Ecology of an urban-adapted species over an urbanization gradient

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I am the author of the thesis entitled

Ecology of an urban-adapted species
over an urbanization gradient

submitted for the degree of

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Brooding male tawny frogmouth on the nest, Westerfolds Park, Melbourne, Victoria, Australia. Photo: Marian Weaving.
Preface

This thesis is a compilation of my own work, where I designed the method for the study with guidance from my supervisors Dr Raylene Cooke, Associate Professor John White and Dr Fiona Hogan. I conducted all of the fieldwork, collected and organised all data and undertook all the analyses associated with this research. I drafted and revised this entire thesis and all photographs are my own except where credited. All of the thesis chapters have been written as manuscripts for publication. Each chapter is therefore self-contained and some repetition occurs, especially in the methods sections. As required by Deakin University all references have been placed at the end of the thesis not at the conclusion of each chapter. Two chapters (2 and 3) have been published with chapter 4 in press and chapter 5 under review. These manuscripts have been co-authored with the above mentioned supervisory panel and they have therefore contributed to the ideas presented in each.

Chapter 2:

Chapter 3:


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It’s been quite a journey. My fellow travellers, companions, contributors and supporters are gratefully acknowledged in the following pages.

Without being too biblical, in the beginning there was Dr Raylene Cooke, Dr John White and Dr Fiona Hogan. What an incredible team you make. You’re all such a credit to your profession. Ray, your skills and personal qualities are too many to list here but your faith in my abilities and your love and curiosity for nocturnal birds kept me on track and got me to the end. Similarly for you John but with a couple of additions. Your capacity to enthusiastically bring together ideas and concepts; and your uncanny ability to recognise when it was time to shove me out of my comfort zone to take my learning to another level! Thank you so much Fiona, your skills and enthusiasm for all things molecular was inspiring as was your patience in teaching me how to extract DNA and more importantly, to understand what it was telling me. I discovered an entirely new and fascinating field that added greatly to this project.

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Finally, to Barbara Goddard who died in 2005. Undertaking life changing projects like a PhD puts the spotlight on your strengths and your weaknesses. When I needed some strength I thought about her and her life.

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So in the end, Dr Raylene Cooke, Dr John White (now both Associate Professors) and Dr Fiona Hogan are still here. The road to completion (as I now know), is not unlike a road trip. GPS malfunctions, unexpected discoveries, on-the-road repairs, bad food and lots of “are we there yet?” comments from the back seat (friends and family). So yes, we are there now. Congratulations to us all.

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Abstract

Urbanization continues to intensify, transforming the planet into areas dominated by human habitation and anthropogenic activities. Australia, similar to many other countries, is already highly urbanized with predictions that this trend will escalate in the coming decades. Urbanization results in a loss and reduction of biodiversity values, producing highly modified ecosystems that support biologically homogeneous communities of taxa. Native species are often greatly reduced, while exotic species are frequently over-represented. Resource specialists such as hollow-dependant species and those requiring large areas of natural habitat frequently decline, while others with greater ecological flexibility and adaptive traits can thrive in urban landscapes. One such species is the tawny frogmouth (*Podargus strigoides*), a species which appears to have adapted to and flourished in urban habitats. Identifying the factors that support their occupation of urban systems forms the basis of this research.

The aim of this research was to investigate the response of the tawny frogmouth to an urbanization gradient. Specifically, how urbanization impacts on various ecological functions. By utilizing a range of methods and approaches we (1) investigated the distribution and individual response to urbanization of three common and wide-spread nocturnal bird species; (2) investigated how urbanization influences the spatial ecology of the tawny frogmouth; (3) examined the impact of urbanization on tawny frogmouth reproduction; and (4) investigated whether urbanization influences the genetic profile of the species.
Abstract

This research was undertaken across an area representing a gradient of urbanization ranging from forested environments to suburban locations in Melbourne, Victoria, Australia. The distribution of the tawny frogmouth was ascertained by day-time detection, call playback and spotlighting techniques. Ecological information was obtained by systematically searching locations throughout the study area to locate birds, obtain data on nesting and roosting activities and to collect genetic samples. Intensive night-time field-work was undertaken to capture individual birds and to radio-track their activities and movements.

The tawny frogmouth, along with the southern boobook and Australian owlet-nightjar, represent three key members of the nocturnal bird community in Australia. All three species are widespread and common but differ substantially in their ecological requirements. The southern boobook and Australian owlet-nightjar are obligate cavity users while the tawny frogmouth is a non-hollow dependant species. The effects of urbanization on all three species were investigated at several scales by comparing broad landscape attributes with species distributions, and by modelling the influence of site level attributes on species presence. While all three species occurred in the urban-fringe environment, the presence of the tawny frogmouth increased with increasing levels of urbanization while the presence of both the southern boobook and Australian owlet-nightjar showed a corresponding decline. These results indicate the significance of urban-fringe environments to all three species but in particular, highlights the capacity of tawny frogmouths to tolerate urban environments.
Abstract

The capture and radio-tracking of individual tawny frogmouths highlighted two important aspects of their spatial ecology; that habitat features including trees and grassy mown areas are important components of the tawny frogmouth home-range, and that home-range size is sex-biased. Male mean home-range was 17.65 ± 4.35 ha (n=7) and female 6.55 ± 1.40 ha (n=5). In the broader urban landscape, and within the core activity areas of their home-range, tawny frogmouths located their home-range in areas containing more trees, avoiding impervious surfaces and utilizing open mown grassy areas. As urbanization levels intensified, male home-range size increased whereas female home-range remained static in size. These results highlight the importance of trees and grassy areas to tawny frogmouths. Trees in particular are a key habitat resource used by the species for day-time roosting, night-time foraging and for important life-cycle events such as breeding.

An assessment of tawny frogmouth reproductive behaviour indicated that in urban environments tawny frogmouths experience high reproductive success. One hundred and fifty eight nest sites were located and 189 breeding attempts monitored across four breeding seasons. One hundred and thirty three of these attempts successfully fledged 177 chicks. Seventy-five of these attempts were categorised as first attempts for the season resulting in 77 fledged chicks. Tawny frogmouths demonstrated rapid and multiple re-nesting attempts after nesting failure and double brooding behaviour. Highly vegetated areas of the gradient were selected for nest site location while more highly urbanized areas were avoided. No particular land-use type impacted on breeding success at both broad and local scales, however, birds selected native rough-barked trees more frequently than any other tree species as a nest site. Climatic variables, in particular rainfall was a key driver for commencement of breeding. These results
highlight the capacity of tawny frogmouths to synchronize their breeding to optimal
environmental conditions indicating successful adaptation to local environmental
conditions and high individual fitness.

Landscape modification by urbanization had little impact on the genetic profile of
tawny frogmouths with analysis showing high genetic diversity and structure with no
evidence of population sub-structure. Resistance modelling revealed that increasing
urbanization (impervious surfaces), did not impede tawny frogmouth movements
across the landscape. Results showed that tawny frogmouths do not disperse over large
distances in urban environments. While shorter dispersal distances may be indicative
of barriers to movement, these findings are driven by female birds, indicating that
dispersal in the species is biased to males. For the non-dispersing sex the benefits
derived from remaining close to the natal territory include resource familiarity, which
is important for successful reproduction and survival. Female philopatry in tawny
frogmouths may be a factor that underpins their high reproductive success in urban
systems.

This research has significantly expanded our knowledge of the tawny frogmouth, in
particular, how the species responds to urban environments. While tawny frogmouths
are widespread in these systems, in highly urbanized areas where tree cover may be
substantially reduced, populations are likely to decline or become locally extinct.
Practical conservation of the tawny frogmouth should aim to preserve highly
heterogeneous urban landscapes, in particular, maintaining and prioritizing the
inclusion of urban greenspace into new housing developments.
Chapter 1: Introduction

Tawny frogmouth adults with fledged chick (centre) roosting in manna gum tree (*Eucalyptus viminalis*) in a suburban park in Melbourne, Victoria, Australia.

Photo: Peter Bermingham.
1.1 Introduction

Urbanization is occurring at a rapid and unprecedented rate across the globe (United Nations 2014). Over half of the world’s population (54%), live in urban centres, and by 2050 this figure is predicted to increase to 66% (United Nations 2014). The rate of urbanization in Australia is one of the highest in the world with over 89% of the population occupying urban centres and recent estimates predict this figure to rise to over 93% by 2050 (United Nations 2014).

The process of urbanization converts natural environments into landscapes characterised by an abundance of impervious surfaces and built structures (McKinney 2002; Pickett et al. 2001). The process begins with the removal of natural vegetation to accommodate the construction of cities, towns and associated infrastructure (Alberti 2005). Remaining natural vegetation is often confined to small patches scattered throughout the landscape and surrounded by a matrix of differing land-use types (McKinney 2006; Niemelä 1999). Over time these patches become increasingly fragmented and spatially disjunct from each other and modified internally by a range of anthropogenic pressures (Bastin and Thomas 1999; Fernandez-Juricic 2000a).

The unprecedented consumption of land for urban use has devastating and profound consequences for biodiversity worldwide (McKinney 2002; Seto, Güneralp and Hutyra 2012). Despite our limited understanding of the response of many organisms to urbanization, much ecological research still continues to focus on biodiversity in more natural environments. This may be due to the difficulties associated with integrating human processes into ecological research (Grimm et al. 2000; Pickett et al. 2001). With
urbanization rates predicated to escalate in coming decades, this situation is rapidly changing with more research focusing on urbanizing landscapes in order to halt the loss, decline and displacement of species worldwide (Chace and Walsh 2006; McKinney 2002; Vitousek et al. 1997).

Urbanization results in multiple land-use types spatially interspersed with each other throughout the landscape (Luck and Wu 2002; McKinney 2002). Urban landscapes typically range from highly urbanized city centres to moderately wooded urban-fringe or peri-urban environments to large tracts of forested lands on the city margin (McDonnell and Hahs 2008). In urban ecological research the urbanization gradient approach (also termed urban-rural gradient, urban-exurban gradient) is used to examine the response of species to different intensities of landscape modification (McDonnell and Pickett 1990; McDonnell et al. 1997).

1.2 Species response to urbanization

In urban systems the predominance of impervious surfaces, artificial structures and the loss and reduction of vegetation, produces environmental conditions vastly different to those in more natural environments (Botkin and Beveridge 1997; McKinney 2002). Elevated temperatures, altered hydrology, homogenous vegetation types and pollutants including chemical, noise and artificial night light, are features commonly associated with urban environments (Bridgman, Warner and Dodson 1995; Svensson and Eliasson 2002). These conditions produce highly altered and modified ecosystems that influence the spatial arrangement and functioning of many organisms (Alberti 2005; McKinney 2002).
Introduction

The dramatic changes to the natural environment resulting from urbanization acts as a filter selecting against species or groups of species dependant on factors such as species-specific traits and behavioural flexibility (Croci, Butet and Clergeau 2008; Lizée et al. 2011; Smart et al. 2006). Urban studies describe compositional changes to mammalian community structure (Bonnington, Gaston and Evans 2014; Prange and Gehrt 2004; Riem et al. 2012), invertebrate communities (Blair and Launer 1997; Niemela et al. 2002), reptile populations (Germaine and Wakeling 2001) and avian community composition (Blair 1996; Bolger, Scott and Rotenberry 1997; Melles, Glenn and Martin 2003).

Taxa commonly found in urban systems often demonstrate particular physical characteristics and ecological traits including a broad dietary base, high annual fecundity rates and sedentariness (Kark et al. 2007; Moller 2009; Prange and Gehrt 2004). They also frequently display a level of behavioural adaptation or tolerance, adjusting their ecological behaviour to interact with, and survive in urban environments (Lizée et al. 2011; Sol, Lapiedra and González-Lagos 2013). Termed urban-adaptors (McKinney 2006), adjustments commonly observed include altered spatial behaviour (Dowding et al. 2010; Gese, Morey and Gehrt 2012; Hodgson, French and Major 2007), altered foraging behaviour due to human-mediated food resources (Gehlbach 2012; Prange, Gehrt and Wiggers 2004) altered reproductive behaviour (Ancillotto, Tomassini and Russo 2015; Chamberlain et al. 2009) and modified vocalizations in response to urban noise (Nemeth et al. 2013).
1.3 Impacts of urbanization on avifauna

Bird species, due to their conspicuousness and sensitivity to landscape change and modification (MacGregor-Fors 2008; Savard, Clergeau and Mennechez 2000) feature prominently in research investigating the effects of urbanization. Studies show that as urbanization intensifies urban bird assemblages typically contain low native species richness, with avian biomass highly elevated, often by a disproportionate number of introduced and exotic species (Beissinger and Osborne 1982; Blair 1996; Clergeau et al. 1998; Sewell and Catterall 1998). Native species associated with more natural environments, including habitat specialists, generally disappear or decline as urbanization increases (Crooks, Suarez and Bolger 2004; Donnelly and Marzluff 2006). Some foraging guilds including nectivorous and omnivorous species appear advantaged by resources common to the urban environment, while others including insectivores are most impacted due to a decline in resources associated with native vegetation loss (Lim and Sodhi 2004; White et al. 2005). The gradual replacement of native species with non-indigenous and exotic biota described as “biotic homogenization” (McKinney and Lockwood 1999), has been observed both internationally (Blair 1996; Clergeau et al. 1998; Melles, Glenn and Martin 2003) and in Australia (Sewell and Catterall 1998).

Although many species are impacted negatively by urbanization, there is evidence that others demonstrate a tolerance to urbanization and an ability to establish and maintain populations in these systems. Examples of urban-adapted avian species include the northern mockingbird (*Mimus polyglottos*), Cooper’s hawk (*Accipiter cooperii*), wheatear (*Oenanthe oenanthe*), great tit (*Parus major*), and Florida scrub-jay (*Aphelocoma coerulescens*) (Boal and Mannan 1998; Fleischer, Bowman and Woolfenden 2003; Meffert, Marzluff and Dziock 2012; Slabbekoorn and Peet 2003;
Introduction

Stracey and Robinson (2012) identified factors and attributes common to urban systems as highly important to a species’ capacity to adapt and remain in urban environments (Anderies, Katti and Shochat 2007), including higher ambient temperatures, reliable and constant water sources, stable and multiple prey types, and human-derived food resources (Chace and Walsh 2006). For some native urban-adapted species, the benefits derived from living in urban environments result in abundances higher than those in more natural environments, suggesting that urban environments may not function as sink environments for some species (Stracey and Robinson 2012).

Comprising numerous types of artificial structures and a multitude of greenspace, urban systems are highly heterogeneous environments. As a unique landform, the built environment and urban greenspace now represent a growing and important land-use type for many avian species (Bryant 2006; Sandström, Angelstam and Mikusiński 2006). In its many forms, the importance of greenspace to avian biodiversity is well documented with findings demonstrating the importance of native remnants (Crooks, Suarez and Bolger 2004; Donnelly and Marzluff 2004), planted and managed parks and gardens (Loss, Ruiz and Brawn 2009; Sewell and Catterall 1998), residential properties (Boal and Mannan 1998; Lerman and Warren 2011), urban wastelands and vacant blocks (Meffert, Marzluff and Dziock 2012), streetscape vegetation (Fernandez-Juricic 2000; White et al. 2005) and small parks (<2 ha) (Carbo-Ramirez and Zuria 2011; Ikin et al. 2013).

At a local scale, greenspace can sustain a diverse avifauna, although species richness depends on factors including patch size, vegetation characteristics of the patch,
structure and function of the patch and characteristics of the surrounding matrix (Clergeau et al. 2006; Fernández-juricic and Jokimäki 2001; Fitzsimons, Antos and Palmer 2011). Remnant patches can support high species diversity independent of bird communities in neighbouring landscapes (Clergeau, Jokimaki and Savard 2001), while greenspace networks provide movement corridors for dispersing individuals, linking populations by maintaining gene flow across the landscape (Bolger, Scott and Rotenberry 2001). In fragmented landscapes such as urban systems, maintaining connectivity and subsequently gene flow is of particular importance in order to insulate species from some of the more detrimental genetic consequences of population isolation (Fahrig 2003). Remnant patches provide refuge for threatened species (Ives et al. 2016; Meffert and Dziock 2012), resources for overwintering migratory species (Carbo-Ramirez and Zuria 2011), and for species considered habitat specialists more commonly associated with natural landscapes (Caula, Villalobos and Marty 2014; Mörtberg and Wallentinus 2000).

An example of a habitat specialist demonstrating an adaptive response to urban environments is Cooper’s hawk (*Accipiter cooperii*), a native American raptor species which has successfully colonised and established populations in Tucson, Arizona. In a study investigating reproductive behaviour, nest densities were found to be higher in urban locations than in exurban sites. Factors associated with these higher densities included high prey availability, permanent water sources and the abundance of large trees as nest sites. In this study, breeding pairs selected exotic and introduced trees species more frequently than native species with most nest trees situated in the gardens of residential properties and in high-use recreational areas such as large parks (Boal and Mannan 1998). Another northern-hemisphere species, an insectivorous native passerine
the wheatear (*Oenanthe oenanthe*), is regarded as an open-land species inhabiting rural landscapes and more recently, urban areas (Meffert and Dziock 2012). A recent study of urban breeding pairs in Berlin, Germany, report high reproductive success attributed primarily to their use of sparsely vegetated urban wastelands scattered throughout the city (Meffert, Marzluff and Dziock 2012).

In comparison to diurnal species, the ecological response of nocturnal birds to urbanization is less studied and consequently less understood. Much research to date has focused on nocturnal raptors comparing species occupying urban and suburban (Ranazzi, Manganaro and Salvati 2000; Zalewski 1994) and urban and rural environments (Minor, Minor and Ingraldi 1993; Smith, Bosakowski and Devine 1999). Research examining nocturnal bird species response to gradients of urbanization have occurred less frequently. Notable exceptions include research investigating various ecological requirements of the powerful owl (*Ninox strenua*) an iconic Australian apex predator (Cooke et al. 2006; Cooke, Wallis and Webster 2002; Isaac et al. 2013).

Even less represented in the literature is the response of non-raptorial nocturnal species (frogmouths and nightjars) to urbanization (Liley and Clarke 2003). In Australia, members of the *Aegothelidae* and *Podargidae* families are key representatives of the nocturnal bird community yet there exists a paucity of information regarding many aspects of their ecology (Hollands 1991). With few exceptions, most research to date has focused on populations inhabiting rural or forested environments (Beruldsen 2003; Brigham et al. 1999; Doucette 2010; Geoffrey and Benjamin 2009; Kavanagh and Bamkin 1995). Their response to habitat loss and fragmentation in urban areas is almost virtually unknown. Unlike many owl species, frogmouths and nightjars are not reliant
on large hollow bearing trees for shelter and breeding and are not constrained by specialist dietary requirements. In Australia, both the Australian owlet-nightjar (*Aegotheles cristatus*) and the tawny frogmouth (*Podargus strigoides*), are common and widespread throughout a range of habitats including urban environments (Schodde and Mason 1980).

1.4 The tawny frogmouth

The tawny frogmouth, (Latham, 1801) is a long-lived and sedentary nocturnal species endemic to Australia (Higgins 1999). The species is one of three frogmouths found in Australia, the other two being the Papuan frogmouth (*P. papuensis*) and marbled frogmouth (*P. ocellatus*), both of which occupy more forested habitats in the northern part of the continent (Higgins 1999). Currently listed by the IUCN as of Least Concern (IUCN 2012, IUCN Red List of Threatened Species), the tawny frogmouth is common and widespread throughout Australia occupying a range of habitats including forest, woodlands heathlands and urban parks (Higgins 1999; Schodde and Mason 1980). The tawny frogmouth is a medium sized bird 35-50cm in length with males weighing 350gm and females 280gm (Higgins 1999). Plumage colour and pattern is principally light silvery grey to dark grey with white or buff spots and streaking. During the daytime, to avoid detection by potential predators, the tawny frogmouth adopts a cryptic stick like posture mimicking a tree branch or trunk (Schodde and Mason 1980). This behaviour, combined with plumage colouration and patterning which resembles bark structure, provides an effective camouflage ensuring the tawny frogmouth remains virtually undetectable (Kaplan 2007; Schodde and Mason 1980). Sexing is difficult due to plumage and size similarities in both sexes (Higgins 1999; Kaplan 2007). Considered a dietary generalist, main prey species are terrestrial and aerial invertebrates with small
vertibrates including mice and reptiles forming part of the diet (Rose and Eldridge 1997).

Unlike many nocturnal species, the tawny frogmouth is not reliant on cavities or tree hollows for roosting or breeding. A variety of native and non-native trees species are selected for diurnal roosting and for nesting and rearing young during the breeding season (Körtner and Geiser 1999a; Körtner and Geiser 1999b). Common roost and nest trees used by the species in urban environments include native eucalypts (Eucalyptus spp.), wattles (Acacia spp.), and she-oaks (Casuarina spp.) and several introduced tree species including pine (Pinus spp.), willow (Salix spp.) and poplar (Populus spp.). The same roost tree may be used over many weeks or months and multiple trees (5-8) can be used over a small area (Körtner and Geiser 1999b).

The tawny frogmouth breeding season is protracted (July to January) with the species capable of repeated attempts if nesting fails, and of multiple broods if conditions are favourable (Higgins 1999). Tawny frogmouth nests are an open and often flimsy platform constructed from small twigs and typically located in or on a horizontal or vertical fork of a tree branch or trunk (Schodde and Mason 1980). Between one and three eggs are laid per clutch with incubation taking between 28-31 days and nestlings fledging after another 30-32 days (Higgins 1999). Post-fledging, juveniles will remain in the natal territory roosting with parents for several weeks or until the commencement of the next breeding season (Higgins 1999; Schodde and Mason 1980).

Research undertaken on tawny frogmouth’s has focused primarily on dietary preferences (Rose and Eldridge 1997), roosting behaviour (Körtner and Geiser 1999a)
nesting densities (Rae 2009), and physiological behaviour (Kortner, Brigham and Geiser 2001) of woodland and forest dwelling birds. Very little is known about the species response to urbanization and landscape modification. In urban environments, long-lived sedentary species are identified as those most vulnerable to landscape modification and resource shifts associated with urbanization (Sekercioglu, Daily and Ehrlich 2004). While the tawny frogmouth is both sedentary and long-lived, several physical and behavioural characteristics may insulate the species from some of the more detrimental effects associated with urban living. Although current populations of tawny frogmouths appear to be substantial and widespread, as urbanization intensifies, tawny frogmouth populations may be impacted by factors such as habitat loss and fragmentation resulting in population declines or extinctions.

For the purposes of this research, the use of the terms “adaptive”, “adapted” and “adaptation” is not intended to be used in a genetic context. Instead, these terms are used to convey a species capacity to align its ecological traits with aspects of the urban environment to its ultimate advantage.

1.5 Thesis aims and structure
The aim of this thesis is to investigate and identify how an urbanization gradient impacts on various ecological aspects of the tawny frogmouth.

In chapter two we investigate how the distribution of three key members of the Australian nocturnal bird community, the southern boobook, Australian owlet-nightjar and the tawny frogmouth is impacted by a gradient of urbanization. While all three species are common and widespread throughout Australia, we seek to determine how three landscape types classified as; suburban, urban-fringe and forest, impact on their
distribution. The effects of urbanization on individual species will be determined by a comparison of broad landscape attributes and species distribution. Modelling of site-level attributes will be undertaken to determine their influence on the presence of all three species in the landscape.

In **chapter three** we investigate tawny frogmouth home-range size and land-use in response to a gradient of urbanization. By using radio-tracking techniques, GIS and various modelling approaches we seek to identify the key land-use types that influence tawny frogmouth home-range size and location in the urban landscape. We also ask whether urbanization exerts an influence on home-range size and whether the response to urbanization is gender specific.

In **chapter four** using a range of modelling approaches and GIS techniques, we investigate the response of tawny frogmouth reproductive behaviour to a gradient of urbanization. Firstly, we ask if the degree of urbanization across the gradient influences the availability of suitable nesting locations for breeding pairs. Secondly, we ask does landscape and site level habitat factors around a nest site exert an influence on the success of nesting attempts. Finally, we test whether the degree of urbanization is a key driver of commencement of breeding.

In **chapter five** using tawny frogmouth DNA and various molecular techniques we take a landscape approach to examine the genetic structure and diversity of the species in response to a gradient of urbanization. By utilizing various genetic materials collected from tawny frogmouths we construct a genetic profile of the species which will be used to assess how genetic structure and diversity is impacted by varying levels of urbanization. In addition, we investigate tawny frogmouth population structure, within-
Introduction

population relatedness and dispersal patterns and further, whether there are sex differences in these responses.

Chapter six represents a synthesis of all four data chapters providing an overview of the major findings of this research. We highlight several issues that may affect tawny frogmouth populations, identify how current urban planning trends and other forms of urban management may impact on those populations and propose future management actions to ensure these populations remain sustainable into the future. We conclude with several suggestions for future research.
Chapter 2:

The distribution of three nocturnal bird species across a suburban–forest gradient

This chapter has been published as:


Tawny frogmouth family group (two adults & two juveniles) roosting in a backyard tree (*Eucalyptus nicholii*) in suburban Melbourne. Photo: Janet Flinn.
2.1 Introduction

The transformation of natural landscapes into urban areas has led to losses of biodiversity on a global scale (Garden et al. 2006; McKinney 2002). To date, ecologists have largely focused on the examination of natural landscapes (Collins et al. 2000; McDonnell and Hahs 2008) but, with urbanization predicted to be the dominant form of land-use within the next decade (United Nations 2014), studies of urban ecology are needed to examine the effects of urbanization on biodiversity (Beck and Heinsohn 2006; Isaac et al. 2008; Melles, Glenn and Martin 2003). One approach, the urban gradient model, provides an opportunity to examine the processes that drive patterns of species richness and abundance at various scales throughout the landscape (McDonnell and Pickett 1990; McDonnell et al. 1997).

Because birds are sensitive to the effects of urbanization, they feature prominently in urban-gradient studies (Savard, Clergeau and Mennechez 2000). Increasing urbanization is generally associated with declining avian species richness, with urban communities dominated by a small number of species, often introduced species, which occur in high densities (Beissinger and Osborne 1982; Blair 1996; Clergeau et al. 1998; Sewell and Catterall 1998). This is likely to result from the original forest habitat remnants being small, linear and isolated from each other (McKinney 2006; Medley and McDonnell 1995), with native vegetation quality and quantity typically reduced and highly altered owing to disturbances associated with urbanization (Donnelly and Marzluff 2006; White et al. 2005). Species more generally associated with woodland or forested habitats are often absent, in decline or marginalized to urban-fringes (Crooks, Suarez and Bolger 2004; Donnelly and Marzluff 2006) where the forest remnants are larger, have increased connectivity and greater structural diversity.
Three nocturnal species compared to those closer to the urban centre (McKinney 2002; Medley and McDonnell 1995).

In comparison to diurnal species, the ecological response of nocturnal birds to urbanization is less well understood. The little research which has been undertaken has generally focused on comparisons between urban and suburban populations (Ranazzi, Manganaro and Salvati 2000; Zalewski 1994) and urban and rural populations (Minor, Minor and Ingraldi 1993; Smith, Bosakowski and Devine 1999) rather than the urban gradient model (Cooke et al. 2006; Cooke, Wallis and Webster 2002). Although there is some information suggesting that nocturnal species appear to be advantaged by their association with urbanization (Bouskila 1995; Clarke 1983), there is still a paucity of information regarding the response of this important group of species to factors such as habitat loss and fragmentation in urban and urbanizing environments.

The complex spatial variation in resource distribution and abundance in the urban environment highlights the importance of undertaking research at multiple scales. Therefore, the aim of this research was to identify factors which influence the distribution of nocturnal species across a gradient of urbanization by examining large-scale (i.e. landscape level) and smaller-scale (i.e. site level) variation in environmental variables.

Because they are highly vocal, common and widespread in a range of habitats throughout Australia (Higgins 1999; Schodde and Mason 1980), the tawny frogmouth \((Podargus strigoides)\), Australian owlet-nightjar \((Aegotheles cristatus)\) and southern boobook \((Ninox novaeseelandiae)\) were chosen as the target species for this research.
The Australian owlet-nightjar and southern boobook are hollow-dependent species that use hollows of various sizes for roosting and nesting (Higgins 1999; Schodde and Mason 1980). In contrast, the tawny frogmouth roosts and nests on tree branches or forks of branches, relying on its cryptic plumage as a protection from potential predators (Kaplan 2007; Rose and Eldridge 1997). The tawny frogmouth and southern boobook consume a variety of invertebrate and small vertebrate prey (Penck and Queale 2002; Rose and Eldridge 1997), whereas the Australian owlet-nightjar is mainly insectivorous (Higgins 1999; Schodde and Mason 1980).

2.2 Methods

The study area was in the north-east of Melbourne, Australia (38°S, 145°E). With a human population of ~3.5 million people, Melbourne has a large urban sprawl that extends to the north, east and west of the city centre, containing a broad range of landscape elements including remnants of native vegetation of varying size and type throughout suburban and urban-fringe areas (White et al. 2005). Melbourne has a temperate climate characterized by warm to hot summers and cool wet winters. The annual average rainfall is 1000 mm (Bureau of Meteorology 2010).

In urban studies, the range of definitions used to quantify and describe the term ‘urban’ differs considerably (Collins et al. 2000). It is thus necessary to quantify which measures were used in defining levels of urbanization so that between-study comparisons can be made (McIntyre, Knowles-Yanez and Hope 2000). For this study, the measure used to define the urban component was the percentage of vegetation cover within landscapes and defined on this basis as ‘suburban’, ‘urban-fringe’ and ‘forest’.
Nine 10 x 10km study landscape plots were selected to represent a suburban–forest gradient based on the percentage of dense tree cover (Fig. 2.1). The percentage of dense tree cover was derived by geographical information system (GIS) mapping of tree cover at a scale of 1:25 000. The derived GIS layer (VICMAP Vegetation) displays the proportion of dense tree cover, with dense defined as vegetation having a crown-cover density >80% (Radford 2005). Landscape plots were classified as: suburban, containing <5% dense tree cover (n = 3 sites); urban-fringe, containing between 30 and 40% dense tree cover (n = 3); and forest, containing >90% dense tree cover (n = 3).

**Figure 2.1.** Location of suburban, urban-fringe and forest landscapes in Melbourne, Australia. Inset map shows Victoria.
Three nocturnal species

A total of 54 sampling sites were located within the nine study landscape plots (six sampling sites per study landscape). Sampling sites were classified into three broad types according to level of urbanization (determined by the percentage of dense tree cover as discussed above) and human population densities (ABS 2001). Suburban and urban-fringe streetscapes were classified as extreme, high and low density (Table 2.1).

Remnant native vegetation, located throughout suburban and urban-fringe landscapes, was classified according to remnant size: small (5–15 ha; n=6), medium (15–30 ha; n=6) and large (30–45 ha; n=6). Forest sites were classified using Ecological Vegetation Classes (EVC), into Wet Forest (n=6), Damp Forest (n=6) and Riparian Forest (n=6) (DSE 2010). Sites were located at least 1 km from each other to try and ensure their independence.

Table 2.1. Suburban and urban-fringe streetscape classification. Under ‘Tree-cover classification’: Moderate, 50-80% crown-cover density; Scattered, 10-50% crown-cover density; <Scattered, <10% crown-cover density. Tree-cover classifications according to Radford (2005).

<table>
<thead>
<tr>
<th>Streetscape</th>
<th>N</th>
<th>Tree-cover classification</th>
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</tr>
</thead>
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<td>&gt;2000</td>
</tr>
<tr>
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<tr>
<td>Low</td>
<td>6</td>
<td>Moderate</td>
<td>&lt;1000</td>
</tr>
</tbody>
</table>

2.2.1 Survey techniques

A 500m transect was established at each sampling site. For access purposes, forest transects were located on forestry roads whereas suburban and urban-fringe transects were located along footpaths and walking tracks.
Survey techniques largely followed standard methods used for surveys of large forest owls in south-eastern Australia (Debus 1995). Throughout the study, from February to August 2008, each transect was surveyed five times. Surveying only occurred on fine, still nights, with 4–5 sites surveyed within any one night, commencing 30 minutes after dark and continuing to 0100 hours. Call playback and spotlighting were used together to maximize detection of birds. Surveys involved call playback using a portable MP3 player (Samsung YP-K3) and speaker system (Sony SRS- A5S) and pre-recorded calls (including territorial and contact calls) of each species. Calls were broadcast at the 100 and 500m points of each transect at a fixed volume based on volumes similar to those of naturally calling birds. At each of the two points on the transect 5 minutes were spent listening for and noting any birds calling naturally before broadcast of recorded calls. Calls of each species were then broadcast for 3 minutes, with an interval of 5 minutes between calls of each, to elicit responses from any birds present; the number of birds responding were noted. After broadcasting at each site was complete for all species, a further 5 minutes were spent listening for the last species, then 5 minutes were spent spotlighting the surrounding vegetation to check for birds attracted to, but not vocally responding to, the playback of calls. During site visits, the order of calls and survey times were randomized to avoid potential bias. To determine whether the number of repeat visits to sites was sufficient to detect each species, a series of random-block analyses of variance (ANOVA) were conducted. These analyses examined the proportion of sites within each site type where a species was detected over the five repeat visits.
Three nocturnal species

2.2.2 Landscape-level attributes

Using ArcView 3.3 (ESRI 2010), GIS layers at 1:25 000 under license from Department of Sustainability and Environment, Victoria (DSE), and VICMAP were used to derive landscape level attributes. The total extent of dense tree cover, moderately dense tree cover, and scattered tree cover was calculated as a percentage in each landscape plot. This information was derived from the TREEDEN25 layer produced by DSE from satellite data. The density of roads, sealed and unsealed, was calculated by summing the length of all roads in each landscape. The density of rivers was measured as the total sum of the length of all rivers in each landscape. According to GIS classification, the river category is defined as any above ground waterway including urban spillways and culverts.

Attributes selected for this study represent elements commonly found along a suburban–forest gradient. Riparian systems are a predominant feature in many landscapes. Studies highlight the importance of riparian systems, in particular the role of remnant vegetation associated with riparian systems for avian species richness (Palmer and Bennett 2006; Palmer et al. 2008; Trollope, White and Cooke 2009). Roads form extensive transportation networks across the gradient. Roadside vegetation also provides habitat for a range of species, including those more generally regarded as forest dependent (Fernandez-Juricic 2004). The value of such habitat is, however, dependent on the ecological capabilities of a species and on factors including the size and type of road (Forman and Deblinger 2000). The density of tree cover varies significantly across the gradient. Variations in density have been shown to have a substantial effect on bird species richness and community composition overall (Crooks, Suarez and Bolger 2004; Sewell and Catterall 1998).
2.2.3 Site-level attributes

Using Arc View 3.3 (as above), data layers were further modified to obtain six spatial attributes. From the centre of each transect a 500 m buffer was applied. Within the radius of the buffer, attributes were derived by calculating the proportion (%) of tree cover classified as dense, moderate and scattered, and the densities (kilometers per square kilometer) of sealed roads, unsealed roads and rivers. Buffer size was based on known dispersal capabilities and home-ranges of all three species (Higgins 1999; Kaplan 2007; Schodde and Mason 1980).

2.2.4 Statistical analysis

At the landscape level, occurrences for each species detected during playback and spotlighting were pooled across each of the nine landscape plots and calculated as a percentage based on the number of sites in each landscape. One-way ANOVA using SPSS v14 (SPSS Inc 2009), were run to determine any differences between landscape type and species presence. Bivariate correlation using SPSS v14 was used to examine associations between the percentage occurrence of each species at a landscape level and the landscape-level attributes. To determine the site-level attributes that influence the presence of each species within a landscape type, an information-theoretic approach based on Akaike’s Information Criterion (AIC) was performed (Burnham and Anderson 2002). Because sample sizes were fairly small, the second-order AIC corrected for small sample sizes (AICc) was utilized. Generalized linear models using a binomial distribution were used to investigate the relationship between the three target species and the predictor variables (R Development Core Team 2009).
Three nocturnal species

Akaike differences ($\Delta$AIC) were used to determine the level of support for each model in the candidate set. Candidate models with $\Delta$AIC <2 have substantial support as being among the best models of the candidate set of models. Akaike weights ($w_i$) were additionally used to determine the evidence of support for each model. $w_i$ are the proportional weight of evidence in support of the particular model being the best model for the situation (Burnham and Anderson 2002). Summed $w_i$ were also used to help identify influential predictor variables in the model. $w_i$ are summed for all models that include a particular variable, with a highly influential variable having a maximum weight of 1.

Model averaging was used to give unconditional model variances when the $w_i$ suggested no individual model was clearly the best ($w_i > 0.9$) (Anderson et al. 2001). Weighted model averaging based on 1000 bootstrapped samples was used to reduce model selection bias. Hierarchical partitioning was used to determine the independent contribution of each predictor variable to the overall model. Models were developed using the R statistical package (R Development Core Team 2009) using algorithms to calculate AICc, bootstrap frequencies, and model averaged estimates (M. Scroggie, Arthur Rylah Institute for Environmental Research, unpubl. code). Hierarchical partitioning was undertaken in R using their hier.part package (Walsh and MacNally 2003).

2.3 Results

2.3.1 Survey effort

For all species there was a significant difference in the proportion of sites where a species was detected between repeat visits (Australian owlet-nightjar: $F = 5.745$, d.f. =
Three nocturnal species

4, 32, \( P < 0.001 \); southern boobook: \( F = 14.464, \) d.f. = 4, 32, \( P < 0.001 \); tawny frogmouth: \( F = 5.821, \) d.f. = 4, 32, \( P < 0.001 \). For all three species there was no significant improvement in the proportion of sites where a species was detected beyond the third visit (Tukey \( P > 0.05 \)). These results suggest the sampling regime was adequate across all habitat types with similar trends observed for each species.

2.3.2 Species response to landscape-level attributes

Throughout the entire study area the southern boobook was detected in the highest proportion of sites (53%), followed by the tawny frogmouth (43%), and the Australian owlet-nightjar (40%).

The presence of the tawny frogmouth was significantly affected by landscape type (\( F = 10.842, \) d.f. = 2, 6, \( P = 0.01 \)). The species was most common in suburban landscapes (73% of sites) and urban-fringe landscapes (50%) but was not recorded from forests (Tukeys: \( P < 0.05 \)). The tawny frogmouth showed a strong positive correlation with the density of sealed roads (\( r_p = 0.817, P = 0.007 \)), the percentage of moderate tree cover (\( r_p = 0.707, P = 0.033 \)), and the percentage of scattered tree cover (\( r_p = 0.862, P = 0.003 \)). In contrast, the tawny frogmouth showed a strong negative correlation with the percentage of dense tree cover (\( r_p = -0.880, P = 0.002 \)). In an urban context, the tawny frogmouth displayed a high level of tolerance to both the suburban and urban-fringe landscapes and a very strong threshold response to forest areas.

The occurrence of the southern boobook differed across landscape types (\( F = 27.730, \) d.f. = 2, 6, \( P < 0.001 \)). The species was most common in forested landscapes (94% of sites) and urban-fringe landscapes (64%) but reporting declined sharply in the suburban.
Three nocturnal species

landscape (13% of sites) (Tukeys: $P < 0.05$). The southern boobook showed strong positive correlations with the density of unsealed roads ($r_p = 0.768$, $P = 0.016$), the percentage of dense tree cover ($r_p = 0.902$, $P = 0.001$) and density of rivers ($r_p = 0.864$, $P = 0.003$) and, conversely, strong negative correlations with the density of sealed roads ($r_p = –0.930$, $P < 0.001$), and the percentage of scattered tree cover ($r_p = –0.911$, $P < 0.001$). In marked contrast to the tawny frogmouth, the southern boobook appears to be positively influenced by forest and demonstrates a threshold response to urbanization beyond which the species rapidly declines.

The Australian owlet-nightjar showed no significant landscape-level differences ($F = 4.020$, d.f. = 2, 6, $P = 0.078$). Although not significant, the species was most common in urban-fringe landscapes (64% of sites) and forest (50%) and was least common in suburban landscapes (18%). The Australian owlet-nightjar showed a strong positive correlation with the density of rivers ($r_p = 0.722$, $P = 0.028$) in all three landscapes. Despite the non-significance of the results, the overall statistical trend suggests some form of decline in response to higher levels of urbanization.

Site-level model selection using AICc identified three models for the tawny frogmouth, all of which had similar support ($\Delta AIC_c < 2$; Table 2.2). All three models contained sealed roads, scattered tree-cover and river variables, indicating that these are significant predictors for the presence of this species. The top-ranked model containing dense tree cover, scattered tree cover, rivers and sealed roads accounted for 50% of the variation in the presence of the species.
Three nocturnal species

With the addition of the moderate tree-cover and unsealed road variables, the second and third highest ranked models showed similar strength, both accounting for 50% of the variation in species presence. As no one model had strong support ($w_i > 0.9$), model averaging was undertaken. Dense tree cover had a strong negative influence, and summing Akaike weights of each variable showed dense tree cover had very high relative importance (99%). Conversely, the density of rivers (99%) and sealed roads (91%) variables both had a strong positive influence on the presence of the tawny frogmouth (Table 2.3).

Hierarchical partitioning supported the selection of dense tree cover recording the highest independent contribution (30%) of all the variables, with sealed roads and rivers adding 25% and 18% respectively.

Model selection using $\text{AIC}_c$ produced eight models for the southern boobook, all of which had similar support ($\Delta \text{AIC} < 2$; Table 2.2). All eight models contained the scattered tree-cover variable indicating that this is an important predictor for the species. The top-ranked model, comprising scattered tree cover and unsealed roads, accounted for 47% of the variation in the presence of the species. The inclusion of the dense tree-cover variable to the third-highest ranked model showed greater strength than the top-ranked model, accounting for 56% of the variation in species presence. The dense tree-cover variable also provided greater strength to models 6, 7 and 8 than that of the top-three ranked models. As no one model had strong support ($w_i > 0.9$), model averaging was undertaken. Summing the Akaike weights for each variable showed that scattered tree cover had a high overall value (88%), with dense tree cover accounting for 47% (Table 2.3). Hierarchical partitioning also supported this selection with
Three nocturnal species

scattered tree cover having the highest independent contribution (36%) followed by
dense tree cover (29%).

Model selection using AICc produced five models for the Australian Owlet-nightjar, all
of which had similar support (ΔAIC < 2; Table 2.2). All five models for the Australian
Owlet-nightjar contained the river variable, indicating its importance for this species.
The top-ranked model contained the river variable, which accounted for 33% of the
variation in species presence. As no one model had strong support (wi > 0.9), model
averaging was undertaken. Summing the Akaike weights for each variable showed that
the river variable had the highest relative importance (99.6%), with sealed roads (34%)
and unsealed roads (29%) having weak support. Hierarchical partitioning confirmed the
significance of rivers with an independent contribution of 70%, sealed roads 10% and
unsealed roads 7% (Table 2.3).
Table 2.2. AICc based model selection for the tawny frogmouth, southern boobook and Australian owlet-nightjar (A.o.n). All models with ΔAIC <2 are reported. Models based on the presence of species at each site. Values represent the number of parameters (K), Akaike information criterion corrected for small sample size (AICc), AICc differences (ΔAIC), Akaike weights (wi), bootstrap selection frequencies (i) and regression explanation scores (R^2) for the best models and evidence ratios (wi/wj). The highest five models are provided. Model variables include: Sealed roads, Unsealed roads, Rivers, Dense tree cover, Moderate tree cover, Scattered tree cover.

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<tr>
<td><strong>A.o.n</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rivers</td>
<td>2</td>
<td>57.5</td>
<td>0</td>
<td>1</td>
<td>0.174</td>
<td>0.36</td>
<td>0.327</td>
<td>-</td>
</tr>
<tr>
<td>Rivers + Sealed Roads</td>
<td>3</td>
<td>58.6</td>
<td>1.09</td>
<td>2</td>
<td>0.101</td>
<td>0.123</td>
<td>0.341</td>
<td>1.72</td>
</tr>
<tr>
<td>Rivers + Unsealed Roads</td>
<td>3</td>
<td>59.0</td>
<td>1.50</td>
<td>3</td>
<td>0.082</td>
<td>0.118</td>
<td>0.336</td>
<td>2.11</td>
</tr>
<tr>
<td>Scattered + River</td>
<td>3</td>
<td>59.1</td>
<td>1.60</td>
<td>4</td>
<td>0.078</td>
<td>0.03</td>
<td>0.334</td>
<td>2.22</td>
</tr>
<tr>
<td>Dense + Rivers</td>
<td>3</td>
<td>59.5</td>
<td>1.97</td>
<td>5</td>
<td>0.065</td>
<td>0.04</td>
<td>0.332</td>
<td>2.67</td>
</tr>
</tbody>
</table>

*Three nocturnal species*
### Table 2.3. Model averaged coefficients, conditional and unconditional standard errors, Z-scores and significance of each variable for the tawny frogmouth, southern boobook and Australian owlet-nightjar (A.o.n) and summed AIC weights (total AIC weight for each model including that model). Results from hierarchical partitioning are shown with the percentage independent contribution.

| Variable  | Co-efficient | Conditional | Unconditional | Z     | Pr(>|z|) | Contribution | Summed AIC weights |
|-----------|--------------|-------------|---------------|-------|---------|--------------|-------------------|
| **tawny frogmouth** |              |             |               |       |         |              |                   |
| Intercept | -1.87303     | 1.95527     | 1.97434       | -0.9487 | 0.34278 |              |                   |
| Dense     | -0.1201      | 0.07365     | 0.05689       | -2.1111 | 0.03477 | 30.1         | 0.997             |
| Moderate  | -0.02688     | 0.08592     | 0.06131       | -0.4384 | 0.66107 | 13.1         | 0.324             |
| Scattered | -0.10469     | 0.08591     | 0.07563       | -1.3843 | 0.16627 | 12.9         | 0.786             |
| Rivers    | 2.82832      | 1.54546     | 1.28126       | 2.2075  | 0.02728 | 17.9         | 0.995             |
| Sealed Roads | 0.49027   | 0.30142     | 0.27694       | 1.7703  | 0.07668 | 24.6         | 0.912             |
| Unsealed  | -0.06887     | 0.38507     | 0.20831       | -0.3306 | 0.74094 | 1.4          | 0.293             |
| **southern boobook** |              |             |               |       |         |              |                   |
| Intercept | 0.90828      | 1.9021      | 2.041         | 0.445  | 0.6563  |              |                   |
| Dense     | 0.01648      | 0.0253      | 0.0233        | 0.7081 | 0.4789  | 29.3         | 0.474             |
| Moderate  | 0.00525      | 0.0358      | 0.0284        | 0.1847 | 0.8534  | 5.2          | 0.262             |
| Scattered | -0.184       | 0.1106      | 0.0899        | -2.0475| 0.0406  | 36.2         | 0.882             |
| Rivers    | 0.18915      | 0.4841      | 0.3291        | 0.5748 | 0.5655  | 6.7          | 0.401             |
| Sealed Roads | -0.00594   | 0.1637      | 0.0786        | -0.0755| 0.9398  | 15.1         | 0.25              |
| Unsealed  | 0.14917      | 0.3048      | 0.2316        | 0.644  | 0.5196  | 7.6          | 0.414             |
| **A.o.n** |              |             |               |       |         |              |                   |
| Intercept | -2.214365    | 1.023778    | 1.04167       | -2.1258| 0.03352 |              |                   |
| Dense     | 0.000274     | 0.006336    | 0.00621       | 0.0441 | 0.96485 | 5.15         | 0.254             |
| Moderate  | 0.002749     | 0.018983    | 0.01815       | 0.1515 | 0.8796  | 1.97         | 0.259             |
| Scattered | -0.001341    | 0.011766    | 0.0115        | -0.1166| 0.90718 | 5.39         | 0.273             |
| Rivers    | 1.116374     | 0.340979    | 0.34999       | 3.1898 | 0.00142 | 70.35        | 0.996             |
| Sealed Roads | -0.033383 | 0.07087     | 0.07296       | -0.4576| 0.64727 | 9.75         | 0.342             |
| Unsealed  | 0.04221      | 0.115574    | 0.12003       | 0.3517 | 0.72509 | 7.39         | 0.292             |
2.4 Discussion

The principle assumption of this study, that habitat attributes at multiple scales would influence the distribution of three nocturnal bird species across a gradient of urbanization, has largely been met. The response of all three species to urbanization appears to be consistent with the ‘intermediate disturbance hypothesis’ in that intermediate levels of urbanization, such as urban-fringe environments, often record the highest level of avian species richness throughout the gradient (Beissinger and Osborne 1982; Blair 1996; Clergeau et al. 1998).

The tawny frogmouth was detected frequently in urban-fringe environments but was detected even more frequently in suburban sites, suggesting that the species is tolerant of, or even prefers, habitats provided by urbanization. The extensive changes to the natural environment as a result of urbanization appear to suit tawny frogmouths. The reduction of vegetation density in suburban areas, owing to residential and urban development, the increase in the number of parks and residential gardens and the presence of urban features, such as street lights, increases prey availability and enhances foraging activity and success for this species (Kaplan 2007; Rose and Eldridge 1997). In addition, unlike the southern boobook and Australian owlet-nightjar, the tawny frogmouth is not dependent on hollows for roosting or breeding, further enhancing its ability to occupy more highly urbanized environments (Kaplan 2007).

Both the southern boobook and Australian owlet-nightjar showed a marked sensitivity to urbanization. Although the southern boobook was detected most frequently in forest areas, both it and the Australian owlet-nightjar were recorded at similar frequencies in
Three nocturnal species

the urban-fringe environment. This may indicate that both are able to endure a threshold to urbanization beyond which they both rapidly decline as urban impacts intensify. Factors such as fragment size and habitat structure (Fernandez-Juricic 2004) and a lack of key habitat resources (Cooke et al. 2006) have been identified as reasons for the absence of species more commonly associated with forest habitats.

The availability of ecological resources such as tree hollows is likely to be a factor influencing the occurrence of the southern boobook and Australian owlet-nightjar in urban-fringe environments. Hollows rarely occur outside of remnants in urban areas, and larger remnants, containing patches of dense and structurally intact vegetation, are more likely to contain hollow-producing trees than smaller remnants (Gibbons and Lindenmayer 2006; Harper, McCarthy and van der Ree 2005). For forest-dwelling hollow-dependent species occupying and populating urban environments is more likely to occur if habitat resources, including suitable tree hollows, are available (Fernandez-Juricic 2000).

Although all three species appear to tolerate the level of disturbance in urban-fringe environments, these areas are also at risk of further degradation. It is critical that continued research is focused on urban-fringe environments to investigate species-specific demographic responses to urban gradients.
Chapter 3:
Sex-biased space-use response to urbanization in an endemic urban adapter

This chapter has been published as:


Tawny frogmouth with tracking device fitted perched on a water feature in a suburban backyard in Melbourne. Photo: Debbie Colbourne.
3.1 Introduction

Globally, urbanization is recognized as a leading cause of biodiversity loss resulting in altered faunal compositions and distributions (Chace and Walsh 2006; Garden et al. 2006). Human activities produce multiple land-use types creating a gradient of urbanization which can be traced from the city centre where impacts are most intense to forested environments where impacts are reduced (McDonnell et al. 1997). The resulting mosaic of land-use types imbedded within a gradient of urbanization provides a model to investigate species responses to differing levels of urbanization (McDonnell and Hahs 2008; McDonnell et al. 1997).

Species respond to urbanization in varying ways but broadly can be referred to as urban avoiders, exploiters and adapters. Those that disappear as urbanization intensifies are termed, ‘urban-avoiders’, species who thrive and expand their distribution in urban environments are described as ‘urban-exploiters’ while urban-adaptors are those species who are able to adapt to moderate levels of urbanization (McKinney 2006). The ability of species to persist in urban environments is linked to their ability to adapt or modify their behaviour in response to resource availability and or distribution (Lowry, Lill and Wong 2011; Prange, Gehrt and Wiggers 2004).

Urban pressures produce altered bird communities, with avian biomass increasing as impacts intensify with a corresponding decline in native species richness (Ortega-Álvarez and MacGregor-Fors 2009). Similar to other taxa, urban-adapted avian species frequently exhibit certain traits (Evans et al. 2011) and demonstrate adaptive responses to anthropogenic impacts and disturbance (Le Viol et al. 2012). Habitat loss and fragmentation often produces such responses including altered movement patterns and
changes to home-range size (Boggie and Mannan 2014; Roth, Vetter and Lima 2008; Rutz 2006). In contrast to diurnal bird species, nocturnal species are less studied. With few exceptions (Doucette 2010), owl species are predominant in many studies investigating how life cycle activities and seasonality influence spatial ecology and habitat use in natural landscapes (Craig, Craig and Powers 1988; Gamel and Brush 2001; Olsen et al. 2011; Salek and Lovy 2012) and in urbanized environments (Bennett and Bloom 2005; Smith and Gilbert 1984).

Long-lived sedentary species are considered to be most affected by shifts in resource distribution and other factors associated with urbanization (Burger et al. 2004; Sekercioglu, Daily and Ehrlich 2004). They therefore make ideal case studies for urban ecological research. In this study we investigated the spatial ecology of a common and long-lived sedentary species the tawny frogmouth (*Podargus strigoides*), in response to increasing levels of urbanization.

The tawny frogmouth is a large-bodied (350–550 g) nocturnal bird species endemic to Australia (Higgins 1999; Schodde and Mason 1980). Widespread throughout a range of habitats (Higgins 1999) in recent times the tawny frogmouth has been found in greater numbers in suburban areas than in more highly vegetated urban-fringe and forested environments (Weaving et al. 2011). With few exceptions (Kortner and Geiser 1999a; Körtner and Geiser 1999b; Rae 2009; Rose and Eldridge 1997), there are many aspects of tawny frogmouth ecology and behaviour still unknown. The aim of this study was to investigate home-range size in response to a gradient of urbanization by determining (a) what are the key land-use types that influence home-range size and
location in the urban landscape; (b) does urbanization impact on home-range size; and
(c) is the response to urbanization gender specific.

3.2 Methods

3.2.1 Study zone

This study was undertaken in parks and reserves located across a 51,783 ha study zone situated in the north-east of Melbourne, Victoria, Australia (Fig 3.1). The study zone represents a gradient of urbanization from a highly urbanized suburban environment to urban-fringe areas. Within this study zone a range of environments are represented including streetscapes of varying age and types and parks and reserves of differing size and usage. In order to assess how different levels of urbanization impact on tawny frogmouth home-range size. We used ArcGIS (ESRI 2011) to derive the level of urbanization at each site and classify according to the proportion of impervious surface in the landscape (Fig 3.1).
Fig. 3.1. Map of the study zone showing its location relative to Melbourne and the extent of the five land-cover categories. Capture location of birds are indicated by black triangles.
3.2.2 Land-use classification

We used a Normalized Difference Vegetation Index (NDVI) created in Environment for Visualizing 4.7 (ENVI 4.7) to determine tawny frogmouth land-use. NDVI is a greenness index used to measure the amount of live, green vegetation in the landscape (Leslie et al. 2010). From the NDVI we derived a categorical layer classifying the landscape into the five broad land-use types: grass, impervious surfaces, trees, rivers and water-bodies e.g. dams and lakes (see in Isaac et al. 2014b).

3.2.3 Survey methods and capture techniques

Tawny frogmouths were captured from February 2009 until June 2012. Prior to catching, sites were surveyed to assess their suitability e.g. access for net placement, to locate resident birds and to observe their night-time movements and activities. Nylon mist nets were selected to capture birds. Birds were lured into nets by broadcasting recorded tawny frogmouth calls on a portable iPod player and speaker sound system. Calls used included adult and juvenile vocalizations. Captured birds were fitted with a Sirtrack VHF radio-transmitter. The transmitter was fitted to the bird with a lightweight backpack style weak-link harness. The combined weight of the transmitter and harness was <5% of the birds body mass. Radio-transmitters were programmed to operate continuously, providing a predicted duty length of 11 months. After the transmitter was fitted the bird was released at the point of capture.

3.2.4 Radio-tracking data collection

We used a hand held 3-element Yagi antenna and a Telonics TR-4 receiver on foot to locate day roosts and nest sites. Locations were entered into a GPS unit and recorded
Home-range

on a high resolution aerial photo. During the breeding season nest sites were identified by the presence of brooding birds. Night-time radio-tracking commenced approximately 30 min after sunset during all weather conditions. Bird locations were recorded on a high resolution aerial photo. To increase independence between observations and reduce sampling bias, where practicable, a minimum of 1 hr occurred between each consecutive reading (Swihart and Slade 1985). A maximum of five readings were taken per bird per night. On the few occasions that a bird could not be sighted e.g. perched in private property, triangulation was used to determine the location.

3.2.5 Calculating home-range size

A minimum of 45 nocturnal location fixes were collected for each bird with 60 fixes per individual being preferred. This number of fixes was selected to provide a more accurate representation of home-range size, to compare land-use type selection between individual birds and to enable a greater variety of analyses to be undertaken (Borger et al. 2006; Seaman et al. 1999). Diurnal fixes of birds (day roosts) and nest sites were included in all home-range calculations. Each diurnal location was used only once as birds often used the same tree on multiple occasions.

We used Geospatial Modelling Environment (GME) (Beyer 2012) to estimate size of home-ranges and core-use areas. We used minimum convex polygons (MCP) to enable comparisons with other studies and kernel density estimators (KDE) which calculate both home-range size and core areas of use in the home-range. We used 95% fixed-kernel isopleths to estimate home-range size and 50% fixed-kernel isopleths to estimate core areas within the home-range. Due to the number of repeated points in the nocturnal
data the smoothing parameter used was Plug-in (Gitzen, Millspaugh and Kernohan 2006). All outputs from GME were imported into ArcGIS10 to calculate area.

We used ArcGIS 10 to calculate the proportion of three land-use categories occurring within each bird’s home-range and within a 1 km buffer zone around each home-range. Rivers and water body categories were excluded from the analysis due to their low occurrence both in and around the home-range of the birds studied.

We used 95% fixed-kernel home-ranges to calculate the 1 km buffer zone around the home-range and the proportion of each category within the home-range. These proportions were used to determine land-use type selection at two orders (Johnson 1980). For second order selection, land-use availability was the proportion of each category type in the 1 km buffer zone and type used was the proportion of each category type in the 95% fixed-kernel home-range of each bird. For third order selection, land-use availability was the proportion of each category type within the 95% fixed-kernel home-range and type used was the proportion of each category type used in the 50% fixed-kernel core activity area.

3.2.6 Second order land-use type selection

To determine if tawny frogmouths position their home-ranges randomly in the landscape or select for particular land-use types, the difference between category availability in the 1 km buffer zone and type used within each bird’s home-range was calculated and a Random Block ANOVA test performed using the three categories as the predictor variable and individual birds as the block. A Tukey’s test was performed to identify if birds were preferentially selecting or avoiding category types.
3.2.7 Third order land-use type selection

To establish whether tawny frogmouths select particular land-use categories within their home-range, the difference between land-use type availability within the home-range and type used within core activity areas was calculated and a Random Block ANOVA test performed using the three categories as the predictor variable and individual birds as the block. A Tukey’s test was performed to identify if birds are preferentially selecting or avoiding category types.

To determine what factors influence the home-range size of tawny frogmouths, an information-theoretic approach was taken, as described by (Burnham and Anderson 2002). As this study had a small sample size and the data were not over-dispersed, the second order Akaike information criterion corrected for small sample sizes (AICc) was utilized. We used linear models to investigate the relationship between the home-range size of tawny frogmouths and a series of pre-determined models which we considered may explain the home-range of tawny frogmouths in urbanized environments. We used the following variables for modelling: – weight of the individual frogmouth (g), the sex of the frogmouth, the proportion of the home-range that was comprised of trees and the proportion of the home-range that was comprised of impervious surfaces. We chose to test six different models that could potentially explain trends in home-range size (Table 3.1).
Table 3.1. Models proposed to explain potential trends in the home-range size of tawny frogmouths. The response variable for all models is home-range size (ha).

<table>
<thead>
<tr>
<th>Model</th>
<th>Variables</th>
<th>Model justification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex-biased model</td>
<td>Sex</td>
<td>Home-range size has been shown to be sex-biased in numerous studies. Consistent trend towards males maintaining larger home-ranges than females in birds.</td>
</tr>
<tr>
<td>Energetic demand model</td>
<td>Weight</td>
<td>Increased body weight has often been shown to lead to increased home-range sizes. This is associated with increased energetic demands of larger animals.</td>
</tr>
<tr>
<td>Sex-biased energetic demand model</td>
<td>Sex, Weight, Sex * Weight</td>
<td>There may be an interaction between energetic demands of animals of differing sizes and the sex of the individual.</td>
</tr>
<tr>
<td>Resource model</td>
<td>Tree cover</td>
<td>Home-range size will be affected by the amount of available habitat in an area. Trees are a critical habitat element for frogmouths, and as such it could be expected that increased tree cover would lead to altered home-range sizes.</td>
</tr>
<tr>
<td>Impact of urbanization model</td>
<td>Impervious surface cover</td>
<td>The degree of urbanization in the home-range may lead to increases in home-range size.</td>
</tr>
<tr>
<td>Sex-biased impact of urbanization</td>
<td>Sex, Impervious surface cover, Sex * Impervious surface cover</td>
<td>The response to urbanization may be sex-biased. This will be particularly important if there is role separation between the sexes.</td>
</tr>
<tr>
<td>Null model</td>
<td>N/A</td>
<td></td>
</tr>
</tbody>
</table>

\[\text{Table 3.1.} \] Models proposed to explain potential trends in the home-range size of tawny frogmouths. The response variable for all models is home-range size (ha).

Home-range

We developed models using the R statistical package (Ihaka and Gentleman 1996) version 2.15. The MuMIN package, version 1.9.0 (Barton 2013) was used for all modelling. Akaike differences ($\Delta A_k$) were used to determine the level of support for each model in the candidate set. Burnham and Anderson (2002), suggest that candidate models with Akaike differences less than 2 have substantial support. Akaike weights were produced to establish whether one model had substantial support as the best model. Anderson et al. (2001), suggest an individual model needs an Akaike weight of greater than 0.9 before it can be considered the best model. Multiple $R^2$ values were generated to establish how well the individual models were able to account for variation in the data.

3.3 Results

3.3.1 Home-range size

In total 12 birds, seven males and five females were caught from eight different parks and reserves and a total of 865 nocturnal fixes recorded (Table 3.2). The maximum number of fixes per bird was 93 and the minimum was 42 (Table 3.2). The minimum number of 60 readings was obtained for all birds except for M6 which died during the study (natural causes). Readings were obtained over a minimum of 53 nights and a maximum of 303 nights. Diurnal locations were recorded for all birds (Table 3.2).

All birds were captured at different locations within each park or reserve. Sites varied from highly urbanized, with a high proportion of impervious surfaces to almost exclusively treed and grassed environments. The most urbanized bird, with the highest proportion of impervious surfaces in its home-range was bird M3 with 76.6% of its
home-range consisting of impervious surfaces. The least urbanized bird was M1 with none of its home-range containing impervious surfaces.

Female body weights ranged from 400 g to 450 g while males weighed between 400 g and 570 g (Table 3.2). Home-range size, calculated from minimum convex polygons (MCP), ranged from 1.95 ha to 22.56 ha (Table 3.2). The smallest kernel home-range was 2.80 ha and the smallest core area of use was 0.28 ha (Table 3.2). The largest kernel home-range was 32.16 ha and the largest core area was 9.62 ha (Table 3.2).
Table 3.2. Tawny frogmouths caught in this study, including sex, weight (g), number of nocturnal fixes, period of time tracked, day roost use, the MCP home-range (ha), the 95% fixed-kernel isopleth home-range (ha) and 50% fixed-kernel isopleth core area (ha) for each bird.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Weight (g)</th>
<th>No of nocturnal fixes</th>
<th>Duration Tracked (nights)</th>
<th>Day Roost use frequency (n)</th>
<th>MCP home-range (ha)</th>
<th>95% kernel home-range (ha)</th>
<th>50% kernel core-area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>530</td>
<td>66</td>
<td>273</td>
<td>13</td>
<td>1.95</td>
<td>2.83</td>
<td>0.62</td>
</tr>
<tr>
<td>M2</td>
<td>450</td>
<td>60</td>
<td>53</td>
<td>14</td>
<td>11.11</td>
<td>16.47</td>
<td>3.97</td>
</tr>
<tr>
<td>M3</td>
<td>445</td>
<td>86</td>
<td>124</td>
<td>9</td>
<td>22.02</td>
<td>28.98</td>
<td>9.62</td>
</tr>
<tr>
<td>M4</td>
<td>570</td>
<td>64</td>
<td>64</td>
<td>6</td>
<td>22.33</td>
<td>26.04</td>
<td>4.95</td>
</tr>
<tr>
<td>M5</td>
<td>530</td>
<td>89</td>
<td>303</td>
<td>35</td>
<td>10.78</td>
<td>11.66</td>
<td>2.37</td>
</tr>
<tr>
<td>M6</td>
<td>475</td>
<td>42</td>
<td>102</td>
<td>6</td>
<td>4.64</td>
<td>5.39</td>
<td>0.99</td>
</tr>
<tr>
<td>M7</td>
<td>400</td>
<td>64</td>
<td>135</td>
<td>18</td>
<td>22.56</td>
<td>32.16</td>
<td>7.83</td>
</tr>
<tr>
<td>F1</td>
<td>450</td>
<td>93</td>
<td>124</td>
<td>15</td>
<td>8.26</td>
<td>5.92</td>
<td>0.86</td>
</tr>
<tr>
<td>F2</td>
<td>435</td>
<td>72</td>
<td>90</td>
<td>12</td>
<td>4.73</td>
<td>2.80</td>
<td>0.28</td>
</tr>
<tr>
<td>F3</td>
<td>410</td>
<td>90</td>
<td>155</td>
<td>12</td>
<td>7.78</td>
<td>9.30</td>
<td>2.32</td>
</tr>
<tr>
<td>F4</td>
<td>400</td>
<td>63</td>
<td>79</td>
<td>7</td>
<td>8.17</td>
<td>10.10</td>
<td>2.69</td>
</tr>
<tr>
<td>F5</td>
<td>410</td>
<td>76</td>
<td>103</td>
<td>6</td>
<td>5.82</td>
<td>4.63</td>
<td>0.87</td>
</tr>
</tbody>
</table>
3.3.2 Second order selection – influence of land-use type on home-range location within the landscape

Tawny frogmouths did not position their home-ranges randomly in the broader urban landscape ($F (2, 22) = 8.523$, $p = 0.002$, $n = 12$; Fig. 3.2). Impervious surfaces had significantly lower differential results than trees (Tukey $p < 0.05$) indicating that tawny frogmouths did preferentially locate their home-range in areas containing more trees and avoided impervious surfaces. The use of grassed areas was similar to the proportion available.

Fig. 3.2. Proportional differences between habitat available in the home-range (95% KD), and the availability of habitat in a 1 km buffer around the home-range for each bird. Positive numbers indicate a preference for habitat type and negative numbers indicate avoidance. Black bars = trees; grey bars = grass; white bars = impervious surfaces.
3.3.3 Third order selection – land-use type within the home-range

There was an effect of land-use type on tawny frogmouths core activity areas within the home-range ($F(2, 22) = 13.500, p < 0.001, n = 12; \text{Fig. 3.3}$). Impervious surfaces had significantly lower differential results (Tukey $p < 0.05$) than trees and grass (Tukey $p > 0.05$) demonstrating that tawny frogmouths selected areas with trees and grass preferentially and avoided areas with impervious surfaces within their home-range.

![Graph](image.png)

**Fig 3.3.** Proportional differences of habitat available within the home-range (95% KD), and within the core activity areas (50 % KD) of each bird. Positive numbers indicate a preference for habitat type and negative numbers indicate avoidance. Black bars = trees; grey bars = grass; white bars = impervious surfaces.
3.3.4 Factors influencing home-range size in the urban environment

Only one model, the sex-biased impact of urbanization model, was supported as explaining home-range size (i.e. $\Delta$AIC < 2; Table 3.3). This model had very strong support as being the best model to explain the home-range size of tawny frogmouths in urban environments with an AIC weight of 0.986, and an $R^2$ of 0.927 (Table 3.3).

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>LogLik</th>
<th>AICc</th>
<th>$\Delta$AIC</th>
<th>AIC Weight</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex-biased impact of urbanization model</td>
<td>4</td>
<td>-29.041</td>
<td>78.081</td>
<td>0.000</td>
<td>0.986</td>
<td>0.927</td>
</tr>
<tr>
<td>Impact of urbanization model</td>
<td>2</td>
<td>-39.080</td>
<td>87.161</td>
<td>9.080</td>
<td>0.011</td>
<td>0.610</td>
</tr>
<tr>
<td>Resource model</td>
<td>2</td>
<td>-40.494</td>
<td>89.987</td>
<td>11.906</td>
<td>0.003</td>
<td>0.506</td>
</tr>
<tr>
<td>Sex-biased model</td>
<td>2</td>
<td>-42.622</td>
<td>94.244</td>
<td>16.163</td>
<td>&lt;0.001</td>
<td>0.296</td>
</tr>
<tr>
<td>Null model</td>
<td>1</td>
<td>-44.727</td>
<td>94.787</td>
<td>16.706</td>
<td>&lt;0.001</td>
<td>0.000</td>
</tr>
<tr>
<td>Energetic demand model</td>
<td>2</td>
<td>-44.722</td>
<td>98.443</td>
<td>20.362</td>
<td>&lt;0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Sex-biased energetic demand model</td>
<td>4</td>
<td>-41.412</td>
<td>102.825</td>
<td>24.743</td>
<td>&lt;0.001</td>
<td>0.425</td>
</tr>
</tbody>
</table>

The modelling provides strong support to suggest that the home-range size of tawny frogmouths in urban environments is affected by the degree of urbanization (i.e. impervious surface cover) within the home-range of an animal, but that this trend is sex-biased. The very high $R^2$ values also suggest that this model is capable of explaining much of the variation in home-range size in our observed data. We used the sex-biased impact of urbanization model to generate predictions and plotted them against the actual home-range data for each sex (Fig 3.4). We observed that the home-range size (Fig 3.4) of male tawny frogmouths are substantially affected by the degree of urbanization (impervious surface cover) within their home-range, with males maintaining larger
home-ranges as urbanization intensifies. This trend does not appear to be the case for females (Fig 3.4).

Fig 3.4. Relationship between the degree of urbanization (impervious surface cover) within a home-range and the home-range size (ha). Triangles and circles represent the observed home-ranges of males and females respectively. The solid lines represent the predicted relationships for males and females respectively from the sex-biased impact of urbanization model.

3.4 Discussion

3.4.1 Land-use type selection by tawny frogmouths

In this study, tawny frogmouths aligned their home-range to the least urbanized areas of the broader urban landscape, showing an avoidance of impervious surfaces and preferentially selecting treed and grassed environments. Trees are highlighted as the most important land-use type influencing home-range location with both trees and grassed areas identified as important features of core activity areas within the home-
range. The preferential selection of trees and grassed areas at both orders of selection is not surprising. Tawny frogmouths are dependent on trees for diurnal roosting and for nest construction and raising young during the breeding season (Kortner and Geiser 1999a; Körtner and Geiser 1999b). Treed environments incorporating grassy areas such as mown parklands, sporting fields and backyards, common in urban environments, provide suitable features for nocturnal hunting.

In contrast to more forested and urban-fringe areas, recent research indicates that tawny frogmouths occur in high abundances in urban areas (Weaving et al. 2011). A combination of generalist habitat requirements (Higgins 1999; Rose and Eldridge 1997) and a level of adaptability to urban environments are likely reasons for these findings. Despite these factors, the preferential use of natural areas over urban habitat highlighted that tawny frogmouths are reliant on areas of natural vegetation and the resources they contain. Our results are broadly consistent with other spatial studies where urban-dwelling species adjust their home-ranges to incorporate natural areas for breeding, foraging and shelter from human disturbance (Framis, Holroyd and Manosa 2011; Gese, Morey and Gehrt 2012; Riley et al. 2003; Smith and Gilbert 1984).

3.4.2 Sex-biased home-range size

Several factors that impact on home-range size include sex bias, with males having larger home-ranges than females (Herr, Schley and Roper 2009; Lindstedt, Miller and Buskirk 1986; Tigas, Van Vuren and Sauvajot 2002) and sexual dimorphism with males having larger body sizes and consequently needing to travel further to obtain prey.
A potential explanation may be linked to parental care of young. In many bird species bi-parental care is common (Westneat et al. 2011). The respective contribution of either sex however, varies according to breeding cycle stages and can differ between the sexes (Steen, Sonerud and Slagsvold 2012; Sunde et al. 2009). In this study, radio-tracking was undertaken throughout stages of the protracted tawny frogmouth breeding season (July–January). Comparisons between breeding and non-breeding periods were not possible, as not all birds bred during their individual tracking periods.

Parental care is undertaken by both sexes, however, the relative contribution by either sex is not known. Male birds assume sole responsibility for day-time brooding (Higgins 1999; Kortner and Geiser 1999a; Schodde and Mason 1980) with both sexes sharing night-time incubation (Kortner and Geiser 1999a). Food provisioning to nestlings may be shared by both sexes (Schodde and Mason 1980), however, respective rates are unknown (Kortner and Geiser 1999a). Post fledging, young birds remain with their parents for protection and prey, often for extended periods of time (Higgins 1999). The contribution towards post fledging care by either sex is not known.

Comparing parental care within nocturnal avian species is problematic. Most studies occur in forested areas and raptor species frequently feature as case studies. Several however, highlight a marked division between the sexes, with males maintaining a high
level of provisioning effort throughout breeding cycle stages (Hakkarainen and Korpimaki 1994; Zarybnicka, Sedlacek and Korpimaki 2009).

It may be possible that male tawny frogmouths are assuming a high level of parental care necessitating more frequent movements over a greater area in order to obtain prey. This may be further exacerbated by the species breeding season coinciding with winter months, a low prey resource period for many species.

Another explanation for larger male home-ranges is that they adjust their movements to overlap with multiple females and therefore travel further than females to find multiple mates (Dahle, Oslash and Swenson 2003; Edelman and Koprowski 2006). Recent evidence has found extra pair fertilizations occurring in many avian species previously thought to be monogamous (Wan, Chang and Yin 2013). While tawny frogmouths are assumed to be monogamous (Higgins 1999), it may be possible that males are engaging in extra-pair copulations with neighboring females.

Similar to other urban-dwelling species, this research highlights the importance of retaining treed areas in order for the tawny frogmouth to occupy and persist in urban environments. As proximity to the city centre increases and the loss of vegetation intensifies, a threshold may be reached beyond which tawny frogmouth populations can no longer occur. The paucity of studies regarding tawny frogmouth ecology and behaviour have limited comparisons with other results. However, we believe our results are significant in that they reveal many previously unknown aspects of tawny frogmouth ecology and behavior and highlights the possibility that urbanization is biased against males. We recommend further research specifically investigating how
Home-range

densities of tawny frogmouths change from suburban to highly urbanized landscapes and identifying the potential causes behind the different responses to urbanization demonstrated by both sexes in this study.
Chapter 4:

Adaptation to urban environments promotes high reproductive success in the tawny frogmouth (*Podargus strigoides*), an endemic nocturnal bird species

This chapter has been published as:


Recently fledged tawny frogmouth chick flanked by adults roosting in a swamp paperbark tree (*Melaleuca ericifolia*) in a suburban Melbourne backyard. Photo: Peter Bermingham.
4.1 Introduction

As one of the most extreme forms of landscape transformation, urbanisation substantially modifies natural ecosystems resulting in dramatic and often irreversible changes (McKinney 2002; Seto, Güneralp and Hutyra 2012). Urbanisation creates heterogeneous landscapes characterised by highly modified urban cores, moderately disturbed urban-fringe areas extending to forested landscapes on the city margin (McDonnell and Pickett 1990).

The effects of urbanisation on avian community composition are well described (Blair 1996; Garaffa, Filloy and Bellocq 2009; Sol et al. 2014). Less studied, and subsequently less understood, is how landscape modification by urbanisation impacts on critical life-history elements such as reproduction. The effect of urbanisation on avian breeding is likely to be highly complex and species specific. In addition, factors such as the type and intensity of urbanisation, the related shifts in resource availability and predation are likely to substantially modify breeding responses (Chace and Walsh 2006; Chamberlain et al. 2009).

Studies spanning urban gradients have demonstrated various differences in reproductive behaviour between urban and rural populations, and have suggested the key roles of factors such as prey availability (Newhouse, Marra and Johnson 2008), habitat type (Dykstra et al. 2000), degree of predation (Antonov and Atanasova 2003; Beck and Heinsohn 2006) and human-subsidized food resources (Rollinson and Jones 2002) as influential in these differences. Many studies have highlighted a clear and consistent pattern demonstrating the association between the degree of urbanisation and
the timing of breeding onset, with factors such as food abundance (Eden 1985; Schoech, Bowman and Thompson 2003), elevated prey density (Boal and Mannan 1999) and increased ambient temperatures (Chamberlain et al. 2009) contributing to the early onset of breeding in comparison to their rural counterparts.

Breeding is a critical life-history event, as such, breeding birds will actively select specific habitats and habitat elements that maximise reproductive success (Bailey and Thompson 2007; Degraaf and Wentworth 1986). If resources are unavailable or lack sufficient quality, as is often the case in urban areas, there are significant implications for the demographics of the urban population (Cody 1985). For species with specialised breeding requirements such as hollow-dependant breeders, urbanized environments often lack the resources required for breeding and as such breeding outputs are substantially reduced by urbanisation (Cooke et al. 2006; Hindmarch et al. 2012; Isaac et al. 2014a; Rottenborn 1999). Where species have less demanding breeding habitat requirements, novel habitat types and abundant food resources common to urban systems, may enhance breeding outcomes resulting in population levels higher than those in more natural environments (Stracey and Robinson 2012). Studies that focus on avian reproduction in urban areas are essential as they provide critical information about the patterns and processes driving reproductive outcomes in response to landscape modification.

Identified as sensitive to landscape modification, long-lived sedentary species are considered useful models for investigating ecological responses to urbanisation (Sekercioglu, Daily and Ehrlich 2004). The tawny frogmouth (*Podargus strigoides*), is a long-lived, sedentary, large-bodied (350-550g) endemic nocturnal species widespread
throughout Australia (Higgins 1999). This species exhibits a range of generalist habitat requirements with no apparent dependency on any one or more habitat resources (Higgins 1999). Dietary items consist of terrestrial and aerial invertebrates and some small vertebrates (Rose and Eldridge 1997). The species has a protracted annual breeding season (July to January) with pairs capable of repeated breeding attempts if prior attempts in that season fail (Higgins 1999). As a non-hollow dependant species, tree branches are used for diurnal roosting and nesting (Kortner and Geiser 1999a; Körtner and Geiser 1999b; Rae 2009). Pairs construct very basic nests from small woody twigs, locating them in the fork of a tree branch or trunk/branch junction or occasionally utilizing an abandoned bird nest (Schodde and Mason 1980). Breeding activities are shared between the sexes (Higgins 1999).

Whilst a common species, many aspects of tawny frogmouth ecology and behaviour remain largely unknown. Most studies have focused on birds associated with woodlands or more forested environments (Kortner and Geiser 1999a; Körtner and Geiser 1999b; Rae 2009). In comparison to more wooded areas, high numbers of tawny frogmouths have been shown to occupy urbanized environments (Weaving et al. 2011) suggesting some degree of tolerance to landscape change associated with urbanisation.

Using the tawny frogmouth as a case study, this research investigates whether the degree of urbanisation has an influence on key breeding parameters. Firstly, does the degree of urbanisation influence the availability of suitable nesting locations across a continuum of urbanisation? We predict that nesting habitat will not be uniform across the urban landscape and will become limited as urbanisation intensifies. Secondly, we investigate whether broad and/or local scale factors around a nest site influence the
degree of reproductive success of tawny frogmouths. We predict that breeding success will be negatively associated with the degree of urbanisation around the nest at both broad and local scales. Finally, we investigate whether the degree of urbanisation influences the timing of the commencement of breeding. We predict that the onset of breeding will be earlier at nest sites in more urbanised locations due to the altered physical and environmental conditions generally associated with these landscapes.

4.2 Methods

4.2.1 Study site selection and land-cover quantification

Our study was located in the north-east of Melbourne, Australia and covered approximately 52,000 ha and represents a continuum of urbanisation (Figure 4.1). Our definition of urbanisation was based on the proportion of impervious surfaces occurring in the study zone, with increasing cover of impervious surfaces indicating increasing urban intensification. To quantify the urban landscape a Normalised Difference Vegetation Index (NDVI), which measures the amount of living green vegetation in the landscape (Leslie et al. 2010), was created in Environment for Visualizing 4.7 (ENVI 4.7). The NDVI landscape scale map was created from SPOT 5 (‘Systeme Pour 1’ Observation de la Terre) imagery using four high-resolution satellite images with a pixel size of 10 m x 10 m. These images were corrected for differences in brightness, colour and contrast then mosaicked together, using one image as the base and a feather distance of 100 pixels to overlap the images (ITT Visual Information Solutions 2010a). The resulting image was then processed to create an NDVI layer.

Using the NDVI layer we then classified the landscape into five broad land-use types that could define the urban landscape: - grass, impervious surfaces, trees, rivers and permanent water-bodies. The land-use layer was created by defining Regions of Interest
(ROI’s), with each land-use type being defined by 107 ROI’s. Supervised classification was then undertaken with the ROI’s using the maximum likelihood function. This function gives each pixel a probability of belonging to a land-use type and then assigns it to the type with the highest probability (ITT Visual Information Solutions 2010b).

**Figure 4.1.** Map of the study area showing extent of land-use types and tawny frogmouth nest locations.
4.2.2 Field survey methods

Between July and January, over four consecutive breeding seasons (2010-2013), parks, vacant land, bushland reserves and streetscapes within the study zone were searched on foot, during the daytime to locate nesting birds. Using binoculars, tree branches were systematically scanned to locate nesting or roosting birds. To avoid bias with the data collection, a single data collector (MW) conducted all surveys using a systematic and consistent search method. Breeding bird locations were also reported by members of the public and ornithology groups and these locations were all visited and confirmed by MW. A small set of nest locations were also found by radio telemetry as we were radio-tracking some birds for other research questions (Weaving et al. 2014). Once a nest site was found, the location was recorded and the following attributes measured:- tree type (native, exotic), Genus (*Eucalyptus, Pinus, Acacia,* other), bark type (rough, smooth and flaky), tree diameter (DBH), nest height (m), nest location (trunk, close to trunk, mid branch, branch junction), nest type (stick, trunk/branch junction, hollow, abandoned bird nest) and nest orientation (NE, NW, SE, SW).

4.2.3 Nest monitoring and behaviour

Nests were monitored at least once per week (during the day), until a nesting attempt fledged chicks or the attempt was abandoned. Dates that nesting behaviour (e.g. bird on nest) was first observed and the date that attempts were abandoned or chicks fledged were recorded. We recorded the number of nestlings observed per nest during site visits. We classified a nest as successful where at least one chick successfully left the nest and recorded the number of fledglings per nest that successfully fledged.
Tawny frogmouth nests are built up to 9m off the ground making it difficult to assess clutch size. Disturbance to nesting birds was minimised during visits by making observations through binoculars as far from the nest as practicable. If a nest was found abandoned, return visits to the site were made each week to search for re-nesting attempts. When chicks were close to fledging, nests were checked more frequently, often daily. If the nest was found empty, the surrounding area was searched for roosting adults and fledglings.

4.2.4 Spatial modelling

To establish whether broad landscape characteristics influenced the area available for nesting across the continuum we utilised MaxEnt, a machine learning process that measures the correlation between a presence location and a set of ecological and geographic variables (EGV’S). MaxEnt is able to generate a spatial distribution map that identifies the probability of occurrence or suitability for what is being modelled (Elith et al. 2011; Phillips, Dudik and Schapire 2004). The advantage of using MaxEnt is its presence-only modelling approach, as due to the cryptic nature of tawny frogmouths we could not be confident that a failure to detect a nest in an area meant an absence of a nest. To produce the predictive model of nest site suitability we chose a series of EGV’s based on previous research and the likelihood of influencing key resources for the species (Table 4.1). EGV’s were created as layers with a spatial resolution of 10m x10m. Prior to modelling we used ENM tools Version 1.3 (Warren, Glor and Turelli 2010) to identify correlated variables (R²>0.75). Where correlated variables existed we chose the variable we considered the most ecologically relevant. Model fit was evaluated by the area under the receiver operator curve (ROC). Twenty replications of each model were run incorporating 5000 iterations with no threshold
rule applied. Random selection partitioned the data 75% to 25% per run, where 75% of the data were used to train the model and the remaining 25% for testing. Each model was run with six different beta multipliers (0.5, 1, 2, 3, 4, and 5), in raw output format. Models were entered into ENM tools which produces Akaike Information Criterion (AICc) scores for all models. The model with the lowest AICc score was selected as the best fit, or most parsimonious model. This model was then re-run in MaxEnt with a logistic output format applied then transferred back into ArcGIS to produce a habitat suitability map. The 10th percentile was selected as the threshold value for defining suitable breeding habitat. This value is commonly used in species distribution modelling studies due to its conservative nature (Razgour, Hanmer and Jones 2011).

Table 4.1. Variables used for MaxEnt modelling.

<table>
<thead>
<tr>
<th>Derived layers</th>
<th>Variable type</th>
<th>Data type</th>
<th>Categories</th>
<th>Layer/Data Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lineal density of roads</td>
<td>A</td>
<td>Continuous</td>
<td>-</td>
<td>Roads-VICMAP (VMTRANS)</td>
</tr>
<tr>
<td>Normalised Difference</td>
<td>A,E</td>
<td>Continuous</td>
<td>-</td>
<td>SPOT 5 IMAGERY (System Pour l’ Observation de la Terre)</td>
</tr>
<tr>
<td>Vegetation Index (NDVI)</td>
<td>A,E</td>
<td>Categorical</td>
<td>Impervious surfaces Trees Grass/agriculture Rivers Water-bodies</td>
<td>Digital Terrain Model (DTM), 20m - VICMAP</td>
</tr>
<tr>
<td>Land-use layer</td>
<td>A,E</td>
<td>Categorical</td>
<td>Ridge Upper slope Middle slope Flat slope Lower slope Valley</td>
<td>Digital Terrain Model (DTM), 20m - VICMAP</td>
</tr>
</tbody>
</table>

Variable type: A= Anthropogenic, E= Ecological, G= Geographical.
4.2.5 Land-use type measurements

We defined a 500m buffer around each known nest tree in ArcMap 10.1 (ESRI 2011) then calculated the proportion of the five land-use types; impervious surfaces, grass, trees, rivers and permanent water-bodies, occurring within the buffer. This buffer size was selected based on known movement capabilities and ecological requirements of the species and as such represents the area likely to provide most of the resources required by a breeding pair (Schodde and Mason 1980; Weaving et al. 2014).

4.2.6 Modelling

We used generalized linear mixed models (GLMM’s) run in ‘R’ statistical package (V 3.1.0) (R Development Core Team 2012) using the lme4 package with model selection performed using the MuMIn package to evaluate whether the degree of reproductive success of breeding tawny frogmouths is influenced by broad scale (500m buffer) and tree level factors at each active nest location (Table 4.2). We also modelled the influence of the degree of urbanisation around a nest as well as the role of climatic conditions on the commencement date of breeding (Table 4.2).

Table 4.2. Modelling parameters used for Generalized Linear Mixed Modelling.

<table>
<thead>
<tr>
<th>Model type</th>
<th>Random factor</th>
<th>Model parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest site location</td>
<td>Year</td>
<td>1 No. of fledged chicks #</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2 % proportion of</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grass</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Trees</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Impervious surfaces*trees</td>
</tr>
<tr>
<td>Nest tree</td>
<td>Year</td>
<td>No. of FC #</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tree attributes &amp; measurements</td>
</tr>
<tr>
<td>Time of breeding</td>
<td>Year</td>
<td>3 Julian date #</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4 % Imp. surf</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5 Temp</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6 Rainfall</td>
</tr>
<tr>
<td></td>
<td></td>
<td>7 Temp*rainfall</td>
</tr>
</tbody>
</table>

# Response variable. All other model parameters are fixed affects. 1 Number of fledged chicks (FC), 2 % proportion of three land-use types in a 500m buffer around nest site locations, 3 Julian date, number of days after July 1st, 4 % proportion of impervious surfaces in 500m buffer around each nest tree, 5 Mean minimum monthly temperature (Celsius), 6 Mean monthly rainfall (mm), 7 interaction between rainfall and temperature.
Reproduction

As some pairs undertook multiple breeding attempts in a year and some pairs were sampled over several years, ‘Year’ was included as a random factor in the modelling (Table 4.2), and global models were fitted with a Poisson distribution. All possible subsets were generated to identify key correlates of tawny frogmouth nest location attributes. Akaike Information Criterion corrected for small sample sizes (AICc) was used to select between models. AICc weights (ωi) were calculated, giving the proportional weight for each model within the model set. Where model uncertainty was indicated, model averaging was undertaken.

4.2.7 Breeding commencement

To establish whether breeding commenced earlier in response to increasing urbanisation we needed to determine the date at which the breeding commenced for each pair. For all years, and for breeding attempts that fledged young, we calculated back from the approximate date of the first chick to fledge (60 days; 29 days for incubation and 31 days brooding) to calculate commencement dates (Higgins 1999). After observing how quickly re-nesting could occur in some pairs following failure, only birds with a Julian date between July 1st - JD1 and September 14th - JD76, were selected for our modelling as these were likely to represent the first breeding attempt of the year. We also included ten pairs that failed to fledge young where the date we observed the brooding bird fell within the Julian date index. In addition we added in some breeding attempts by several radio-tracked birds. Although these attempts were made just outside of our Julian date range (i.e. after September 14th) we included them since these birds were under constant observation so we were confident that these attempts were their first. Due to their known effect on avian breeding (Both et al. 2006; Schaper et al. 2012), we also included two meteorological variables: - precipitation and
temperature in our modelling. We obtained data (Mean minimum daily temperatures Celsius) and Mean daily precipitation rates (mm) from the Australian Bureau of Meteorology (Bureau of Meteorology 2015). We calculated the average daily rates of both variables for the thirty days prior to the commencement of breeding for each pair.

4.3 Results

4.3.1 Tawny frogmouth breeding effort

Over all breeding seasons we located 158 active nests across the study zone (Figure 4.1). All breeding attempts were monitored until chicks fledged or the attempt failed. Of the 189 known breeding attempts we monitored, 133 attempts successfully produced 177 fledged chicks. From all breeding attempts we monitored, 75 were classified as the likely first attempt for a pair in that breeding year. Of these, 65 pairs (86.7%) were successful in fledging a total of 77 young. Six of the 10 failed pairs attempted to breed again, where 5 (83.3%) were successful at fledging 6 young. The one pair that was unsuccessful in its first two breeding attempts was subsequently able to successfully fledge a single young on their third attempt. Overall, for nests where we could confidently assign the first breed for a year, 71 of the nests (94.7%) were able to successfully fledge young.

There were a further 114 nesting pairs where we were able to monitor breeding. As the nests were often found later in the breeding season, we could not assign them to the group where we had confidence it was their first breeding attempt. From these nests 77 were successful at fledging 88 chicks. Of the 40 nests that failed only 8 pairs attempted breeding again. Five of these nests were successful at fledging 5 young.
Ultimately, of this group of nests where we could not establish whether it was the first breed of the year, 71.9% of pairs were able to successfully fledge young.

We recorded three pairs double brooding after successfully producing fledged chicks from a previous attempt. One of which fell within our Julian date index for first known breeding attempts. All three double brooding attempts failed. To our knowledge only one other incident of double brooding has been reported in Australia for tawny frogmouths (Debus 1997).

We calculated brood size based on the maximum number of hatched chicks observed in the nest during all site visits and fledging rates as the total number of chicks that successfully fledged per successful breeding attempt. For all breeding attempts, the mean brood size was 1.1 and fledging rate was 0.9. For first known breeding attempts mean brood size was 1.3 and fledging rate was 1.1.

4.3.2 Is breeding habitat influenced by urbanisation?

Across the four years in which we monitored tawny frogmouth breeding we established the locations of 158 active breeding nests across the gradient (Figure 4.1). To determine whether urbanisation has an influence on the availability of nest sites across the landscape we developed presence-only models based on the 158 active nest locations. Utilizing a set of ecological, geographical and anthropogenic variables we generated a number of potential spatial models to explain the distribution of nest sites across the gradient (Table 4.1). Of the potential set of six models to explain tawny frogmouth nest locations across the gradient, AUC values ranged from 0.78 to 0.85. These models have a strong capacity to explain the distribution of potential nest site habitat across the landscape. The most parsimonious model, as defined by the lowest AICc values, had a
regularisation beta-multiplier of 2 and a good fit for the nest locations with AUC_{train} = 0.804 and AUC_{test} = 0.768.

The key drivers in the models that explained nest site locations were the classified land-use layer and lineal density of roads which together contributed 92.9% of the total model performance. The environmental variable with the highest gain when used in isolation was the lineal density of roads with a contribution of 56.4%. The variable that decreased the gain the most when omitted was the lineal density of roads indicating that it has the most information not accounted for by other variables. The presence of the road density variable in our model suggests that the degree of urbanisation does influence the availability of nest locations for this species across the gradient. This relationship, however, breaks down beyond 12 lineal kilometres of roads per square kilometre (Figure 4.2).

The high contribution of the land-use layer to model performance was driven by a clear preference to areas of the urban landscape with trees (Figure 4.3). The addition of NDVI into the models also influenced nest site locations throughout the gradient. NDVI represents actively growing vegetation and as such is seen as a surrogate for vegetation productivity. As NDVI values increased there was a distinct increase in the probability of an area having a higher capacity of being a good nest location (Figure 4.4).
Figure 4.2. Lineal density of roads (km per km²).

Figure 4.3. Land-cover categories: 1= Grass, 2= impervious surfaces, 3= trees, 4= rivers, 5= permanent water-bodies.

Figure 4.4. NDVI (greenness index).

Figures 4.2 - 4.4. Red represents the mean response of the individual variable over MaxEnt replicate runs. Blue represents the mean response of the variable over the 20 replicate runs ± one standard deviation. Categorical variables contain two shades of blue.
Reproduction

To identify which areas of the gradient constituted potential breeding habitat, we applied the 10th percentile threshold value to our best model and classified the gradient into two categories; potential and non-potential nest site habitat. Potential breeding habitat accounted for 26,796 ha (51.7%) of the total study area.

4.3.3 Do particular habitat characteristics of the nest tree influence nest site location at a local scale?

We sought to establish whether there were any obvious consistencies in the type of trees and nest characteristics that were utilised by tawny frogmouths for nesting. Using the 158 nests, we found that even when other options are available, birds preferentially select trees with specific attributes. Native tree species (95%) were selected over exotic (5%) species with *Eucalyptus* spp. selected over any other genus (94%). Trees with rough (57%) and flaky barks (26%) were selected over smooth barked species (17%). All pairs constructed a nest from sticks and twigs as opposed to selecting abandoned bird nests. In most instances (70%), birds chose a branch junction (a branch fork under the canopy of the tree) on which to locate their nest, followed by tree trunk junction (16%), mid branch location (13%) and on a branch where it connects to the trunk (1%). Nest orientation varied with no one particular direction being favoured. The mean height of nests were 9.8 m and the mean DBH of nest trees were 0.61m. These results indicate that tawny frogmouths show a strong preference for native tree species in particular *Eucalyptus* spp. with a rough or flaky bark structure within which to build their nests.
4.3.4 Do land-use type and characteristics of the nest tree impact on breeding success?

To determine which factors or set of factors contributed to successful reproduction, we developed models based on the number of fledged chicks produced from all breeding attempts. For our modelling we used eight habitat variables associated with nest trees and the proportion of three land-use types (grass, trees and impervious surfaces) occurring within a 500m buffer around each nest tree (Table 4.2). These land-use types, in particular, open grassy areas and trees are highly represented in tawny frogmouth home-ranges, being used by the species for a range of ecological and behavioural functions (Weaving et al. 2014).

Using this set of variables model selection identified two models (ΔAIC<2). Our top model was the null model indicating that none of the land-use types had a significant effect on tawny frogmouth breeding success (Table 4.3 Model a).

For nest tree modelling, model selection identified two models (ΔAIC<2). The null model had top support indicating that none of the attributes associated with the nest tree supported breeding success (Table 4.3 Model b). While tawny frogmouths are clearly selecting trees with particular attributes over others our modelling indicates that no one attribute influences breeding outcomes. Despite our prediction that breeding success would be negatively associated with the degree of urbanisation around the nest at several scales, our modelling results suggest that once a nest location is established, these factors do not impact on breeding success.
Reproduction

4.3.5 Does urbanisation influence time of breeding?

We now ask whether the onset of tawny frogmouth breeding is affected by the degree of urbanisation. To build our models we used 75 nests where the first known breeding attempt for the year was established (based on Julian date July 1st = day one of breeding). We modelled this against the proportion of impervious surfaces within the 500m buffer around each nest site and temperature and rainfall rates in the month prior to nesting. Model selection using AICc identified two models (ΔAIC <2; Table 4.3 Model c). In the top model, the meteorological variables (temperature and rainfall) were supported as the most influential variables linked to the commencement of breeding. The impervious surfaces variable, (our indicator of the degree of urbanisation), was not supported as important in driving the commencement date of breeding. Despite our prediction that increasing levels of urbanisation may promote earlier onset of breeding, the modelling suggest that the main drivers of breeding commencement are based on climatic conditions.

Table 4.3. AICc based model selection for explaining the effect of (a) the proportion of land-use types occurring within a buffer around nest trees and (b) nest tree characteristics and attributes on tawny frogmouth breeding success. Model (c) explains factors influencing commencement of breeding time. All models with ΔAIC<2 are reported. The top models are provided.

<table>
<thead>
<tr>
<th>Model (a)</th>
<th>df</th>
<th>Loglik</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>2</td>
<td>-216.450</td>
<td>437.0</td>
<td>0.00</td>
<td>0.362</td>
</tr>
<tr>
<td>Impervious surfaces</td>
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<td>438.9</td>
<td>1.98</td>
<td>0.134</td>
</tr>
<tr>
<td>Trees</td>
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</tr>
<tr>
<td>Grass</td>
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<td>0.129</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
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<th>Loglik</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
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<td>-216.450</td>
<td>437.0</td>
<td>0.00</td>
<td>0.156</td>
</tr>
<tr>
<td>Nest height</td>
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<td>437.4</td>
<td>0.41</td>
<td>0.127</td>
</tr>
<tr>
<td>DBH</td>
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<tr>
<td>Tree (native/exotic)</td>
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<td>439.0</td>
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<td>0.056</td>
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</table>

<table>
<thead>
<tr>
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<th>df</th>
<th>Loglik</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rain+Temp+Rain *Temp</td>
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<td>0.00</td>
<td>0.490</td>
</tr>
<tr>
<td>Rain+Temp</td>
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<td>-252.749</td>
<td>516.4</td>
<td>1.97</td>
<td>0.183</td>
</tr>
</tbody>
</table>

Model (a): Models based on the proportion (ha) of five land-use types within a 500m buffer around each nest. Land-use types are: - grass, trees, impervious surfaces, rivers and permanent water-bodies. Model (b): Models based on nest tree attributes and measurements. Model (c): Models based on the proportion of impervious surfaces within a 500m buffer around each nest, start of breeding date (Julian date - July 1), rainfall (mm) and temperature (Celsius) rainfall and temperature interaction.
To assess how rainfall and temperature impact on the temporal distribution of breeding we plotted start of breeding dates (Julian date) against the average rainfall rates and temperature that occurred in the 30 days prior to start of breeding. Overall there was a strong negative linear association between rainfall rates and breeding commencement dates (Figure 4.5 a). Higher rainfall rates resulted in earlier start of breeding dates. Conversely, there was a strong positive linear relationship between temperature and start of breeding dates with rising temperatures correlated with later start of breeding dates (Figure 4.5 b). The positive relationship between temperature and start of breeding was not surprising since as the season progresses temperatures increase.

**Figure 4.5.** Scatterplots showing the relationship between Julian date and (a) rainfall rates and (b) temperature.
4.4 Discussion

Generalist habitat requirements and flexible behavioural traits are likely factors for the reproductive success of tawny frogmouths observed in this study. Research investigating avian reproduction in urban environments report similar levels of productivity in species with comparable ecological traits and characteristics (Antonov and Atanasova 2003; Stracey and Robinson 2012). Termed urban-adaptors or exploiters (Le Viol et al. 2012), these species frequently develop adaptive responses to landscape modification to occupy urban systems in high numbers (Lizée et al. 2011).

Tawny frogmouths select potential nest site locations based on a decision making process that occurs at multiple scales. Firstly, we predicted that nesting habitat will not be uniform across the urban gradient and would become limited at high levels of urbanisation. Spatial modelling confirmed this prediction indicating that pairs were avoiding more extreme levels of urbanisation across the gradient and selecting areas containing moderate levels of urbanisation combined with increasing tree cover in which to locate their nests. These areas represent the intermediate level of landscape modification along a continuum of urbanisation (McKinney 2006). They typically comprise wooded suburban streetscapes and parks containing high levels of floral diversity capable of supporting elevated abundances of avian taxa (Carbo-Ramirez and Zuria 2011; Loss, Ruiz and Brawn 2009). Regarded as an open woodland species, these environments suit many aspects of tawny frogmouth ecology providing varied tree species for day-time roosting and breeding. The profusion of open mown grassy areas and abundance of artificial and natural perch types creates an ideal environment for nocturnal foraging. A recent spatial study highlighted the importance of trees and open
tended grassy areas in the species home-range with an avoidance of areas with
impervious surfaces (Weaving et al. 2014).

Secondly, we predicted that breeding success would be negatively associated with the
degree of urbanisation around the nest at both the broad and local scales. Our results
did not support this predication. At both scales, the level of urbanisation was not
supported in our models as influential to breeding success. We did however, identify
that breeding birds were selective in their choice of a nest tree with tree species
containing certain structural attributes selected over others. Other studies illustrate
similar behaviour where habitat characteristics of the nest tree and the area surrounding
the nest, drive nest site selection at the local level (Bailey and Thompson 2007; Stout,
Temple and Papp 2006; Wagner and Islam 2014).

As a non-hollow dwelling species, tawny frogmouths rely on a range of behavioural
and physical characteristics to maintain low day-time visibility (Körtner and Geiser
1999b; Rae and Rae 2014). During breeding, the selection of a nest tree must maintain
this status for both adults and growing young. By selecting a tree with characteristics
that minimize predation threats, provide stability and maximises thermoregulation
properties, their chances of reproductive success are thus increased.

Our final prediction that breeding will commence earlier in response to more highly
urbanized locations was also not met. The key drivers for the commencement of
breeding were climatic variables in particular rainfall. Rainfall variations impact on the
breeding performance of many avian species, with effects more pronounced at
particular phases of the breeding cycle (Mattsson and Cooper 2009; Peach et al. 2008).
Assessing the effect of climate, especially precipitation on nocturnal avian species can be challenging as most studies feature raptorial species occupying natural or agricultural environments. Several however, emphasise the effect of precipitation on reproductive success (Bionda and Brambilla 2012; Ogada and Kibuthu 2012) in particular how rainfall variations influence time of breeding and subsequently reproductive success. For diurnal and nocturnal species, food availability is a key factor associated with enhanced breeding performance (Bionda and Brambilla 2012; Hakkarainen, Koivunen and Korpimaki 1997; Schoech, Bowman and Thompson 2003). Climatic conditions, in particular rainfall and rising temperatures, stimulate ecosystem productivity leading to increases in food availability and thus providing a cue for the onset of breeding. In south-eastern Australia, September marks the cessation of winter and the start of spring, resulting in more stable weather patterns, warmer temperatures and high levels of invertebrate abundance.

The timing of seasonal reproduction to occur when environmental conditions are optimal is a major contributing factor to reproductive success in many avian species (Blackmer et al. 2005; Both et al. 2006). The capacity for tawny frogmouths to synchronize their breeding to coincide with peak environmental conditions is a strategy that allows them to maximise their reproductive output. Across the urban landscape tawny frogmouth pairs in this study achieved extremely high reproductive success and low failure rates. The capacity for breeding pairs to quickly re-nest and attempt breeding again after a failed nesting attempt provides a key advantage for the species over a single annual nesting attempt. For a large, long-lived, sedentary bird such as the tawny frogmouth this ability suggests high individual fitness and indicates a successful adaptation to local environmental conditions (Blackmer et al. 2005)
Chapter 5:

Highly heterogenous environments facilitate gene flow for an urban-adapted endemic species

This chapter is under review as:


Tawny frogmouth adult (far right) and two recently fledged juveniles roosting in a she-oak (*Allocasuarina verticillata*) in a suburban Melbourne park. Photo: Debbie Lustig.
5.1 Introduction

Habitat loss and fragmentation caused by urbanization transforms once continuous tracts of natural vegetation into patches dispersed throughout the landscape (Botkin and Beveridge 1997). Floristically and structurally diverse, these patches are typically smaller than those in more wooded areas and spatially isolated from each other by an abundance of impervious surfaces, fabricated structures and transportation networks (Collins et al. 2000; Medley and McDonnell 1995). Species once widespread with few barriers to movement are often confined to these patches, dependent on the resources they provide for functioning (Bowler and Benton 2005; Crooks et al. 2001; Major et al. 2014).

For species that remain common and widespread throughout fragmented landscapes, maintaining functional connectivity across the landscape is essential in order for these populations to persist (Crooks and Sanjayan 2006). If landscape connectivity is reduced, genetic exchanges facilitated by dispersing individuals may be impaired resulting in physically and genetically isolated sub-populations prone to inbreeding, loss of genetic diversity and local extinction (Frankham 2006; Reed 2004).

Understanding the effects of habitat loss and fragmentation on wildlife populations has, in recent times gained prominence in the field of landscape genetics (Manel et al. 2003; Storfer et al. 2007). Of benefit has been the development of genetic techniques, in particular, measures that test the relatedness between individuals of a species (Banks and Peakall 2012). When integrated with landscape information, these techniques create opportunities for investigating and testing assumptions regarding the dispersal...
Due to their ability to fly, birds are thought to be less impacted by landscape modification (Henle et al. 2004), although impacts may differ between species dependent on factors such as dispersal capabilities (Delaney, Riley and Fisher 2010; Harrisson et al. 2013), and behavioural responses to movement barriers such as roads (Forman and Alexander 1998; Harris and Reed 2002). Although some avian species become wide-spread and abundant in urban environments, (Chace and Walsh 2006; Stracey and Robinson 2012), as urban development intensifies even the most resilient species may experience a reduction in genetic diversity through population isolation resulting from reduced landscape connectivity.

Common and wide-spread throughout a range of habitats, the tawny frogmouth (Podargus strigoides) is a large bodied nocturnal bird species endemic to Australia. While current populations appear to be large and stable, due to several life-history traits, tawny frogmouths are likely to be impacted by fine-scale disturbances such as a reduction of nest trees and foraging areas due to urban growth and development.

Using the tawny frogmouth as a case study, we took a landscape approach to examine the genetic structure and diversity of the species across a gradient of urbanization. We had two main objectives. The first was to examine population structure, within-population relatedness and dispersal patterns and further, whether there were sex differences in these responses. We predict that tawny frogmouths will experience a
reduction in genetic diversity in response to urbanization. Secondly, we aimed to
determine whether landscape modification resulting from urbanization, reduces
functional connectivity and subsequently limits tawny frogmouth gene flow. We
predict that urbanization will limit tawny frogmouth movements at high levels of
resistance, thereby impeding gene flow.

5.2 Methods

5.2.1 Study area and land-cover quantification

Our study was located in the north-east of Melbourne, Australia and covered
approximately 52,000 ha and represents a gradient of urbanization (Figure 5.1). The
area contains multiple land-use types including neighbourhoods of varying age and type
and public land comprising parks, areas of remnant bush land and reserves of differing
size and use. Our definition of urbanization was based on the proportion of impervious
surfaces occurring in the study zone. To quantify the urban landscape a Normalized
Difference Vegetation Index (NDVI), which measures the amount of living green
vegetation in the landscape (Leslie et al. 2010), was created in Environment for
Visualizing 4.7 (ENVI 4.7). The NDVI landscape scale map was created from SPOT
5 ("Systeme Pour 1" Observation de la Terre) imagery using four high-resolution
satellite images with a pixel size of 10 m. These images were corrected for differences
in brightness, colour and contrast then mosaicked together, using one image as the base
and a feather distance of 100 pixels to overlap the images (ITT Visual Information
Solutions 2010a). The resulting image was then processed to create the NDVI layer.
From the NDVI layer we then produced a categorical map, classifying the landscape into five broad land-use types that could define the urban landscape: grass, impervious surfaces, trees, rivers (flowing water) and permanent water-bodies (lakes and dams). The land-use layer was created by defining Regions of Interest (ROI’s), with each land-use type being defined by 107 ROI’s. Supervised classification was then undertaken with the ROI’s using the maximum likelihood function. This function gives each pixel a probability of belonging to a land-use type and then assigns it to the type with the highest probability (ITT Visual Information Solutions 2010b).
Figure 5. 1. Map of the study area including land-use type, extent and DNA sample locations.
5.2.2 Study site and DNA sampling

From 2010 to 2015 parks, reserves, streetscapes and private properties within the study area were searched to locate the presence of tawny frogmouths. DNA samples were obtained invasively (blood) and non-invasively (tissue and feathers) during this study. Over a three year period (2010-2013), tawny frogmouths were netted and captured at parks and reserves in the study zone. A blood sample (~70 μl), was taken from the brachial vein of each bird using a VITREX® capillary tube. Each sample was transferred to a Whatman FTA Card® and stored at room temperature in paper envelopes. Between 2010 and 2015, deceased birds (road-killed or by causes unknown), were collected opportunistically from locations throughout the study area. Tissue samples were taken from these birds and stored in absolute ethanol at -20°C. Over the five year period, naturally shed feathers were obtained from beneath roosting and nesting tawny frogmouths by actively searching territories on a monthly basis. Feathers were assessed for quality and condition as described by Hogan et al. (2008). Feathers of poor condition were discarded, other feathers were placed into a clean dry paper envelope and stored at room temperature. Feather samples were also obtained from members of the public which were collected from locations within the study area. All DNA sample locations were georeferenced with a GPS.

5.2.3 DNA isolation

Genomic DNA was isolated from tawny frogmouth blood (n=8), tissue (n=9) and feathers (approx. 5 mm feather tip) (n=402) samples using the QIAGEN DNeasy Blood and Tissue kit (QIAGEN, Inc.) as per the manufacturer’s protocol. DNA isolates were quantified using a Qubit® fluorometer kit (Invitrogen). Only samples with
concentrations of >2.0 ng/μl were profiled. DNA profiles were obtained by genotyping a suite of six tawny frogmouth microsatellite markers (Pst05, Pst07, Pst12, Ps13, Pst20 and Pst24) (Hogan et al. 2012) (Appendix 1.), and by amplifying the CHD-1(chromohelicase-DNA-binding) to determine gender (Griffiths, Daan and Dijkstra 1996). Genotyping was performed by the Australian Genome Research Facility (AGRF) Melbourne, Australia. As non-invasively sampled DNA, such as shed feathers, can have reduced DNA quality and quantity, amplification errors rates were determined by using the error rates estimation calculator in GIMLET v 1.3.3 (Valiere 2002). DNA isolated from shed feathers (n=107) were genotyped four times. Consensus genotypes were generated with GIMLET using the threshold rule where an allele must appear at least three times to be accepted. Loci giving ambiguous results were omitted (scored as a failed reaction). DNA profiles for all samples were compared using Microsatellite toolkit (Excel Microsatellite Toolkit v. 3.1), to identify samples originating from a single individual i.e. shed feathers. From the 419 DNA samples collected, 124 individual tawny frogmouth DNA profiles were obtained from feather (n=107), blood (n=8) and tissue (n=9). The DNA profiles of 124 individuals were subsequently used for genetic analysis and resistance modelling and 120 individuals were used in the spatial autocorrelation analysis.

5.2.4 Characterization of loci

For each locus we calculated the number and range of alleles, observed and expected heterozygosity, polymorphic information content and estimated null allele frequencies using CERVUS (Kalinowski, Taper and Marshall 2007). Deviation from Hardy–Weinberg Equilibrium (HWE) and linkage disequilibrium was determined using
GENEPOP 3.4 (Raymond and Rousset 1995). We used MICROCHECKER 2.2.3 (Van oosterhout et al. 2004) to check each locus for further evidence of null alleles, scoring error due to stuttering, and large allele drop out.

5.2.5 Population structure

To determine if population structuring was present in the tawny frogmouths sampled across our study area, we used STRUCTURE 2.3., a modelling program widely used in landscape genetic studies (Gil and Brumm 2014). The program groups individuals using genotype data to infer the presence of distinct population clusters \((K)\) in the absence of spatial data (Pritchard 2000). We ran STRUCTURE using an admixture model allowing allele frequencies to be correlated. Twenty replicate runs were performed with a burn-in period of \(10^6\) repetitions for each \(K\) followed by \(3 \times 10^6\) MCMC (Markov Chain Monte Carlo) iterations, where \(K=1\) to 10. We visualized results in STRUCTURE HARVESTER (Earl and vonHoldt 2012), and estimated the most likely number of populations \((K)\) from the log normal probability of data values.

5.2.6 Isolation by distance and dispersal patterns

To investigate potential isolation by distance effects and evidence of sex-biased dispersal behaviour amongst tawny frogmouths, we compared all sampled individuals together \((n=120)\) and then males \((n=65)\) and females \((n=55)\) separately. We used GenAlEx 6.5 (Peakall and Smouse 2012), to construct pairwise matrices of genetic and geographic distance between sampling sites. From these matrices we then undertook spatial autocorrelation analysis to generate the coefficient \((r)\) which calculates relatedness levels amongst individuals which are attributed to a designated distance.
Landscape connectivity

class bin. We selected ten distance class bins based on prior knowledge of the species spatial behaviour and other observational data (Weaving et al. 2014). Distance class bins increased in increments of 250m ranging from 250m – 2500m. We used 999 random permutations to test for significance. To estimate the 95% confidence interval around the $r$ coefficient value, the number of bootstraps were set at 999.

5.2.7 Circuitscape modelling

Circuitscape combines graph theory with electrical circuit theory to measure habitat connectivity across a given landscape (McRae et al. 2008). The program calculates the cumulative flow of current through each cell of a resistance map between a set of nodes set pairwise as sources of current and ground (McRae et al. 2008). Circuitscape has distinct advantages over other connectivity modelling approaches due to its ability to evaluate multiple dispersal pathways which can then be applied to ecological processes such as species movements and gene flow (McRae and Beier 2007). Circuitscape provides a method to assess and predict connectivity for a range of species across both large landscapes and highly heterogeneous areas such as urban habitats (Amos et al. 2012; Braaker et al. 2014; McRae and Beier 2007; Munshi-South 2012).

5.2.8 Rationale for creation of resistance surfaces for Circuitscape modelling

We decided on two approaches to test whether tawny frogmouth gene flow is reduced or impeded by urbanization. Our first approach was to build resistance surfaces based on increasing degrees of urbanization (impervious surfaces). Our rationale for this approach was that urban intensification (increasing levels of impervious surfaces),
Landscape connectivity would reduce and remove both habitat and potential dispersal paths. Landscape resistance would thus be increased with increasing increments of urbanization.

Our second approach was to construct resistance surfaces based on habitat suitability. While tawny frogmouths are considered an urban-adapted species they demonstrate a reliance on natural features including trees and open grassy areas used for various ecological functions (Weaving et al. 2014). We hypothesized that based on these known requirements and tawny frogmouth behaviour, a reduction of these features would therefore reduce landscape connectivity creating greater resistance to movement. Conversely, areas containing a greater abundance of these features would pose less resistance to movement.

5.2.9 Resistance surfaces based on impervious surfaces

As map boundaries are known to effect current flow (Koen et al. 2010), we used ArcMap 10.1 (ESRI 2011) to create a buffer consisting of the extended land-use layer around the study zone. To increase computational speed we re-sized our map cell size from 10x10m to 20x20m. We felt that this resolution was coarse enough to allow processing with a basic desktop computer but still fine enough to capture the features of tawny frogmouth home-ranges (McRae and Beier 2007; Weaving et al. 2014). We assigned each cell of our land-use layer that was classified as trees, grass, water-bodies and water courses as 1 (least resistant to movement). We then assigned resistance values (in increasing increments) to each cell of the land-use layer classified as impervious surfaces (Table 5.1). We also constructed one resistance surface, a resistance by Euclidian distance ‘Null’ model, where all land-use types exhibited similar resistance.
Landscape connectivity
to movement (Table 5.1). This surface would enable us to calculate appropriate values
that could be used in partial Mantel tests to condition for the effect of geographic
distance.
### Landscape connectivity

Table 5.1. Values used for resistance surfaces for developing each landscape model.

<table>
<thead>
<tr>
<th>Model type</th>
<th>Model number</th>
<th>Model code</th>
<th>Source</th>
<th>Grass</th>
<th>Trees</th>
<th>Rivers</th>
<th>Water-bodies</th>
<th>Impervious surfaces</th>
<th>Potential habitat</th>
<th>No-potential habitat</th>
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<td>1</td>
<td>1</td>
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<td>1</td>
<td>1</td>
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<td>1_2</td>
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<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
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<td>1_3</td>
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<td>1</td>
<td>1</td>
<td>3</td>
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<td>1</td>
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<td></td>
<td></td>
<td></td>
<td>1</td>
<td>10</td>
</tr>
</tbody>
</table>

*Species Distribution Model: - Model constructed from tawny frogmouth capture locations, breeding sites, roosts and genetic material collection locations and a set of ecological, geographical and anthropogenic variables.*
5.2.10 Resistance surfaces based on habitat suitability derived from Species Distribution Models (SDM)

We constructed a SDM in MaxEnt V3.3.3., a computational program that measures the correlation between a presence location and a set of variables (Elith et al. 2011). We used the geographic co-ordinates of nesting and roost sites, catch sites and DNA sampling locations, with a range of spatially explicit environmental and anthropogenic variables. We removed highly correlated variables (correlation coefficients ≥ 0.8), after testing with ENM tools v1.3 (Warren, Glor and Turelli 2010), and variables that did not contribute to the model. The following variables were used for our resistance model. A digital terrain model (for slope classification), a Normalized Difference Vegetation Index (NDVI), a categorical land-use layer comprising five land-use types derived from satellite images and a road density layer (lineal). Modelling outputs were converted to produce a binary result and classified as either potential or no-potential habitat for tawny frogmouths. From this model we then created two resistance surfaces assigning potential habitat as 1 and no-potential habitat with resistance values of 2 and 10 (Table 5.1).

For modelling we used Circuitscape version 4.0, selecting the pairwise mode with focal nodes consisting of a single cell, and adjacent cells connected to eight neighbours by average resistances (McRae et al. 2008). To reduce computational time, current maps were produced post hoc to visualize significant results.

5.2.11 Mantel and partial mantel analyses of Circuitscape models

We used Mantel and partial Mantel tests implemented in the ECODIST package in R (R Development Core Team 2012), to test the correlation between genetic distances
and pairwise resistance distances generated by Circuitscape modelling. We computed two sets of Mantel tests; simple Mantel tests between genetic and resistance distance and partial Mantel tests. Partial Mantel tests enable testing for a relationship between two variables, while controlling for a third. We used partial Mantel tests within a causal modelling framework, where the correlation between each landscape model was tested with the other models partialled out. The results from this analysis are then used to assess the degree of support for each model (Cushman et al. 2013). Both sets of analyses compared all individuals together and each sex separately and were run with 10,000 permutations.

5.3 Results

5.3.1 Genetic diversity and population structure

Genetic diversity across tawny frogmouths was high with the number of alleles per locus ($N_a$) ranging from 10 to 15, mean 12.0 (Table 5.2). Observed heterozygosity ($H_o$) ranged from 0.55 – 0.85 (mean 0.78) with expected heterozygosity ($H_e$) ranging from 0.54 – 0.84 (mean 0.77; Table 5.2). All loci conformed to HWE expectations and there were no consistent patterns of linkage disequilibrium amongst the loci. Genotypic data analysis in STRUCTURE indicated $K=1$ as the most likely number of clusters for samples collected from tawny frogmouths. These results indicate no evidence of population sub-structure and that individuals sampled are representative of a single continuous population.
Landscape connectivity

Table 5.2. Characterization of six microsatellite loci of the tawny frogmouth. N, sample size; N_a no. of alleles; H_o and H_e observed and expected heterozygosity respectively; PIC Polymorphic Information Content; HWE Hardy-Weinberg Equilibrium.

<table>
<thead>
<tr>
<th>Locus</th>
<th>N</th>
<th>Allele Size range</th>
<th>N_a</th>
<th>H_o</th>
<th>H_e</th>
<th>PIC</th>
<th>Null Allele Freq</th>
<th>HWE P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pst05</td>
<td>124</td>
<td>83-117</td>
<td>14</td>
<td>0.815</td>
<td>0.826</td>
<td>0.809</td>
<td>-0.0001</td>
<td>0.7577</td>
</tr>
<tr>
<td>Pst07</td>
<td>124</td>
<td>129-171</td>
<td>10</td>
<td>0.831</td>
<td>0.844</td>
<td>0.821</td>
<td>+0.0059</td>
<td>0.9782</td>
</tr>
<tr>
<td>Pst12</td>
<td>124</td>
<td>202-218</td>
<td>10</td>
<td>0.823</td>
<td>0.814</td>
<td>0.785</td>
<td>-0.0080</td>
<td>0.9860</td>
</tr>
<tr>
<td>Pst13</td>
<td>123</td>
<td>78-182</td>
<td>15</td>
<td>0.846</td>
<td>0.818</td>
<td>0.791</td>
<td>-0.0208</td>
<td>0.4152</td>
</tr>
<tr>
<td>Pst20</td>
<td>122</td>
<td>215-290</td>
<td>14</td>
<td>0.549</td>
<td>0.538</td>
<td>0.524</td>
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<td>0.7303</td>
</tr>
<tr>
<td>Pst24</td>
<td>124</td>
<td>116-150</td>
<td>12</td>
<td>0.823</td>
<td>0.801</td>
<td>0.775</td>
<td>-0.0197</td>
<td>0.8376</td>
</tr>
</tbody>
</table>

5.3.2 Isolation by distance and dispersal patterns

To identify whether the spatial genetic structure of tawny frogmouths was a function of geographic distance we used spatial autocorrelation analysis. Our results identified a positive genetic structure in tawny frogmouths at a fine-scale \((p<0.001)\). This pattern indicates that birds were more genetically similar at shorter distances. As distances increased, relatedness declined (Fig. 5.2 a). This pattern suggests that dispersal distances for tawny frogmouths may be relatively small. When individuals were analyzed independently, female birds showed a positive genetic structure \((p<0.001)\), indicating that females were more closely related to each other at shorter distances (Fig 5.2 b). This pattern suggests that females are not dispersing far beyond the natal territory and its immediate surrounds. In contrast to female, males did not show elevated levels of genetic relatedness, the positive genetic structure at a fine spatial scale is therefore being driven by females, suggesting that dispersal is male-biased in tawny frogmouths (Fig 5.2 c).
Figure 5.2 a-c. Spatial autocorrelation values ($r$) calculated for increasing distance size classes for (a) all tawny frogmouths ($n=120$), (b) females ($n=55$) and (c) male ($n=65$), 95% CI about the null hypothesis, 95% confidence error bars about the $r$ as determined by bootstrapping. Upper (U) and lower (L) confidence limits bound the 95% confidence interval about the null hypothesis of no spatial structure for the combined dataset.
5.3.3 Mantel and partial mantel testing

We evaluated the Mantel and partial Mantel correlation between 11 landscape resistance models (isolation by resistance; IBR), plus the Null model (isolation by distance; IBD) and tawny frogmouth genotypes within the study area. Modelling produced three landscape models all of which had a similar level of support. The highest ranking landscape model was Model 11, (SDM 1_2); $r = 0.090$, $P = 0.03$. Second and third highest ranked models respectively were Model 2, (1_2); $r = 0.075$, $P = 0.04$ and Model 1, (Null); $r = 0.066$, $P = 0.03$; Table 5.3). No other landscape models were supported and none were significant for either sex. In addition, none of the three models were significant with the other models as partial variables. Given the shared basis from which the resistance models were derived (the categorical land-use layer), and the relatively low differences between resistance values, meant that all three models were highly correlated with each other (ranging from 0.8 – 0.9). In addition, all of the $r$ values were weak which makes distinguishing differences between models difficult. We could adopt the approach of Cushman et al. (2013), who recommends that model comparison is best accomplished by the magnitude of the Mantel $r$ value, however, none of our partial Mantel results were significant. While Model 11 has the highest $r$ value we cannot discount Model 1 and Model 2. A more parsimonious approach therefore would be to suggest that our results indicate weak support for both IBD and IBR. A similar approach was taken by Amos et al. (2012), to the more mobile and tolerant avian species in a multi-species study.
Table 5.3 Results from Mantel tests where each resistance model and the null model was tested against individual tawny frogmouth genetic distances.

<table>
<thead>
<tr>
<th>Model Number</th>
<th>Model code</th>
<th>Overall rank</th>
<th>Mantel correlation coefficient ($r$)</th>
<th>$P$ value</th>
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<tr>
<td>Model 1</td>
<td>Null</td>
<td>3</td>
<td>0.066</td>
<td>0.03*</td>
</tr>
<tr>
<td>Model 2</td>
<td>1_2</td>
<td>2</td>
<td>0.075</td>
<td>0.04*</td>
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<tr>
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<td>1_3</td>
<td>5</td>
<td>0.070</td>
<td>0.09</td>
</tr>
<tr>
<td>Model 4</td>
<td>1_4</td>
<td>6</td>
<td>0.066</td>
<td>0.12</td>
</tr>
<tr>
<td>Model 5</td>
<td>1_5</td>
<td>7</td>
<td>0.064</td>
<td>0.14</td>
</tr>
<tr>
<td>Model 6</td>
<td>1_10</td>
<td>8</td>
<td>0.059</td>
<td>0.17</td>
</tr>
<tr>
<td>Model 7</td>
<td>1_20</td>
<td>9</td>
<td>0.057</td>
<td>0.18</td>
</tr>
<tr>
<td>Model 8</td>
<td>1_30</td>
<td>11</td>
<td>0.057</td>
<td>0.19</td>
</tr>
<tr>
<td>Model 9</td>
<td>1_40</td>
<td>10</td>
<td>0.057</td>
<td>0.19</td>
</tr>
<tr>
<td>Model 10</td>
<td>1_50</td>
<td>12</td>
<td>0.057</td>
<td>0.19</td>
</tr>
<tr>
<td>Model 11</td>
<td>SDM 1_2</td>
<td>1</td>
<td>0.090</td>
<td>0.03*</td>
</tr>
<tr>
<td>Model 12</td>
<td>SDM 1_10</td>
<td>4</td>
<td>0.089</td>
<td>0.07</td>
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</table>

*Indicates $P$ value significance.

5.4 Discussion

Information on how landscape modification influences within-population genetic structure can highlight the effect of habitat loss and fragmentation on ecological processes such as dispersal (Amos et al. 2012; Braunisch, Segelbacher and Hirzel 2010; Cushman and McGarigal 2002). This information is particularly critical for long-lived and sedentary species like the tawny frogmouth, as these taxa are considered most sensitive to fine-scale changes associated with landscape modification (Sekercioglu, Daily and Ehrlich 2004). In contrast to diurnal species, cryptic and nocturnal species are less studied resulting in data deficiencies for population monitoring. Data obtained from this research therefore provides information previously unknown regarding the effects of urbanization on the genetic profile of tawny frogmouths.
5.4.1 Genetic structure and diversity of tawny frogmouths

Our first prediction that urbanization would result in a reduction of genetic diversity in tawny frogmouths was not met. In fact, landscape modification by urbanization appears to have little impact on the genetic profile of tawny frogmouths. Genetic diversity was high with no evidence of population sub-structure detected. The highly heterogeneous and patchy environment of the study area may provide an explanation for these results. These environments comprise diverse and abundant areas of greenspace which, for the mobile and ecologically flexible tawny frogmouth, represent potential habitat for a range of ecological functions. Furthermore, these habitats improve landscape connectivity providing movement corridors for taxa to disperse throughout the landscape (Bolger, Scott and Rotenberry 2001). Genetic studies of other urban-dwelling species including the striped skunk (*Mephitis mephitis*) (Brashear, Ammerman and Dowler 2015), and an endemic species of sparrow (*Passer italiae*) (Fulgione, Procaccini and Milone 2000), also show little within population genetic differentiation, due to their adaptive responses to urban habitats and their capacity to utilize urban corridors to facilitate movements.

5.4.2 Resistance by urbanization

Our prediction that urbanization would limit tawny frogmouth movements thereby reducing gene flow, was also not met. Our first modelling approach, resistance surfaces based on increasing levels of urbanization (impervious surfaces), produced models showing that increasing levels of urbanization posed limited resistance to tawny frogmouth movements. Our second approach, to rank landscape resistance based on habitat suitability derived from a Species Distribution Model (SDM), produced models that showed a similar result. Previous SDM modelling (Weaving et al. 2015) and the
SDM constructed here had very high predictive ability with both indicating that significant proportions of the urban environment constituted potential habitat for tawny frogmouths. For both of our modelling approaches the landscape within the study area provides little resistance and sufficient connectivity to enable birds to undertake movements thereby providing few restrictions to gene flow.

5.4.3 Dispersal patterns and male-biased dispersal

Our results indicate that tawny frogmouths do not disperse over large distances in urban environments. Short distance dispersal can be indicative of restricted dispersal related to factors such as behavioural capabilities and physical barriers (de Ita et al. 2012). Our analysis however, shows that tawny frogmouth fine-scale dispersal patterns are driven by female birds. Avian species generally demonstrate female-biased dispersal (Gowaty 1993; Greenwood 1980; van Dijk et al. 2015). While uncommon, male-biased dispersal does occur, primarily for inbreeding avoidance and to increase access to females (Greenwood 1980; Harrison, York and Young 2014). Prior research indicates that spatial behaviour in tawny frogmouths is sex-biased with males maintaining larger home-ranges than females in urban areas (Weaving et al. 2014).

Our results also provide support for female philopatry. While the reasons for philopatry are complex and differ between and within taxonomic groups (Greenwood 1980), for the non-dispersing sex there are significant benefits for remaining close to the natal territory including local resource familiarity which may be important for successful reproduction and survival (Greenwood 1980; Tomas 1995). Until recently, many aspects of tawny frogmouth breeding behaviour in urban systems was largely unknown, however, recent studies have found that birds in these systems experience a very high
degree of reproductive success. If female birds are remaining in close proximity to the natal area the benefits derived from this behaviour may be an underlying factor that contributes to this success (Weaving et al. 2016). While comparisons are limited, high natal philopatry is exhibited by another long-lived and sedentary member of the Caprimulgiformes order, the red-necked nightjar (*Caprimulgus ruficollis*) (Camacho and Roskaft 2014).

Studies using genetic data highlight the genetic consequences of reduced functional connectivity for urban-dwelling taxa (Major et al. 2014; Munshi-South and Kharchenko 2010). Some however, provide evidence that human-modified landscapes with their complex patchworks of habitat types can provide conduits for species movements (Brashear, Ammerman and Dowler 2015; Santonastaso et al. 2012). By using a landscape genetics approach in combination with SDM and resistance modelling, we have shown that highly heterogenous landscapes provide limited resistance to dispersing tawny frogmouths resulting in high genetic diversity and structure. Resistance modelling did not detect strong patterns of resistance however, this in itself is a significant outcome, indicating that these landscapes facilitate rather than impede tawny frogmouth gene flow. This factor, combined with generalist resource requirements, high mobility and behavioural adaptability, further reinforces the emerging status of the tawny frogmouth as an urban-adapted species.
Chapter 6: Discussion

Tawny frogmouth adult and chick on the nest in a Red Box (*Eucalyptus polyanthemos*), located in a suburban streetscape in Melbourne. Adult is using mimicry to avoid detection. Photo: Matt Oliver.

“To keep every cog and wheel is the first precaution of intelligent tinkering”

Aldo Leopold.
6.1 Urban impacts on biodiversity

Australia, similar to other countries of the world is experiencing rapid urban growth with predications that by 2050 ~ 93% of Australians will live in urban environments (United Nations 2014). On an unprecedented and global scale, urbanization is converting vast tracts of the natural environment into landscapes characterised by fabricated structures, transportation networks and human habitation (Seto, Güneralp and Hutyra 2012). Aside from the physical and visual impacts of urbanization, urban development alters the structure and function of natural ecosystems modifying the distribution and composition of the biodiversity these systems support (Alberti 2005). Floral and faunal communities become increasingly homogenous, comprising few abundant and often introduced species replacing rich native communities (McKinney 2006; Smart et al. 2006). Some species may decline due to the pressures exerted by urban affects (Germaine and Wakeling 2001; Pauw and Louw 2012), while others appear to thrive in urban systems occupying these habitats in high abundances (Martin, French and Major 2010; Prange, Gehrt and Wiggers 2004).

Landscape homogenisation by urbanization and associated pressures acts as a biological filter creating communities of species that exhibit similar traits and behaviours (Croci, Butet and Clergeau 2008). Several key studies have highlighted this phenomenon and formulated an index by which species, based on their individual response to urbanization, are classified into three broad categories (Blair 1996; McKinney 2006; McKinney and Lockwood 1999). “Urban avoiders”, those species that frequently decline as urbanization intensifies, “urban exploiters”, species that
thrive and expand their distribution in urban environments, and “urban adaptors”,
species that tolerate low to moderate levels of urbanization.

6.2 Urban avoider, urban adaptor or urban exploiter?

Characterising species into three broad groups based on their response to a gradient of
urbanization can be a useful theoretical concept in urban ecology (Blair 1996; McKinney and Lockwood 1999). This method of classification however, can also be
simplistic as it assumes that all species within each category will demonstrate an
equivalent response to urbanization (Evans et al. 2011). Species specific traits, the
ability of species to undertake behavioural adjustments and the dynamic nature of urban
environments, may suit the assignment of some species to more than one classification
(Kark et al. 2007; Sol, Lapiedra and González-Lagos 2013). For example, some urban
adapters and exploiters share similar ecological traits (Kark et al. 2007), while others
may exhibit traits common to urban avoiders (Conole and Kirkpatrick 2011). Habitat
specialists (termed urban avoiders), may tolerate moderate forms of urbanization but
their expansion to areas with increased human habitation may be constrained by a lack
of specialist habitat resources (Christina and Marzluff 2005; Degraaf and Wentworth
1986; Lim and Sodhi 2004). One such example is the powerful owl, a nocturnal species
that demonstrates a tolerance to moderate forms of urbanization but is limited from
colonising more intensively urbanized areas due to a lack of hollow-bearing trees
required for breeding (Cooke, Wallis and Webster 2002; Isaac et al. 2014a).

The tawny frogmouth is a large bodied and endemic bird species widespread and
common throughout a range of Australian habitats. Nocturnal and highly cryptic habits
has to date, resulted in a lack of information regarding many ecological aspects of the
Discussion

species. This thesis investigated the response of the tawny frogmouth to a gradient of urbanization. Specifically, to identify some of the factors that drives their colonisation of urban habitats.

Contrary to my initial predictions, the tawny frogmouth has consistently demonstrated a strong tolerance and adaptability to urban environments. As this research progressed it became clear that this capacity is due to the species generalist ecological traits and its ability to make behavioural adjustments to occupy urban systems. Tawny frogmouths also have the ability to exploit certain elements of urban environments which works to their ecological advantage. Features common to urban environments including artificial structures and night-time lighting are used by tawny frogmouths to enhance their nocturnal foraging success (Rose and Eldridge 1997; Weaving and Cooke 2010). The tawny frogmouth thus displays a range of traits and behaviours that extends its urban-adaptor status into the urban exploiter range.

In Australia many taxa rely on hollows and cavities for ecological functioning (Gibbons and Lindenmayer 2006). In urban areas the paucity of hollow-bearing trees resulting from human activities and management practices can have a dramatic effect on the distribution and abundance of hollow-dependant species (Davis, Major and Taylor 2014; Harper, McCarthy and van der Ree 2005). Unlike many other Australian nocturnal bird species, tawny frogmouths are not dependent on hollows instead selecting a range of tree species both native and exotic for roosting and breeding (Körtner and Geiser 1999b; Schodde and Mason 1980). This independence from hollows enables the tawny frogmouth to occupy a unique ecological niche, reducing the potential for resource conflicts with other hollow-dependant nocturnal and diurnal
species. Their lack of dependence on hollows likely plays a significant role in the widespread distribution and high abundances of tawny frogmouths detected in moderately and highly urbanized environments. (Chapter 2).

Many native bird species exhibit a reliance on high quality native remnant vegetation, with studies highlighting a strong positive correlation between native vegetation and native species richness and diversity (Germaine et al. 1998; Lim and Sodhi 2004; Sewell and Catterall 1998; White et al. 2005). Maintaining the habitat values of native remnants in urban areas can be problematic, as remnants are frequently small and subject to a range of degrading processes by anthropogenic activities (McKinney 2006). Tawny frogmouths will utilize these remnants however, their lack of reliance on native vegetation enables them to permeate out into the urban matrix to use non-native street trees and other vegetative resources for foraging, roosting and breeding (Chapter 2, 3, 4 and 5). The spatial behaviour of tawny frogmouths identified in chapter three, highlights both urban adaptor and avoider traits, with birds adjusting their movement patterns to incorporate natural features into their home-ranges while avoiding the more urbanized areas of the landscape. This chapter also revealed a dependence on tree cover indicating that a threshold may exist for tawny frogmouths. In intensively urbanized areas, tree cover may be substantially reduced suggesting that tawny frogmouth populations may be unsustainable in these landscapes.

In urban landscapes patterns of human occupation over time create complex mosaics of built structures and greenspace networks (Alberti 2005). At both a landscape and neighbourhood scale, neighbourhood streetscapes reflect these transitions by the presence of abundant and diverse vegetation types (Heezik and Adams 2014). The
Discussion

configuration of greenspace comprising open mown areas, native remnants, gardens and parklands, creates an environment that benefits individual bird species and can elevate species richness and abundance to high levels (Luck, Smallbone and Sheffield 2013). As an open woodland species, these environments also suit many aspects of tawny frogmouth ecology supplying critical resources for ecological functions such as roosting, foraging and breeding (Chapter 2, 3, 4 and 5).

A key indicator of the successful adaption of tawny frogmouths to urban environments, is outlined in chapter four which examined the species reproductive response to urbanization. Tawny frogmouth reproductive behaviour merges both urban adaptor and exploiter traits resulting in a reproductive strategy that yields high reproductive success. Coupled with a protracted breeding season, low failure rates and the capacity to produce multiple broods in a single season, tawny frogmouth breeding efforts resulted in a high rate of fledging success. The non-uniformity of habitat along the gradient resulted in breeding pairs preferentially selecting sites within the more moderately disturbed areas of the gradient to locate their nest. Once birds had located their nest, irrespective of land-use type surrounding the nest tree, a high percentage of breeding attempts successfully fledged young. This suggests that once breeding birds have selected a nest site the likelihood of producing young to fledging is high. Breeding birds showed a preference but not dependence on native tree species as a nest tree. Their choice of a nest tree was based on attributes and features common to both native and several exotic tree species. The ability to use both native and exotic tree species increases their capacity to colonise urban environments particularly in areas of the gradient where vegetation loss may be pronounced.
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The spatial configuration of urban greenspace and the often inhospitable nature of the intervening landscape, can impede the movements of less mobile and ecologically flexible species (Delaney, Riley and Fisher 2010) (Chapter 5). The collective abundance of urban greenspace can enhance landscape connectivity by creating movement corridors that can mitigate the detrimental genetic effects of population isolation (Bolger, Scott and Rotenberry 2001; Frankham 2006) (Chapter 5). Highly mobile and ecologically flexible species such as the tawny frogmouth can utilize these corridors thereby avoiding some of the cumulative effects of population isolation including reduced reproductive output (Kuitunen et al. 2003) and survival (MacDougall-Shackleton et al. 2011) (Chapter 4 & 5). A high level of genetic diversity in populations reflects high fitness amongst individuals, a factor that enhances the capacity of these populations to adjust to landscape modification and synchronize life-cycle events such as breeding to local environmental conditions (Chapter 4).

6.3 Issues affecting tawny frogmouth populations

Modelling of tawny frogmouth home-ranges highlighted a sex-biased response to urbanization with male birds maintaining larger home-ranges than females (Chapter 3). Contractions and expansions of home-range size in modified landscapes is not uncommon with differences observed between species and between the sexes arising from factors such as resource availability (Riley et al. 2003), and life-cycle events such as breeding (Framis, Holroyd and Manosa 2011) (Chapter 3). Maintaining large home-ranges however, comes with associated costs including increased metabolic demands which has the potential to impact on individual fitness (Harestad and Bunnel 1979). In urban environments, larger home-ranges can result in greater contact with predators.
such as cats (*Felis catus*) (Balogh, Ryder and Marra 2011), and a heightened risk of death through collision with cars (Rose and Eldridge 1997; Santos et al. 2013).

The disproportionate loss of one sex can also have significant implications for population demographics with the potential for biased population sex ratios, a recognised problem in wildlife management and conservation (Donald 2007; Grayson et al. 2014). A further issue, is the finding that male tawny frogmouths are the more dispersive sex (Chapter 5), a behaviour that may expose them to greater risks as they leave the natal area to disperse across unfamiliar territory. Whilst current populations of tawny frogmouths appear stable, the cumulative effect of these behaviours may have future implications for urban populations.

A trend occurring globally with negative impacts for urban biodiversity (Heezik and Adams 2014; Loram et al. 2007), is the loss of garden vegetation including large trees for housing densification. Replacement gardens frequently incorporate more simplified vegetation forms interspersed by large areas of impervious surfaces (Loram et al. 2007). In many cities and towns, urban street trees are regularly assessed by management bodies to ensure their condition does not pose a threat to public safety (Sæbø et al. 2005). Subsequently, many of these trees undergo intensive pruning regimes, removing large branches which changes the character, structure and shape of the original tree (Sæbø et al. 2005). These structural changes can reduce their ecological value as a nest tree for tawny frogmouths and other species that require large branches as a nesting platform (personal observation, M. Weaving).
6.4 Future management actions

The theoretical concept of “sparing or sharing” has to date, focused primarily on agricultural land-use (Lin and Fuller 2013). The concept involves two models (1), high intensity food production on smaller land areas while reserving land for conservation (“sparing”) and (2), food production over a greater area with the conservation of natural vegetation for biodiversity gains (“sharing”) (Lin and Fuller 2013). While there is much debate on the relative merits of the model and its application to varying landscapes (Grau, Kuemmerle and Macchi 2013; Law et al. 2015), parallels can be drawn between agricultural development and current patterns of urban development and growth. Intensively urbanized areas are characterized by high housing density interspersed with native vegetation remnants of varying type and size while more sprawling forms of urbanization contain vegetation values in the form of streetscape vegetation distributed throughout the landscape. With threats to biodiversity escalating from rapid urbanization on a global scale, there is an urgent need to assess the respective effects on biodiversity from both forms of urban development with a view to developing a more spatially integrated approach to urban planning that considers both human and wildlife needs.

The practical application of the “sharing and sparing” model could be of benefit to the tawny frogmouth, in particular the “sharing” model of urban development would match with its urban-adapted status. Lower density housing (“sharing”) interspersed with streetscape vegetation, parklands and gardens, provide many of the resources required by the species. These resources are common to many suburban neighbourhoods contributing substantially to local and regional avian diversity and abundance (Chamberlain, Cannon and Toms 2004). The consequences of the “sharing” model for
urban-avoider species however, would be high, as many demonstrate a reliance on the habitat values provided by native remnant vegetation. (Isaac et al. 2013; Trollope, White and Cooke 2009). Maintaining their presence in urban areas would require the retention of remnant vegetation which is associated with more intensive forms of urbanization (“sparing”). While the tawny frogmouth does utilizes native vegetation this model of urban development would disadvantage the species through a net loss of greenspace associated with more intensive land development. Despite the scale and intensity of urbanization globally there is limited evidence on how to design and grow our cities to minimize their ecological impact on biodiversity (McDonnell 2009). In particular there is very limited research at a city scale as to how both urban-growth scenarios will impact on biodiversity (Sushinsky et al. 2013). Assessing these impacts will require long-term and targeted urban ecological research with a view that research findings will underpin future urban planning policies and urban development.

6.5 Future directions and research
This research contributes to the very limited information available on the tawny frogmouth and its response to an urbanization gradient. In the construction of this thesis many questions arose from the data collected indicating much potential for future research. Currently, research of avian diversity in urban areas rarely includes nocturnal bird surveys which has led to substantial data deficits for this important group of birds. This may be due to the assumption that nocturnal species have a strong association with forest and woodland habitats and that urban areas are unlikely to provide the resources they require for survival. It is strongly recommended therefore that future studies incorporate nocturnal surveys into their study design. Secondly, to investigate if
Increasing levels of urbanization creates thresholds for tawny frogmouths and thirdly, to assess the post-fledging survival rates of tawny frogmouth juveniles.
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References


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Authorship Statement: Chapter 2.

1. Details of publication and executive author.

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<td>Marian Weaving</td>
<td>School of Life and Environmental Sciences</td>
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Signature and date: 17/12/2015

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**Authorship Statement: Chapter 3**

1. Details of publication and executive author.

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<tr>
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<tr>
<td>Sex-biased space-use response to urbanization in an endemic urban adapter</td>
<td>Landscape and Urban Planning</td>
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Signature and date: 17/12/2015

*Signature Redacted by Library*
Kara Hower  
School of Life and Environmental Sciences  
Deakin University, Melbourne, Victoria, Australia  
Field work assistance.

5. Author Declarations.
I agree to be named as one of the authors of this work, and confirm: that I have met the authorship criteria set out in the Deakin University Research Conduct Policy, that there are no other authors according to these criteria, that the description in Section 4 of my contribution(s) to this publication is accurate, that the data on which these findings are based are stored as set out in Section 7 below. If this work is to form part of an HDR thesis as described in Sections 2 and 3, I further consent to the incorporation of the publication into the candidate’s HDR thesis submitted to Deakin University and, if the higher degree is awarded, the subsequent publication of the thesis by the university (subject to relevant Copyright provisions).

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1. Details of publication and executive author.

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<th>Title of Publication</th>
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<tbody>
<tr>
<td>Adaptation to urban environments promotes high reproductive success in the tawny frogmouth (<em>Podargus strigoides</em>), an endemic nocturnal bird species.</td>
<td>Landscape and Urban Planning</td>
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<td>Highly heterogeneous environments facilitate gene flow for an urban-adapted endemic species.</td>
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<tr>
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Isolation and characterization via 454 sequencing of microsatellites from the tawny frogmouth, *Podargus strigoides* (Class Aves, Family Podargidae)

Fiona E. Hogan\textsuperscript{A},\textsuperscript{E}, Marian Weaving\textsuperscript{B}, Gregory R. Johnston\textsuperscript{C} and Michael G. Gardner\textsuperscript{D}

\textsuperscript{A}School of Applied Sciences and Engineering, Monash University, Northway’s Road, Churchill, Vic. 3842, Australia.
\textsuperscript{B}School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, Vic. 3125, Australia.
\textsuperscript{C}Vertebrates Section, South Australian Museum, North Terrace, Adelaide, SA 5000, Australia.
\textsuperscript{D}School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, SA 5001, Australia; Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, Adelaide, SA 5005, Australia; and Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide, SA 5000, Australia.
\textsuperscript{E}Corresponding author. Email: Fiona.Hogan@monash.edu

Abstract. We isolated 24 novel polymorphic microsatellite markers from the tawny frogmouth, a nocturnal bird endemic to Australia, which has successfully adapted to urban environments. Initially, 454 shotgun sequencing was used to identify 733 loci with primers designed. Of these, we trialed 30 in the target species of which all amplified to expected size. Subsequently, all 30 of these loci were screened for variation in 25 individuals, from a single population in Melbourne, Victoria, Australia. Twenty-eight loci were polymorphic with observed heterozygosity ranging from 0.03 to 0.96 (mean 0.58) and the number of alleles per locus ranged from 2 to 18 (average of 6.5); we confirmed that 24 loci conformed to Hardy–Weinberg expectations. The 24 loci identified here will be useful in understanding the reproductive ecology, population genetics and the gene flow amongst localities in urban environments where this bird thrives.

Additional keywords: 454 GS-FLX, nocturnal, shotgun sequencing, urban.

Received 14 June 2012, accepted 2 August 2012, published online 17 September 2012

The tawny frogmouth, *Podargus strigoides* (Latham, 1801), is an urban survivor. It is a nocturnal bird endemic to Australia and is common in Australian cities (Weaving et al. 2011). The tawny frogmouth typically preys upon insects and small vertebrates such as mice, which are abundant in built environments. It roosts and nests on tree branches, and is therefore not hollow dependent, which reduces competition with other comparable species such as owls. The ecology of the tawny frogmouth is therefore suited to urban environments and, as such, it readily occupies a diverse range of habitats including urban parks, reserves, private property and public localities.

Although considered common, little is known about many aspects of the tawny frogmouth’s ecology and behaviour. Weaving et al. (2011) highlights the species’ ability to occupy urban streetscapes and reserves in unusually high densities; however, the breeding and social mechanisms that support this behaviour are unknown and difficult to infer from purely observational studies. Microsatellite loci can be used to unequivocally identify individuals and have been used to assess the reproductive ecology, population structure and dispersal of urban birds (Selkoe and Toonen 2006). In order to assess the ecology and behaviour of the tawny frogmouth inhabiting urban environments, we developed a suite of species-specific polymorphic microsatellite markers.

Genomic DNA (5 mg) was isolated from blood taken from a single *Podargus strigoides* using the QIAGEN DNeasy Blood and Tissue kit (QIAGEN Inc., Valencia, CA, USA) as per the manufacturer’s protocol. The DNA was then sent to the Australian Genomic Research Facility in Brisbane, Australia, for shotgun sequencing on a Titanium GS-FLX (454 Life Sciences/ Roche FLX) following Gardner et al. (2011). The sample occupied 12.5% of a plate and produced 198 838 individual sequences, with an average fragment size of 356. We used the program QDD ver. 1 (Meglecz et al. 2010) to screen the raw sequences with 8 di-, tri-, tetra-...
Table 1. Characterisation of polymorphic loci

<table>
<thead>
<tr>
<th>Locus</th>
<th>Primer sequence (4'-3')</th>
<th>GenBank accession number</th>
<th>Repeat motif</th>
<th>N</th>
<th>Allele range</th>
<th>Na</th>
<th>Ho</th>
<th>He</th>
<th>PIC</th>
<th>Null allele frequency</th>
<th>HWE</th>
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<td>117–119</td>
<td>0.120</td>
<td>0.393</td>
<td>0.311</td>
<td>+0.5244*</td>
<td>&lt;0.001*</td>
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</tr>
<tr>
<td>Pst04™</td>
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<td>25</td>
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<td>0.080</td>
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<td>Pst09™</td>
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<td>86–156</td>
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<td>0.824</td>
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<td>25</td>
<td>202–216</td>
<td>0.800</td>
<td>0.804</td>
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<td>25</td>
<td>78–162</td>
<td>0.960</td>
<td>0.864</td>
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<td>T: CTGCTAATACCTGACCC</td>
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<td>25</td>
<td>83–93</td>
<td>0.840</td>
<td>0.782</td>
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<td>143–175</td>
<td>0.727</td>
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<td>0.634</td>
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<td>+0.1005</td>
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<td>25</td>
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<td>0.520</td>
<td>0.431</td>
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<td>JX157907 (CTG)₁₀</td>
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<td>215–278</td>
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<td>JX157908 (GAG)₁₀</td>
<td>25</td>
<td>166–181</td>
<td>0.600</td>
<td>0.651</td>
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<td>19</td>
<td>214–226</td>
<td>0.158</td>
<td>0.326</td>
<td>0.294</td>
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<td>24</td>
<td>114–136</td>
<td>0.625</td>
<td>0.680</td>
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<td>JX157911 (AT)₁₀</td>
<td>25</td>
<td>116–140</td>
<td>0.880</td>
<td>0.813</td>
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<td>JX157912 (GA)₁₀</td>
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<td>93–95</td>
<td>0.2</td>
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<td>88–118</td>
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<td>183–187</td>
<td>0.333</td>
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we chose loci with more than eight repeats, tetra- and pentanucleotide loci for ease of scoring and supplemented with di- and trinucleotides to allow more complete utility of the capillary fragment separation range. Subsequently, 30 loci were chosen for further development. DNA was extracted from blood samples from eight individual *Podargus strigoides* using the QIAGEN DNeasy Blood and Tissue kit. Extracts were trialed for amplification in a 10-μL reaction containing 4 μL Go Taq (Promega), 1 μL each forward and reverse locus-specific primers (10 mm) and 1 μL DNA. The following PCR conditions were used: 95°C for 2 min followed by 40 cycles at 95°C for 20 s, 54°C for 20 s, and 72°C for 5 min. PCR products were visualized on a 1.5% agarose gel stained with SYBR® safe DNA gel stain. All loci amplified an unambiguous product of the expected size. PCR products from all 30 loci were then screened for polymorphism on an 8% polyacrylamide gel, where all loci appeared polymorphic. The loci were organized into three panels and the forward primer of each was 5′ labelled with an appropriate fluorescent tag: FAM (Gene Works), NED, PET or VIC (Applied Biosystems) (Table 1). Twenty-five samples were then genotyped on an AB3730 capillary sequencer and analyzed using GENEMAPPER3.7 software (Applied Biosystems) by the Australian Genomic Research Facility. Sex (*P = 0.001) was inferred by amplifying the CHD-1 gene (Grifiths et al. 1998), and products were separated on 8% polyacrylamide gel stained with SYBR gold (Invitrogen).

For each locus we calculated the number and range of alleles, observed and expected heterozygosity, polymorphic information content and estimated null allele frequencies using CERVUS (Kalinowski et al. 2007) and deviation from Hardy–Weinberg Equilibrium (HWE) using GENEPOP 3.4 (Raymond and Rousset 1995) (Table 1). We used MICROCHECKER 2.2.3 (Van Oosterhout et al. 2004) to check each locus for further evidence of null alleles, scoring error due to stuttering, and large allele drop out.

Genotypic data was not obtained for Pst01 and Pst02 as these loci failed to optimize due to non-specific amplification and stuttering. The mean number of alleles per locus was 6.50, the mean observed and expected heterozygosity was 0.58 and 0.63 respectively and the mean polymorphic information content was 0.58. None of the loci showed evidence of large-allele drop out, or evidence of scoring error due to stuttering; however, five loci showed significant null allele frequencies. Six loci deviated from HWE in the tested population (Table 1); three of these (Pst03, Pst18 and Pst26) were sex-linked, with heterozygotes found only in the heterogametic (female) sex. We checked all pairs of loci for linkage disequilibrium in GENEPOP and results for one pair, Pst18 and Pst21, were significant (*P < 0.001) after sequential Bonferroni adjustment (Hochberg 1988). According to Waits et al. (2001), seven loci with *H* = 0.6 are required to provide a probability of identity (*Pid*) of 0.0001 (1 in 10 000) for unrelated individuals and 15 loci with *H* = 0.6 provides a *Pid* of 0.0001 for siblings. From the 30 loci screened, 24 loci were polymorphic, conformed to HWE and showed no evidence of null alleles, stuttering or allelic dropout; of these, 16 had an observed heterozygosity >0.6. This suite of loci will therefore be sufficient to provide unequivocal identification of individuals and will be useful for inferring information about the reproductive ecology, population genetics and gene flow amongst tawny frogmouths in urban environments.

**Acknowledgements**

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Appendix 1.

References


