for other bird species (Smith and Shugart 1987; Rolstad *et al.* 1998; Bonar 2001; Schwarzova and Exnerova 2004). If small territory size is a general indicator of high territory quality, then measurements of territory size in this study indicate that more suburban landscapes are of higher quality for superb fairy-wrens than remnant edge habitat. However, this contradicts the findings of Berry (2001) and the data on food availability found in this study.

Utilising different methods for calculating territory size allowed me to further explore the relationship between size, quality and habitat use. Superb fairy-wrens were shown to occupy smaller territories in suburban landscapes compared to non-suburban (remnant edge habitat) using 95% minimum convex polygon (MCP), a calculation that simply joins 95% of the outermost fixes recorded for an individual. This method has the potential to overestimate territory size in poorer quality habitats where there are areas of unsuitable habitat within territories (Harris *et al.* 1990). However, this difference in territory size was not observed for the 95% fixed kernel method. Fixed kernel calculations determine the actual proportion of time which individuals spend in each location, and therefore give an indication of habitat usage (Worton 1987). Comparisons of these two methods of territory calculation allow conclusions of habitat usage within territories to be made (Van Winkle 1975; Worton 1987). Differences in the sizes of territories calculated by the two methods here suggest that suburban fairy-wrens were using their habitat more extensively than non-suburban fairy-wrens. Non-suburban superb fairy-wrens had larger territories overall but spent most of their time in part of their territory equivalent in size to suburban territories. Birds were therefore maximising habitat usage within suburban territories but had larger areas of unused habitat within

non-suburban territories. Therefore greater energy would be expended by non-suburban birds defending larger boundaries and making occasional forays into infrequently used parts of their territory. Previous comparisons of territory size calculated by fixed kernel and MCP methods have shown a similar pattern of habitat usage for a range of fauna, including the migratory passerine cerulean warbler (*Dendroica cerulean*)(Barg *et al.* 2005), red-cockaded woodpecker (*Picoides borealis*)(Franzreb 2006) and the komodo monitor (*Varanus komodoensis*)(Ciofi *et al.* 2007).

Estimates of territory sizes of superb fairy-wrens calculated here (for both urban and rural/remnant sites) were indicative of higher quality superb fairy-wren territories calculated elsewhere. The high quality habitat of ironbark forest in the Australian National Botanic Gardens has resulted in a habitat saturated with superb fairy-wren territories averaging 0.6 ha (Mulder 1992). This habitat is not part of a natural system, being largely planted and managed and therefore this high quality and small territory size is unlikely to be represented in other natural forests and woodlands. Territories of 1.25 ha and 1-2 ha were also recorded in rural fragmented habitats, where not all available habitat was suitable (Tidemann 1983; Nias 1987). However limited resources in fragmented Acacia woodlands resulted in territory sizes of 8.6 ha (Chan and Augustyn 2003). Given the similarity of territory sizes here (suburban: 1.4 ha both MCP and fixed kernel; non-suburban: 2.6 ha MCP and 1.7 ha fixed kernel) to other comparatively high quality habitats in fragmented environments it appears both these urbanised environments provide comparatively high quality habitat for this species in terms of vegetation requirements.

Despite both suburbs and remnant edges being overall high quality habitat as determined by territory size, there were differences in food availability and consequently differences in foraging behaviour observed. The total diversity of orders available, the numbers of individuals sampled and the total biomass did not differ between suburban habitat and habitats found along rural/remnant edges. However, the average biomass of individuals at each site was smaller in suburban wild habitat, suggesting that, overall, suburban habitats tend to be characterized by smaller individuals. Individual arthropods tended to be smaller in suburban habitats, both in long and short grass than in non-suburban habitats.

Generalist insectivores, such as the superb fairy-wren, are less likely to be affected by a loss of the arthropod diversity, and more by a decrease in overall abundance. Previous analyses of diets of superb fairy-wrens have indicated that this species feeds upon over 40 families of arthropods (Rowley 1965; Tidemann *et al.* 1989; Barker and Vestjens 1990). With the exception of the Acari order, the six other orders sampled that comprised 97% of the total biomass in this study have been previously represented in the diet of superb fairy-wrens (Barker and Vestjens 1990). While adults feed upon small items, large arthropods are identified as important resource for nestlings. However, previous studies have not indicated what size constitutes ‘small’ or ‘large’ items. This study is the first to examine the arthropod biomass that can potentially be obtained as a food source for this species as opposed to diversity only. The biomass of individual arthropods was, on average, smaller in suburban habitats than in non-suburban, remnant-edge habitat. If the biomass of the arthropods available for nestlings is smaller and members of the group are unable to compensate for this by increasing feeding

frequency, then there may be impacts on the fitness and survivorship of urban nestlings, however as yet this is unknown. Insufficient food availability has been demonstrated to be responsible for higher nestling mortality for a range of urban-dwelling species including European starlings (*Sturnus vulgaris*) (Mennechez and Clergeu 2006), common blackbirds (*Turdus merula*) and song thrush's (*Turdus philomelos*) (Schnack 1991). Solonen (2001) demonstrated that, while great tits (*Parus major*) and blue tits (*P. caeruleus*) had smaller average clutch sizes in urban versus rural habitats, this was not directly due to a shortage of their arthropod food supply during the breeding season (Solonen 2001). Still, poor food quality prior to the breeding season in urban habitats may have been partially responsible for smaller clutch sizes.

Adult superb fairy-wrens appear to have responded to the availability of smaller-sized arthropods by modifying their foraging behaviour. By increasing foraging duration to nearly double that occurring on the remnant edge, individuals are likely to be able to obtain sufficient resources. Such differences in foraging and other behaviours have rarely been examined in the urban landscape. Florida scrub-jays (*Aphelcoma coerulescens*) forage more efficiently in urban areas due to the provisioning of supplementary food which promotes earlier nesting (Fleischer Jr *et al.* 2003). Diet-switching allows this omnivorous species to cope with decreased natural food supplies in the urban landscape (Sauter *et al.* 2006). However, by foraging more frequently in the open, superb fairy-wrens are likely to be more exposed to predation risk. Therefore there are a range of factors that influence the quality of a habitat. Measurements of quality should consider both vegetation requirements as well as the food availability of the habitat.

6.3 Long Term Impacts of Life in Urban Environments

When settling in a habitat patch, individuals must assess the suitability and quality of the site, not only for immediate survival, but also for the potential of successful reproduction (Cody 1985; Charlesworth 1994; Sutherland 1996). Those species in the urban wildlife community that function most successfully within urbanised habitats are those that are not confined to only one habitat type, or patch, but those that can move within and throughout a variety of different patches of varying qualities (Davis and Glick 1978). An optimal patch is therefore one where all the requirements of individuals are all met such that the population can breed at replacement levels, i.e. it is not a 'sink' population (Donovan *et al.* 1995). A reduction in the availability of optimal habitat would therefore force individuals into sub-optimal patches, which would then have consequences for the future reproductive output of the population (Lambrechts *et al.* 2004).

Under normal conditions, individuals would settle preferentially in the best quality habitat available (Fretwell and Lucas 1970). Indeed, habitat preferences have been shown to be positively related to habitat quality (Muller *et al.* 1997; Martin 1998). In this study, there was little difference in the overall quality of urban superb fairy-wren habitat and remnant edge habitat. While territory quality was apparently higher in urban habitats, as indicated by smaller territory sizes, individual food items were smaller, forcing a change in behaviour by foraging individuals.

This study found that the urban environment has good quality habitat patches for the superb fairy-wren to occupy, though occupancy is limited by vegetation suitability. There are long-term consequences of urban habitat selection, however, that have not been

examined here. Particularly important is the ability of superb fairy-wrens to recruit juveniles into the breeding population, thus ensuring the long-term survival of the species in the urban landscape. If the urban landscape is attracting superb fairy-wrens due to food availability and suitable vegetation patches, yet, through predation levels or other detrimental impacts, is unable to support recruitment and survival, then the urban environment may actually be acting as an ecological trap. In some cases, the quality of a habitat becomes mismatched with the reproductive output and survival of the species, usually due to some vegetation characteristics (Dwernychuk and Boag 1972; Gates and Gysel 1978). Rather than an apparently suitable habitat being cued with positive outcomes, those cues become linked with negative ones, resulting in an ecological trap. Such an ecological trap results in a population sink, whereby, a species becomes locally extinct because individuals are unable to be recruited into the breeding population, yet immigration into the habitat still occurs.

In an ecological trap, individuals actively select the poor quality habitat rather than occupying the poor quality habitat once high quality habitat is filled (Battin 2004). These ecological traps are often influenced by some other factor such as increased predation or human disturbance that suppresses reproductive output (Gates and Gysel 1978; Misenhelter and Rotenberry 2000). It is suggested that ecological traps are more common in human-modified landscapes than natural ones (Dwernychuk and Boag 1972; Gates and Gysel 1978; Best 1986; Misenhelter and Rotenberry 2000; Vierling 2000). Cooper's hawks (*Accipiter cooperii*) nesting in Tuscon, Arizona occur in much higher densities in the city than in the surrounding landscape because of greater prey sources found at bird feeders (Boal and Mannan 1999). While urban birds nest earlier and hatch

larger clutches, the mortality of nestlings is much greater in the city (> 50%) compared to exurban areas (< 5%) due to high infection levels of trichomoniasis in their prey items (primarily doves and pigeons)(Boal and Mannan 1999). Population levels are not declining in the city, suggesting that birds are immigrating from outside areas in response to the abundance of nest locations and prey.

Superb fairy-wrens settle preferentially in some urban locations that have high proportions of vegetation (particularly native shrubs or lantana), but there are a range of predation risks that are elevated throughout the urban landscape. The impact of domestic cats (*Felis catus*) on international urban avian populations as a whole is debatable (Churcher and Lawton 1987; Jarvis 1990; Barratt 1997, 1998; Woods *et al.* 2003; Lepzck *et al.* 2004; Baker *et al.* 2005; Sims *et al.* 2008). However, domestic cats are known to prey upon superb fairy-wrens and other small Australian native birds (Barratt 1997), and adult survival and juvenile recruitment may be limited in urban habitats with high cat predation (Barratt 1997). A number of Australian aggressive and predatory birds such as the noisy miner (*Manorina melanocephala*) and pied currawong (*Strepera graculina*) are also in higher numbers in urban and edge habitats compared to their traditional habitats. Noisy miners aggressively exclude other birds, particularly small species, from their territories and are suggested to play a part in the decline of small birds, including the superb fairy-wren from urban habitats (Catterall *et al.* 2002; Catterall 2004; Parsons *et al.* 2006) as well as edge habitat (Dow 1977; Grey *et al.* 1997, 1998). Pied currawongs prey upon the eggs and nestlings of small birds, sometimes also taking adults (Major *et al.* 1996; Wood 1998). They have become abundant in the urban landscape due to the provisioning of fruit-bearing trees such as privet (*Ligustrum sp.*) which provide a year-

round food source (Buchanan 1989; Bass 1995). With urban landscapes subjecting superb fairy-wrens to potentially increased predation pressures, while providing suitable attractive habitat and sufficient food, an ecological trap may be present. However, in addition to knowledge of the mortality rate of adults, reproductive success of superb fairy-wrens in the urban landscape, as well as within equivalent edge habitat is also needed.

Examinations of the response of passerines to urbanisation are often lacking important reproductive information (Van Horne 1983). Of the research that is available, there appears to be no clear relationship between breeding success in urban and natural environments. Some species, such as the Greenfinch (*Carduelis chloris*) show increased success along an urban gradient (Kosinski 2001), whereas other species, belonging to a range of guilds, show decreased nest success with increased urbanisation (Schnack 1991; Matthews *et al.* 1999; Mennechez and Clergeu 2006). Others have shown no change in nest success (Bowman and Wolfenden 2001; Blair 2004; Beck and Heinsohn 2006; Leston and Rodewald 2006). Due to the lack of research it is, as yet, difficult to interpret factors which influence urban breeding success.

As in international studies, the measurement of the breeding success of birds in Australian urban areas is uncommon (but see Major *et al.* 1996). Analysis of the Australian Nest Record database, however, has indicated some species which prefer to breed in urban areas, and some which are more successful at breeding (McMahon 2005). The superb fairy-wren showed a preference for nesting in habitats other than urban ones, however, it fledged young more successfully in urban locations (urban = 72% success; non-urban = 67%)(McMahon 2005). This supports the suggestion that a lack of a suitable

shrub layer is again the limiting factor in the distribution of superb fairy-wrens in urban areas. While superb fairy-wrens appear to breed successfully where nest locations are found and have a high fledging rate, juvenile mortality is unknown. Given juvenile birds are particularly susceptible to cat predation (Barratt 1997), the potential for the urban landscape to be acting as an ecological trap cannot be ruled out.

Under favourable conditions, superb fairy-wrens demonstrate high levels of extra-pair paternity (76% - Mulder 1992). This social monogamy results in the majority of young being raised by fathers and siblings from which they are not directly related. Consequently, when the dominant male in a family group dies, a juvenile from within the same territory or an outsider male may take his place (Rowley and Russell 1997). While the ability of superb fairy-wrens to breed successfully in urban areas has been demonstrated (McMahon 2005), the degree of extra-pair fertilisation is unknown in this habitat.

Rather than occurring in locations saturated with territories as was the case for Mulder's research (1992), territories in urban landscapes as well as in forest interiors and shrublands are generally much more fragmented and isolated. In this study, no more than 2 territories were ever observed adjacent to each other and in most cases, there were no adjacent territories. There may be long term disadvantages to living in an urban habitat that is unknown currently if outsider males are unable to fill territories. In habitats with less isolated territories, such as in the optimal habitat of the National Botanic Gardens in Canberra, high divorce rates and turnovers of dominant females results in most of the males being unrelated to the female (Dunn *et al.* 1996). Young males related to the females do not compete with those that are unrelated for breeding opportunities (Dunn *et*

al. 1996). This type of saturated habitat is generally not found in natural systems (Chan and Augustyn 1996). In heterogenous landscapes such as in urban habitats and forest interiors, spatial patchiness of suitable habitat, resulting in isolation of territories, may restrict the options of the dominant female for mate choice, resulting in poorer quality offspring or reduced mating attempts. Territories may become abandoned or there may be genetic consequences of inbreeding that may result if son-mother pairings occur. There is a need to understand the reproductive response of superb fairy-wrens to the isolation of territories and the ability of superb fairy-wrens to disperse in urban and fragmented landscapes, factors that are currently not understood.

The restriction and isolation of territories in urban habitats may also inhibit the establishment of new superb fairy-wren territories. Juvenile females are driven out from the natal territory at the commencement of the breeding season and dominant females only divorce when their territory changes or a vacancy appears in a nearby one (Cockburn *et al.* 2003). Such behaviour is not only consistent with incest avoidance but also enables sons to compete for within group mating (Cockburn *et al.* 2003; Cockburn 2007). If the area surrounding superb fairy-wren territories is unsuitable then the potential for a dominant female to leave would be expected to be reduced and juvenile females would also be less likely to find suitable habitat in which to establish a new territory. The long term consequences of limited dispersal are unknown.

6.4 Conclusions

There are areas within the urban landscape that provide a quality of habitat for superb fairy-wrens that is equivalent to that of rural-remnant edge locations (thought to

be a preferred location). However, a shortage of suitable vegetation, particularly the shrub layer, appears to be limiting the distribution of this species. While generally found in urban habitats with native shrubs, lantana and other introduced vegetation are also utilized by this species. Males were shown to compensate for a reduction in the size of arthropod prey items (largely due to the comparative rarity of orthopterans in suburban locations) by increasing the duration of foraging without sacrificing other territorial, maintenance and reproductive behaviours such as calling and preening. The non-significant trend found for females (likely to be due to the small sample size) suggests this is the case for both genders. This may, however, expose suburban superb fairy-wrens to greater predation risk. Calculations of territory size performed here show that suburban territories are smaller, and therefore of higher quality for this species, with larger portions of remnant edge territories being unsuitable and therefore unused. Further, the sizes of territories measured in both habitats here fall at higher quality end of the territory size spectrum calculated in previous studies and is similar to sizes calculated for other fragmented habitats, again suggesting that these two habitats, with contrasting degrees of urban impact, provide suitable, successful habitat for this species.

There are long-term effects of life in the urban landscape that are not understood for this, and many other bird species. If unable to breed successfully, and subject to high adult mortality, then the urban environment could be acting as an ecological trap, pulling in superb fairy-wrens from other edge or more traditional habitats nearby with favourable shrub layers (both native and lantana) and available arthropod resources. Given it is a noxious weed, lantana is not suitable for planting to create superb fairy-wren habitat, instead, its removal is necessary for the conservation of other native flora and fauna.

Removal and replacement with alternative shrubs must be done carefully and slowly to avoid disturbance to superb fairy-wrens and other organisms that use lantana for food and/or shelter. There is also a need to understand the reproductive behaviours and breeding success of this species in these types of landscapes to understand the true impact of urbanisation. With present knowledge, the best strategy for enhancing the ability of this species to occupy urban habitats is to increase shrub plantings, particularly native shrubs in gardens, which will complement existing foraging opportunities provided by an abundance of short grass habitat.

6.5 References

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