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Habitat and Resource Utilisation by an Urban Parrot Community

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Abstract

Urbanisation typically results in homogenisation of the constituent avifauna, as generalists that are able to adapt to and persist within the urban landscape replace specialist species whose specific habitat needs are removed. Recently, within some major urban centres, parrots have become a conspicuous component of the avifauna and are present in higher abundance in the urban landscape than in the natural environment. This thesis examines the composition and distribution of the parrot community within a large urban centre and evaluates the relative importance of key abiotic and biotic factors that may explain the increase in abundance of urban parrots.

Firstly, I determined the distribution and abundance of 13 native species of parrot within four major habitat types, distributed throughout four urban zones. I demonstrated that 10 parrot species were present in higher abundance within the urban landscape, compared to natural habitat, and that one species, the rainbow lorikeet, was ubiquitous throughout the urban landscape. Using historical data sets, I then showed that both drought and wild fire resulted in an influx of some parrot species into the urban landscape.

I then investigated the distribution of two key resources, nectar and tree hollows. To determine the amount of nectar available to nectarivorous parrots in the urban landscape, I calculated the amount of energy supplied by nectar in two urban and two non-urban habitats. I also determined whether nectar-providing trees in the urban landscape were more productive than the same species of tree within the non-urban landscape. I demonstrated that the standing crop of nectar was consistently higher within streetscapes compared to the non-urban habitat and is capable of sustaining large populations of large-bodied nectarivores. I also demonstrated that trees within the urban landscape produce more flowers and flower for longer than the same species of tree outside the urban landscape, further adding to the increased nectar resource present in the urban landscape.

There are typically fewer tree hollows in the urban landscape compared to forest and I conclusively demonstrated this, showing that remnants in Sydney contained only half the number of tree hollows present in continuous forest, with even fewer tree hollows present in other urban habitats. Using motion activated video cameras placed in trees, I showed that there were significantly more visitations to hollows by parrots within the urban landscape, compared to forest, as well as significantly more aggressive interactions. Two species featured in the visitor spectrum at tree hollows. The rainbow lorikeet made the highest number of visitations to urban hollows and both the rainbow lorikeet and the sulphur-crested cockatoo were responsible for the majority of aggressive interactions. The rainbow lorikeet and the sulphur-crested cockatoo, as well as the Australian king parrot, were also associated with different types of hollows.

My results demonstrate that the urban landscape is capable of sustaining a diverse community of native parrots, particularly nectarivores such as the rainbow lorikeet. The urban landscape provides food resources in excess of that found in natural habitat, however nesting resources are fewer compared to natural habitat. My research suggest that there may be a shortage of tree hollows and I discuss how, if the density of parrots continues to increase, there may be a simplification in the current avifauna due to a shortage of breeding resources. I present results from applied ecological research and discuss these results in the context of ecological theory and the conservation of urban wildlife within a large city.

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Statement of Authorship

Except where reference is made in the text, this thesis contains no material published elsewhere or extracted in whole or part from a thesis by which I have qualified for or been awarded another degree or diploma.

No other person's work has been used without due acknowledgment in the text of this thesis.

This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

Adrian Davis

The University of Sydney

A Note on the Structure of this Thesis

This thesis is set out as a series of manuscripts for publication and the manuscripts have either been published in or submitted to appropriate journals in the form presented in this document. To maintain consistency as a thesis, some words may have been changed from that which appears in the published manuscripts. As each Chapter has been written as a stand-alone paper, there is some redundancy within the thesis.

This thesis is comprised of three parts. In Part 1 (chapters 2-3), I investigate the historical changes in abundance of parrots within Sydney and the effect of wild fire and drought on these changes, as well as describing the present-day abundance of and habitat utilisation by parrots within Sydney. In Part 2 (chapters 4-5), I investigate the availability and usage of nectar resources by nectarivorous parrots within the urban landscape. In Part 3 (chapters 6-7), I investigate the distribution of and availability for tree hollow resources as well as parrot preferences for particular hollow characteristics. In Chapter 8, I conclude by synthesising findings from Chapters 2-7 and make recommendations for future management of the urban landscape to promote parrot diversity.

Contributions of the Co-authors

Dr Charlotte Taylor (University of Sydney) provided primary supervision and Dr Richard Major (Australian Museum) secondary supervision. Both Charlotte and Richard guided and advised in the design of the projects, with all data collection carried out by Adrian. Adrian carried out all analyses, with advice offered by Charlotte and Richard. Manuscripts were written by Adrian and then examined by Charlotte and Richard.

Charlotte R. Major

Charlotte Taylor Richard Major

Part 1

Historical and Present-Day Abundance and Habitat Utilisation by Parrots: the Effect of Abiotic Factors

Photo: A Davis

Chapter 1: A General Introduction to Urban Ecology and the Effects of Urbanisation on Parrots and Resources in the Urban Landscape

Photo: B. Howard

Urban ecosystems are increasingly common and sometimes play important roles in conservation, such as the protection of local biodiversity (Bolger et al., 1997; Crooks et al., 2004; Dearborn and Kark, 2010; FitzGibbon et al., 2007). Additionally, urban ecosystems provide important benefits to humans, through the provision of services and, in some cases, the only opportunity for urban citizens to connect with nature (Magle et al., 2012). With over half the world's population now living in cities (United Nations, 2004), the conservation of urban biodiversity is receiving increasing human interest.

Despite such benefits, there is still relatively little documented about the historic and recent trends in urban wildlife (Magle et al., 2012). To effect appropriate conservation and management, such information is necessary to begin to understand the factors and the availability and distribution of resources that wildlife relies on to determine whether native species will be winners or losers within the urban environment (van Heezik et al., 2008). Suburban gardens, for example, are the largest collective green space within cities (Gaston et al., 2005; Mathieu et al., 2007), where green space is defined as natural or semi-natural areas or other open spaces that conserve natural ecosystem values and functions and provide benefits to wildlife and people (Benedict and Mcmahon, 2006; Moseley et al., 2013; Sandström et al., 2006). The role of urban green spaces in supporting the diversity and abundance of native wildlife has only recently been addressed (Gaston et al., 2005; Parsons et al., 2006; White et al., 2005). In general, the rate at which natural habitat is conserved is declining globally (Blair and Johnson, 2008) and the conservation of natural habitat in cities will assume increasing importance in the future (Magle et al., 2012) as the world continues to urbanise.

Whilst urbanisation generally has profoundly negative effects on biodiversity (Grimm et al., 2008), birds of the order Psittaciformes (parrots), have increased in abundance in many cities (Lambert et al., 2009; Lowry and Lill, 2007; Shukuroglou and McCarthy, 2006; Smith and Lill, 2008; Strubbe and Matthysen, 2007; Woodall, 2002). They are also conspicuous, colourful and charismatic and may be excellent flagship species to promote the importance of urban biodiversity (Guittar et al., 2009). As cavity-nesters, they are also capable of acting as umbrella species for a range of other hollow-utilising fauna (Politi et al., 2009; Savignac et al., 2000). There is, however, little scientific knowledge on the processes by which parrots have benefitted from urbanisation (Burgin and Saunders, 2007). It is important that we gain an understanding of how parrots utilise the urban landscape, and the resources within, to ensure that conservation is a key component of urban management and planning and can safeguard the current diversity of wildlife within the urban landscape.

1.1 Urbanisation

Urbanisation, the alteration of existing natural ecosystems due to increases in human habitation (Heterick et al., 2013), is considered one of the most important pressures on the environment (Estoque and Murayama, 2013; Heterick et al., 2013). Urbanisation typically results in a reduction of biodiversity and localised extinction of native species as native vegetation is converted into densely populated cities and low-density suburban environments (Cardilini et al., 2013; Chace and Walsh, 2006; Marzluff, 2001; McKinney, 2008). Globally, cities and their associated sprawl now cover 3% of the world's surface, with the number of people living within towns and cities expected to increase by a third over the next thirty years (Heterick et al., 2013; McKinney, 2006).

Australia is highly urbanised with over 80% of its population living in urban regions (Australian Bureau of Statistics, 2008; Bekessy et al., 2012). Whilst most people are familiar with the term 'city', and in this thesis it refers specifically to the built-up central business district, the term 'suburbs' is less easily defined. In Australia, the term 'suburbs' typically refers to the region located mid-way between the city centre and the surrounding rural lands, characterised by freestanding dwellings on relatively large allotments (Johnson, 2006). As Australian cities have continued to grow, the suburban region has moved spatially outward (termed 'urban sprawl') from the 'inner suburban region', characterised by 19th century dwellings on the city side of the suburban midpoint and typically within walking distance to the city (Johnson, 2006). On the other side of the suburban midpoint is the 'outer suburban region', consisting of the land between the suburban region and the rural/forested region (Cardilini et al., 2013; Johnson, 2006) and often contains newer housing estates.

Urbanisation results in changes to the structure of the landscape, transforming previously continuous natural vegetation into isolated patches of native and exotic vegetation, impervious surfaces of buildings and roadways and artificially constructed green spaces, such as golf courses and sporting ovals (Catterall, 2009; Menke et al., 2011). These patches of remnant and surrounding artificial landscape are collectively termed the 'urban matrix' (Meffert and Dziock, 2013). This new habitat, together with the associated altered resource availability (Anderies et al., 2007; Shochat, 2004), changes in predator spectrum (Bonnington et al., 2013; Møller, , 2012; Møller, and Ibanez-Alamo, 2012), water quality (Pinto et al., 2013; Smucker et al., 2013), nutrient cycling (Chudoba et al., 2013; Xia et al., 2013), microclimate (Ding and Shi, 2013; Gero et al., 2006; Kalnay and Cai, 2003) and increases in wildlife stress and disease (Brearley et al., 2012; Davis et al., 2012b; McDonnell and Pickett, 1990) results in a novel ecosystem with a species composition and relative abundances that have not previously existed (Hobbs et al., 2006; Kowarik, 2011).

Birds are considered a good model to understand the effects of urbanisation on habitat structure and composition (Chace and Walsh, 2006; Clergeau et al., 1998; MacGregor-Fors et al., 2010; Reis et al., 2012; Savard et al., 2000). They are highly sensitive to changes in habitat structure and vegetation composition, with different species responding differently to changes in resource distribution (Chace and Walsh, 2006; Clergeau et al., 1998). Typically, urbanisation results in a reduction of species diversity and an overall simplification of the avifaunal community, as a suite of species capable of tolerating the urban matrix replaces regionally distinct communities (Blair, 2001; Chace and Walsh, 2006; Clergeau et al., 2006; McKinney, 2008; McKinney and Lockwood, 1999). In addition, it has been widely documented that successful introduced species are often pre-adapted to the open and disturbed habitats which humans have a propensity for creating, and urban avian communities worldwide may be dominated by a small number of established exotic species (Case, 1996; Chace and Walsh, 2006; McKinney, 2006; McKinney and Lockwood, 1999; van Heezik et al., 2008), such as the house sparrow (*Passer domesticus*) in the Americas, South Africa, Australia and New Zealand (Anderson, 2006; Saetre et al., 2012), monk parrots (*Myiopsitta monachus*) in Europe and North America (Pruett-Jones et al., 2012; Strubbe and Matthysen, 2009) and the common myna (*Sturnus tristis*) in Asia, Australia, New Zealand, Fiji, South Africa, Hawaii and other islands in the Indo-Pacific and Atlantic Oceans (Baker and Moeed, 1987). Established exotic species are often sedentary, may nest within cavities or buildings, roost and forage communally and have either an omnivorous or granivorous diet (Blair, 1996; Jokimaki and Suhonen, 1998; Kark et al., 2007; MacGregor-Fors et al., 2010). They utilise resources within the urban core, where few native species can survive, and may even become dependent upon these resources, for example pigeons that rely on spilled food and deliberate feeding by humans (Kark et al., 2007; Rose and Nagel, 2006; Shochat et al., 2006). Whilst a variety of native and non-native bird species are able to persist within the less dense suburban region, it is these pre-adapted urban exploiters that are able to succeed within the urban core (Blair, 1996; Kark et al., 2007).

In addition to exotic urban exploiters, certain native species are also capable of persisting within, and capitalising upon, the urban landscape, where they can occur in densities higher than in their traditional habitat (Blair and Johnson, 2008; Blair, 1996; Emlen, 1974; French et al., 2005; Major et al., 1996). Such species have been termed 'suburban adapters' (Blair, 1996) and are capable of exploiting additional resources, such as ornamental vegetation, that exist amongst moderate levels of development (Beissinger and Osborne, 1982; Blair, 1996). Several species of parrot have adapted particularly well to the urban environment and, as a group, parrots have exhibited some of the most positive responses to urbanisation (Major and Parsons, 2010). As the model taxon for this thesis, parrots will be used to investigate how resources within the urban landscape are utilised by fauna that appear to be responding positively to urbanisation.

In Europe, 171 species of bird have been introduced, of which 75 have established stable populations (Chiron et al., 2009), with parrots accounting for 18% of the established avifauna (Strubbe and Matthysen, 2009). In the United States, there are at least 25 species of introduced parrot that have established breeding populations (Garrott et al., 1993; Pruett-Jones et al., 2012). The ring-necked parakeet (*Psittacula krameri*), native to Africa and Asia, has established breeding populations throughout 35 countries on five different continents (Butler, 2005) while the monk parakeet has established at least 31 populations throughout Europe and is also well established throughout the United States (Minor et al., 2012; Pruett-Jones et al., 2012; Strubbe and Matthysen, 2009). These populations originated from either deliberate releases or from aviary escapees and, now naturalised, are of both economical and ecological concern, causing damage to infrastructure (monk parakeets) and competing with native secondary cavity-nesting species in urban habitats (ring-necked parakeets) (Pruett-Jones et al., 2012; Strubbe and Matthysen, 2009).

Within Australian cities, certain native species have recently increased in abundance. Unlike many cities within the northern hemisphere however, which are dominated by granivorous and omnivorous generalist species (Garrott et al., 1993), certain nectarivorous species of the family Meliphagidae (honeyeaters) have responded positively to urbanisation and have become a dominant component of the urban avifauna (Ashley et al., 2009). Noisy miners (*Manorina melanocephala*) and red wattlebirds (*Anthochaera carunculata*), two large honeyeaters, have increased in density throughout several major Australian cities since European settlement (Higgins et al., 2001; Hoskin, 1991; Low, 2002). Noisy miners are territorial, sedentary and gregarious birds whose traditional habitat is open woodland and forest edge (Higgins et al., 2001). Their elevated density in urban regions is thought to be due to a combination of the sparse Eucalypt cover (in this thesis, the common term 'Eucalypt' includes species of the genera *Eucalyptus*, *Angophora* and *Corymbia*), due to thinning of the canopy, reduction in shrub cover as a result of creating lawns, and supplementary nectar provided by ornamental shrubs, particularly within suburban regions (Catterall, 2004; Sewell and Catterall, 1998). Noisy miners are considered to be the dominant force structuring urban bird communities (Maron et al., 2013).

The rainbow lorikeet (*Trichoglossus haematodus*), a native nectarivorous parrot, has also benefited from urbanisation, having recently dramatically increased in numbers in several major Australian cities and towns (Shukuroglou and McCarthy, 2006; Veerman, 1991; Waterhouse, 1997). Other species, both nectarivorous and granivorous, also appear to be increasing in density, but aside from the rainbow lorikeet, the effects of urbanisation on parrots has received little attention (Burgin and Saunders, 2007).

1.2 Historical changes in urban parrot communities

Parrot densities have changed considerably in what is now the urban landscape. Prior to 1900, the rainbow lorikeet, eastern rosella (*Platycerus eximius*), musk lorikeet (*Glossopsitta concinna*), little lorikeet (*Glossopsitta pusilla*), king parrot (*Alisterus scapularis*), turquoise parrot (*Neophema pulchella*), swift parrot (*Lathamus discolour*) and ground parrot (*Pezoporus flaviventris*) were sighted in the Sydney region (Burgin and Saunders, 2007; Hindwood, 1939, 1962a) and sulphur-crested cockatoos (*Cacatua galerita*), were present on the western edge of the Sydney 'county', on the Cumberland Plains Woodland (Burgin and Saunders, 2007; Higgins, 1999). The rainbow lorikeet population, first sighted in the Sydney region by the Cook expedition in May 1770 (Hindwood, 1962b), began to decline by the 1900s (North, 1914; Waterhouse, 1997). By the early 1900s, the rainbow lorikeet was rarely, if at all, observed (Crome and Shields, 1992; North, 1914). Similarly, the frequency at which musk lorikeets were sighted also declined by the 1900s (Hindwood, 1939). Both species of birds were heavily trapped prior to 1900 (Hindwood, 1939), which may have resulted in a decline in abundance, however the large-scale clearing of native vegetation since European settlement (Benson and Howell, 1995) is likely to have impacted upon the populations of both species.

Several major Australian cities and towns now have permanently established populations of parrots that had either been absent for a long period of time or were not previously present. Rainbow lorikeets, previously absent in cities since the early 1900's, have now been observed in densities between 1.67 birds per hectare (Melbourne) and 8 birds per hectare (Townsville) (Fitzsimons et al., 2003; Shukuroglou and McCarthy, 2006; Woodall, 1995). In Sydney, the abundance of long-billed and little corellas, once previously absent, has increased dramatically and flocks of more than 50 sulphur-crested cockatoos are now frequently sighted (Burgin and Saunders, 2007). There are now 15 species of parrot that have been recorded within 10 km of the Sydney GPO, of which six are well established and four continue to increase in numbers (Burgin and Saunders, 2007).

Two species that used to be present, the turquoise parrot and the ground parrot, are now absent from the region as a result of urbanisation (Burgin and Saunders, 2007). Both the turquoise parrot and the ground parrot are now listed as vulnerable under the New South Wales (NSW) Threatened Species Conservation Act 1995. The little lorikeet and the swift parrot, which also were once common in the Sydney region, are now both listed as vulnerable in NSW (Threatened Species Conservation Act 1995).

Parrots are now some of the most frequently sighted birds in several major cities in Australia. The galah (*Eolophus roseicapillus*) has increased in abundance in Brisbane over the last 30 years, where it increased from the 44th to the 24th most encountered species and the rainbow lorikeet population changed from the 22nd most encountered species to the most frequently encountered species (Woodall, 2002). Red-rumped parrots (*Psephotus haematonotus*) and musk lorikeets have also become more abundant over the last 30 years in Melbourne (Lowry and Lill, 2007; Shukuroglou and McCarthy, 2006; Smith and Lill, 2008). A large population of rainbow lorikeets has also established in Perth, on the west coast of Australia, but this population resulted from released individuals, as the rainbow lorikeet does not naturally occur on Australia's western coast (Lamont and Burbidge, 1996).

Several hypotheses have been proposed to explain temporal changes in the abundance of particularly parrot species, including impacts of wild fires and mass flowering events, however these have never been empirically tested. An extensive wild fire burned in the bushland surrounding Sydney in 1936 and, throughout the year, increased numbers of rainbow lorikeets were observed throughout Sydney (Hindwood, 1939). A mass flowering of swamp mahogany (*Eucalyptus robusta*) occurred in Sydney in 1939 and large flocks of swift parrots appeared, where they were observed feeding on the flowers (Hindwood, 1939).

Changes in the abundance or distribution of some parrot species may also have occurred as a result of changed rainfall patterns. The population of galahs in Sydney, was believed to have been boosted by a large drought in rural New South Wales in the 1940s (Hoskin, 1991). Budgerigars (*Melopsittacus undulatus)* were recorded during the early 1980s and were believed to have moved into Sydney from west of the Great Dividing Range during an extensive drought (Hoskin, 1991). Increased rainfall may also result in population or distribution changes, with the population of sulphur-crested cockatoos increasing in western Sydney during 1956, following a year of increased local rainfall (Hoskin, 1991).

In addition to environmental events, such as wild fires or droughts, the change in both assemblage composition and species abundance has also anecdotally been attributed to an increased availability of food resources throughout the urban landscape (Burgin and Saunders, 2007; Legault et al., 2012; Lowry and Lill, 2007; Shukuroglou and McCarthy, 2006).

1.3 Food Resources for Urban Parrots

Increased amounts and accessibility of food resources is another possible explanation for the increase in parrot populations in urban regions. Within the urban landscape, seasonal variation in food availability may be buffered, as compared to that in the natural environment, due to the diversity of cultivated shrubs and trees, which produce an almost continual supply of fruits and flowers (Cannon, 1979; Lowry and Lill, 2007; Shukuroglou and McCarthy, 2006). This may be particularly true of the suburban region, which is often a complex matrix of remnant vegetation, green spaces and gardens (Sewell and Catterall, 1998). Within Australia, the move to planting hybrid natives (e.g. *Grevillea* spp.) and other "bird-attracting plants" (Catterall, 2004; French et al., 2005) may have benefitted nectarivorous species, in particular the rainbow lorikeet, whose diet consists almost exclusively of nectar and pollen (Burgin and Saunders, 2007; Cannon, 1979; Sewell and Catterall, 1998). Green spaces, such as golf courses and recreational parks, also frequently contain planted nectar-rich plants, such as *Callistemon* spp (Burgin and Saunders, 2007). The relationship between nectar-providing plants within the Australian suburban landscape and the abundance of nectarivorous parrots has never been empirically tested, nor has any study previously compared the volume of nectar per hectare between urban and natural habitats.

In addition to high volumes of nectar, the urban landscape may also provide increased food resources for granivorous species, when compared to natural habitat. Grassed recreational ovals and road verges are common throughout the urban landscape and the timing of flowering and subsequent seeding of different species of grasses may provide an abundant and continuous supply of food (Hitchmough and Woudstra, 1999; Lowry and Lill, 2007).

As well as being abundant, resources in the urban landscape may also be easier to obtain, compared to the natural environment, as habitats are often intensively maintained, with lawns of parks and ovals frequently watered and fertilised and trees maintained in good condition (mulched and diseased limbs pruned) (Bang et al., 2012; Bertoncini et al., 2012; Neil and Wu, 2006). Well-maintained lawns may be easier to dig into and forage on, and may be closer to water supplies, which are often readily available from public fountains or birdbaths. Compared to the natural environment, the urban landscape may therefore provide a greater amount of food resources that are easier to access.

1.4 Nesting Resources for Urban Parrots

Not all resources may be present in higher abundance within the urban landscape. Tree hollows are a critical breeding requirement for most species of parrots and, with the increasing densities of some species of parrots, may become limiting within the urban landscape. Unlike in Europe, and North and South America, where primary hollow development occurs when fauna, such as woodpeckers (*Picidae* spp.), actively excavate a hole in the heartwood of the tree (Aitken and Martin, 2007; Harper et al., 2005a), within Australia, no primary excavators exist and hollow-utilising fauna must rely on hollows that form via secondary hollow development (Gibbons and Lindenmayer, 1996; Harper et al., 2005a; Saunders et al., 1982; Strubbe and Matthysen, 2007). Secondary hollow development occurs when the tree is damaged (e.g. by wind or wild fire) and the heartwood is exposed (Gibbons et al., 2002; Harper et al., 2005a). Fungi then decompose the heartwood and a subsequent hollow cavity is created. Secondary hollow development is, however, a slow process, and it may take upwards of one hundred years for a suitably sized hollow to develop that is useable for most vertebrate wildlife (Goldingay 2011 and references within; Harper 2005; Cameron 2006; Gibbons 1996).

Even if hollows are abundant within the urbanised landscape, it does not necessarily mean that they are suitable for use by parrots or other urban fauna (Cockle et al., 2010). Hollows vary widely in terms of their physical attributes (e.g. height, entrance diameter, depth etc.) and many hollows may be either sub-optimal or completely unsuitable for some species of parrot to rear young (Cockle et al., 2011; Marsden and Jones, 1997; Politi et al., 2010; Stojanovic et al., 2012). Additionally, some hollows may have poor drainage and may flood when it rains (Heinsohn et al., 2003). A hollow must be large enough to raise young, whilst also providing protection from predators, competitors and weather, and the exact requirements of a suitable hollow will therefore vary for individual species (Aitken and Martin, 2004; Cockle et al., 2011; Gibbons et al., 2002; Newton, 1994).

Extensive clearing has resulted in a reduction of hollow-bearing trees within the urban landscape (Harper et al., 2005a). Within unmanaged eucalypt forest, hollow density has been recorded at between 6 and 27 hollow-bearing trees per hectare (Gibbons et al., 2002; Todarello and Chalmers, 2007). Tree cover within the urban landscape can range from over 50% canopy cover in remnant vegetation through to sparsely vegetated parks and streetscapes (hereafter referred to as 'streets') where hollow density may be as low as 1% of that of natural forest (Shukuroglou and McCarthy, 2006).

If there are comparatively few hollows within the urban landscape, levels of competition may be high as individuals within a high-density community compete for optimal nesting hollows (Ardia et al., 2006; Strubbe and Matthysen, 2007). Competitive interactions between parrots at nesting hollows can be fierce (Heinsohn et al., 2003; Krebs, 1998; Lamont and Burbidge, 1996; Renton, 2004) and the rainbow lorikeet and sulphur-crested cockatoo have been recorded successfully usurping nests from other parrot species, potentially preventing them from breeding (Heinsohn et al., 2003; Higgins, 1999; Lamont and Burbidge, 1996). No study to date has assessed the distribution of hollows throughout the urban landscape or determined the level of competition that exists for tree hollows within any city in Australia.

1.5 Project Aims

This project aims to determine the present day distribution and abundance of parrots within a large city, identify factors that have influenced changes in the composition and abundance of the community and document how parrots utilise the urban landscape. It investigates the usage of, and competition for, both food and nesting resources and how these resources influence parrot abundance.

This project comprises three main parts.

Part 1 addresses the broad scope of the thesis by documenting the distribution and abundance of parrots within a large coastal city and by determining the extent to which this distribution can be explained by commonly held conceptions related to the abiotic environment. Chapter 2 investigates the present-day abundance of parrots throughout the major urban habitat types to provide information for management and future planning of the urban environment. Chapter 3 determines to what extent wild fire and drought could explain changes in the abundance of parrots that frequently occur within the city.

Part 2 addresses a common assertion that nectar, a major food resource for nectarivorous parrots, is elevated in the urban landscape, as compared to natural habitat, such that it may contribute to the increased abundance of nectarivorous parrots. Chapter 4 quantifies the amount of energy supplied by nectar within different habitats to determine if nectar-energy is higher in the urban landscape compared to natural habitat, and to determine the relationship between nectar availability and nectarivore abundance. Chapter 5 investigates the floral resource provided by trees in the urban landscape to determine if they produce more flowers, and flower for longer periods, than the same tree species within the non-urban environment, and whether this may benefit large-bodied nectarivores, including parrots.

Part 3 investigates the nesting resources within the urban landscape by quantifying the number of hollows in different urban habitats and determining how these are utilised by parrots and other hollow-nesting fauna. Chapter 6 addresses the level of visitation and competition between parrots and other hollow-utilising fauna at hollows within remnant vegetation. Chapter 7 investigates the distribution of hollows throughout the urban landscape, and also extends upon Chapter 6 by investigating the characteristics of hollows or hollow-bearing trees and determining the extent to which they are associated with individual species of parrot.

To conclude, Chapter 8 synthesises the findings from Chapters 2-7 to predict future responses of parrots to urbanisation and identify key areas for management attention to maintain urban parrot diversity.

Chapter 2: Seasonal Abundance and Habitat Use of Australian Parrots in an Urbanised Landscape

Photo: B Howard

Davis, A., Taylor, C.E. and Major, R.E. (2012). Seasonal abundance and habitat use of Australian parrots in an urbanised landscape. *Landscape and Urban Planning 106*, 191-198

2.1 Abstract

Certain native species are able to tolerate the urban landscape to the point where they are sometimes found in higher abundance in cities than they are in the surrounding natural vegetation. To improve understanding of the resource requirements of Australian parrots, we investigated the seasonal abundance and habitat use of 13 species in different landscape units in the major urban centre of Sydney, Australia. The urban landscape was divided into four urban zones and 528 surveys were conducted over a period of two years throughout four habitats of remnant vegetation, golf courses, streets and recreational parks, as well as the surrounding natural landscape, during both breeding and non-breeding seasons. Significant seasonal differences in abundance existed for two granivorous and one nectarivorous species. Abundance was significantly higher in the outer urban zone than the non-urban zone and species assemblage differed significantly between all urban zones and the non-urban zone during the breeding season but only between the city and non-urban zone during the non-breeding season. Remnant vegetation was also characterised by a significantly different community to other habitats during the breeding season. Understanding how fauna utilise the urban landscape, particularly high profile fauna such as parrots, has the potential to assist in both management and conservation of urban diversity.

2.2 Introduction

The number of cities, and the amount of land that is occupied by urban sprawl, is extending globally, with the increasing demand for housing resulting in losses of both native vegetation and associated elements of biodiversity (Pećarević et al., 2010; Shwartz et al., 2008; Tratalos et al., 2007). No landform change is as dramatic as urbanisation, which, as well as resulting in large changes to the landscape, also results in the creation of entirely new habitats compared to those which were previously present (Gilbert, 1991; Major and Parsons, 2010; Shukuroglou and McCarthy, 2006). Such newly created habitat is often intensively managed, with activities such as lawn mowing and landscaping which, when combined with the differing physical characteristics of the urban landscape, result in a unique mosaic of residential, commercial, industrial and recreational spaces. These spaces occupy a dynamic continuum from areas of buildings and bitumen, interspersed with street trees and suburban gardens, through to large tracts of semi-intact natural vegetation (Breuste et al., 2008; Crooks et al., 2004; Major and Parsons, 2010; Shukuroglou and McCarthy, 2006; White et al., 2005; Young et al., 2007).

Despite many of these habitat components being isolated and relatively small, the high degree of variation, ranging from semi-natural to completely anthropogenic habitat, results in a high degree of spatial heterogeneity which can occasionally extend right into the urban core (Breuste et al., 2008; Bryant, 2006; McDonnell and Pickett, 1990; Rebele, 1994). This heterogeneity, termed the urban-rural gradient, tends to be highest within the suburban zone and is often characterised by a limited number of bird taxa that are often in high abundance, having successfully colonised the urban landscape (Blair, 2004; Blair, 1996; Green, 1984; Jones, 1981; Lowry and Lill, 2007; Parsons et al., 2006; Rottenborn, 1999; Sewell and Catterall, 1998; Young et al., 2007). Such taxa appear to be pre-adapted to survival in the urban landscape (Major and Parsons, 2010) and are able to both capitalise upon resources in new habitats analogous to those in their natural habitat, or to exploit different resources not present in their natural habitat (Ashley et al., 2009; Blair and Johnson, 2008; Blair, 1996; Emlen, 1966; French et al., 2005; Huhtalo and Järvinen, 1977; Major and Parsons, 2010; Sewell and Catterall, 1998).

Globally, parrots (Psittaciformes) have proved to be a successful group of avian urban adaptors, with many species of introduced parrots now naturalised across the European and North American continents as well as Japan, Israel and New Zealand (Lambert et al., 2009; Lever, 2005). Over the last 30 years, populations have increased throughout major urban landscapes and surrounding suburban and rural zones and appear to be distributed throughout various types of urban habitat (Butler, 2005; Lambert et al., 2009; Strubbe and Matthysen, 2007; Wenner and Hirth, 1984). Many of these populations were originally founded by aviary escapees or from individuals that had been deliberately released, and population sizes of different species now range from sporadic and non-established pairs to rapidly increasing, high-density populations. Increasing population density has raised concerns of both competition within and displacement of other avian fauna and a subsequent reduction in urban biodiversity (Butler, 2005; Lambert et al., 2009; Strubbe and Matthysen, 2007; VanBael and PruettJones, 1996).

Unlike in the northern hemisphere, parrots within countries of the southern hemisphere, such as Australia and South America, are endemic and, although some urban populations were founded by releases and aviary escapees from outside their natural range, others have simply expanded their range to make use of urban resources or have remained in the landscape throughout the urbanisation process. In some cases these urban populations appear to be periodically boosted by environmental stresses such as drought or wild fire (Burgin and Saunders, 2007; Davis et al., 2011; Shukuroglou and McCarthy, 2006) or may exhibit a seasonal shift in abundance (Shukuroglou and McCarthy, 2006; Veerman, 1991; Waterhouse, 1997).

Additionally, southern hemisphere parrots differ from their northern hemisphere counterparts in having a greater proportion of nectarivorous parrots. This may result in differences in habitat or resource utilisation because honeyeaters (Meliphagidae) and lorikeets exploit nectar rich resources in gardens, parks and streets (Fitzsimons et al., 2003; Lim and Sodhi, 2004; Smith and Lill, 2008; White et al., 2005; Young et al., 2007).

Despite both range expansion and increasing population densities, urban populations of parrots have received little research attention and there is a general lack of ecological information on parrots in urban landscapes (Garrott et al., 1993; Guittar et al., 2009; Strubbe and Matthysen, 2007). As large and brightly-coloured birds, parrots are valuable flagship taxa for promoting community interest in biodiversity, particularly in urban centres where they interact with a large human audience, which may not have the opportunity to interact regularly with the natural environment (Butler, 2005; French et al., 2005; Guittar et al., 2009). An important step in managing urban environments to maintain diversity is to understand the distribution and abundance of parrots throughout the heterogeneous urban landscape. This study aims to determine habitat use and abundance of different parrot species, as well as any seasonally related changes in abundance, within Australia's largest urban centre, Sydney. Specifically, we aim to:

1) determine if there is a shift in abundance relating to the parrot breeding season between the urban landscape and non-urban landscape;
2) determine if there is a difference in species abundance and composition between different types of urban habitat, and

3) determine if there is a difference in species abundance and composition between urban zones.

2.3 Materials and Methods

2.3.1 Study Sites

The study area encompassed the Sydney urban landscape on the east coast of New South Wales, Australia, extending over an area greater than 12 000 square kilometres and characterised by a warm, temperate climate. It is an urban island, bounded by the Pacific Ocean to the east and three large national parks to the north, south and west (Fig. 2.1). The area of natural vegetation within these parks surrounding Sydney exceeds 260 000 hectares and is predominantly dry sclerophyll woodland or forest, and heath (Keith, 2006). A series of concentric ellipses extending from the centre of Sydney, demarcate the urban landscape into 'city', 'inner suburban', 'suburban' and 'outer suburban' zones (Fig. 2.1), each based upon distance from the city (using ArcGIS v 9.2) and boundary definitions from the NSW Division of Local Government (www.dlg.nsw.gov.au).

Urban space was classified into four distinct parrot habitats and replicate sites of each habitat were selected in each zone (Table 2.1). Parks were defined as a sporting field or other similar open grassed recreation area with few, if any, trees. Streets were defined as the front gardens of houses and the roadside verge they bordered. Remnant vegetation (hereafter referred to as 'remnants') was defined as patches of fragmented bushland within each urban zone and was typically sandstone sclerophyll forest. The fourth habitat, golf courses, varied in vegetation type and coverage though not in overall

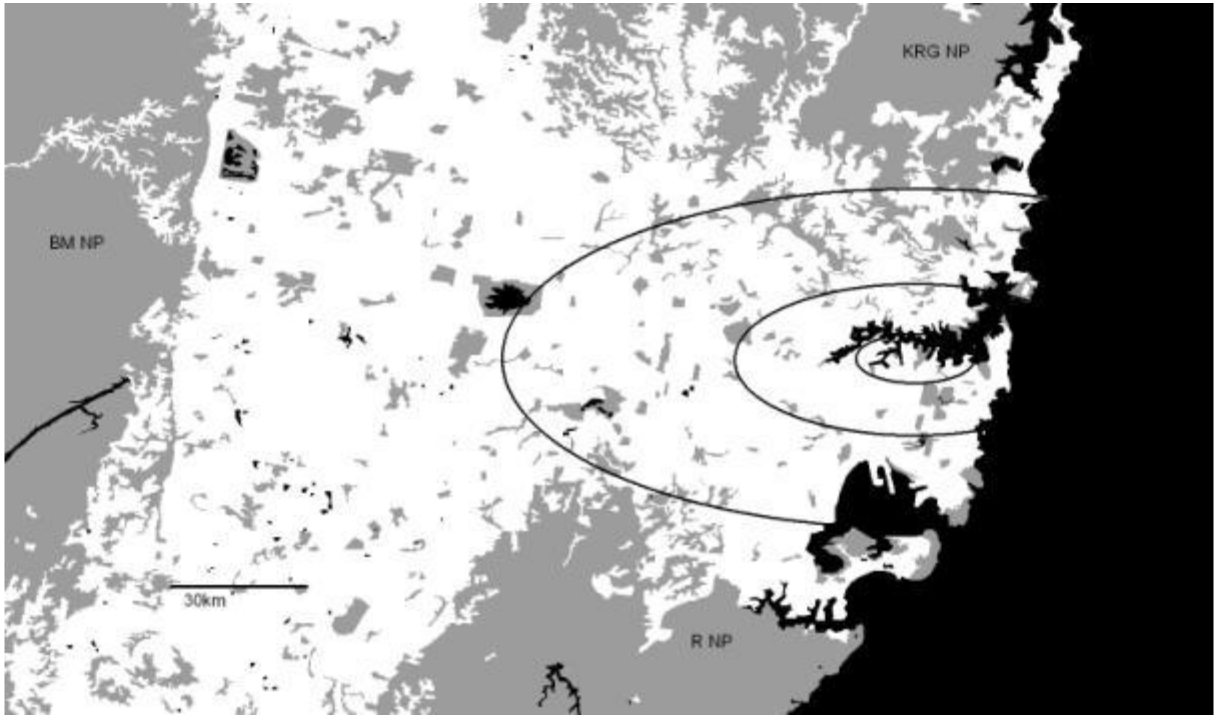

Fig. 2.1 Map of the study region surrounding Sydney, Australia, showing the urban landscape (white) and surrounding vegetation (grey) with Royal National Park (Royal NP), Ku-ring-Gai Chase National Park (KRG NP) and the Blue Mountains National Park (BM NP). Water is coloured black. The centre ellipse demarcates the city with the larger two ellipses demarcating the inner zone and the suburban zone respectively. The outer zone is the land bounded between the suburban zone and the surrounding national parks.

Table. 2.1 The distribution of urban habitat study sites within each urban zone.

Zone		**Habitat**		
	Park	Street	Golf Course	Remnant
City	8	14	0	0
Inner	16	16	8	10
Suburban	8	16	16	16
Outer	16	16	14	16

structure. Sites in each zone were randomly selected from either a listing in a local street directory or from Google Maps, and we attempted to represent each habitat equally within each zone. Differing numbers of habitat sites reflect the variability of certain habitat types throughout each urban zone (e.g. there are no golf courses in the city).

An additional 64 sites were selected from the non-urban landscape of the surrounding national parks (NP) that border Sydney (Royal National Park, Ku-ring-gai Chase National Park and the Blue Mountains National Park). Sites were selected randomly using grids on a topographic map, with the constraint that the site had to be accessible by road or path to be considered for selection.

2.3.2 Bird Surveys

Area-search surveys (Barrett et al., 2003), recording the presence of any species of the order Psittaciformes*,* were conducted over a 2-ha area within each site, for a period of 20 minutes, undertaken in the early morning or late afternoon, up to three hours after sunrise and two hours before sunset.

Surveys were completed once at 132 sites during the breeding months of August to October 2008 and repeated over the same area at the same sites during the non-breeding months of March to May 2009. A different suite of 132 sites was then surveyed once during August to October 2009 and again in March to May 2010.

2.3.3 Analysis

Variation in the abundance of six species and guild variables was identified using linear mixed models. The sulphur-crested cockatoo, eastern rosella (*Platycercus elegans*), galah, red-rumped parrot, little corella (*Cacatua sanguinea*) and long-billed corella (*Cacatua tenuirostris*) were broadly grouped into a single 'total granivore' variable. The rainbow lorikeet, little lorikeet, musk lorikeet, and scaly-breasted lorikeet (*Trichoglossus chlorolepidotus*) were similarly broadly grouped into a single 'total nectarivore' variable, on the assumption that, given the limited literature on feeding in the wild, they are primarily nectar feeders. Due to the high abundance of the sulphur-crested cockatoo and the rainbow lorikeet compared with other species, additional 'granivore' and 'nectarivore' variables were created that excluded the sulphur-crested cockatoo and the rainbow lorikeet. The abundance of sulphur-crested cockatoos and the rainbow lorikeets was analysed separately. The Australian king parrot, crimson rosella (*Platyercus elegans*) and yellow-tailed black-cockatoo (*Calyptorhynchus funereus*) were not included in the grouped foraging guilds due to their broader diets (Higgins, 1999) and they did not fit into the category of either 'nectarivore' or 'granivore'.

Data for the city and inner suburban zones were pooled for analysis to equate sample sizes between urban zones and from here on shall be referred to as 'city'. Data for the non-breeding seasons of 2009 and 2010 were pooled, as were the data for the breeding seasons of 2008 and 2009. All variables were log transformed to improve normality of the data.

Linear mixed models (IBM SPSS version 19.0) were used to account for any variance that may have been due to the unequal distribution of habitat throughout the urban zones. Models were first run with 'season' and 'urban zone' as fixed factors and 'habitat' as a random factor, as the urban habitats sampled were only a selection of a larger suite of available types of habitat

(Garson, 2007). Where 'habitat' was found to be non-significant, it was dropped from the model and the model was run again with either season or urban zone or both factors, and the model with the highest AIC value was retained (Garson, 2007) To determine which of the urban zones accounted for significant zone effects, we undertook multiple comparisons using Fisher's LSD test.

To determine the effects of season, urban zone and habitat on species that were not sufficiently common for abundance data to meet parametric assumptions (all species other than the sulphur-crested cockatoo and rainbow lorikeet), abundance data for these species were transformed into presence/absence data and the same linear mixed model procedure was used to measure variation in the number of sites in which each species was present. We also tested for effects of season, urban zone and habitat on overall parrot diversity by calculating the Shannon-Wiener Diversity Index (Clergeau et al., 1998; Shannon, 1948) for each survey and using this as the dependent variable in the same linear mixed model procedure.

To investigate differences in the bird community between seasons, urban zones and habitat types, we used one-way ANOSIM (PRIMER version 5.3.4) based on a similarity matrix constructed using Bray-Curtis similarities. To determine the percentage contribution of each species to the dissimilarity between factors, we used a SIMPER analysis (PRIMER version 5.3.4).

2.4 Results

2.4.1 Bird Abundance

Significant seasonal differences in the mean abundance of birds were identified for the 'total granivores', with a higher abundance of all granivorous species present in the breeding season (mean =2.01, ± 0.36 (SE) birds per survey) than in the non-breeding season (mean = 1.43*,* ± 0.29 (SE)) ($F_{1,\,502} = 3.40, p < 0.05$). When the sulphur-crested cockatoo was analysed separately, its abundance was higher in the breeding season (mean = 1.04*,* ± 0.24 (SE)) than in the non-breeding season (mean = 0.46, ± 0.12 (SE)) ($F_{1,\,502} = 6.31, p < 0.05$), and there was no significant difference between the two seasons for the remaining pooled granivorous species after the sulphur-crested cockatoo had been removed from the analysis ($F_{1,\,502} = 0.63, p > 0.05$). No significant differences in the abundance of 'total nectarivorous' species between the two seasons were detected ($F_{1,\,502} = 2.49, p > 0.05$). However, when the rainbow lorikeet was removed, the abundance of the remaining nectarivores differed significantly between seasons ($F_{1,\,502} = 7.53, p < 0.01$), with a higher abundance during the non-breeding season. There was no significant difference in the abundance of rainbow lorikeets between the breeding and non-breeding seasons ($F_{1,\,502} = 2.49, p > 0.05$).

Seasonal differences also existed between the numbers of sites at which two of the less common species were present. Musk lorikeets were present at significantly more sites in the non-breeding season (mean = 0.067, ± 0.016 (SE)) than the breeding season (mean = 0.0078, ± 0.0055 (SE)) ($F_{1,\,502} = 13.30, p < 0.01$), and corellas were also present at significantly more sites in the non-breeding season (mean = 0.59, ± 0.15 (SE)), than the breeding season (mean = 0.24, ± 0.0095 (SE)) ($F_{1,\,505} = 4.27, p < 0.05$).

The linear mixed models detected no significant differences between habitats in the abundance of 'total granivores', 'total nectarivores', the remaining granivorous species when the sulphur-crested cockatoo was removed, the remaining nectarivorous species when the rainbow lorikeet was removed, or the rainbow lorikeet and sulphur-crested cockatoo when analysed separately. Habitat, however, accounted for 13% of the variance in the difference in abundance between zones for the 'total granivorous' species. When the sulphur-crested cockatoo was analysed separately, habitat accounted for only 1% of the variance in its abundance between zones, but accounted for 25% of the variance in abundance between zones for the remaining granivorous species. Habitat also accounted for over 19% of the variance in the number of sites between zones at which the red-rumped parrot was present and over 5% of the variance of sites between zones at which the galah was present. Habitat accounted for less than 3% of variance for all other species abundance and presence.

Abundance varied significantly between urban zones for both 'total granivores' ($F_{1,\,502} = 17.46$, $p < 0.01$) and 'total nectarivores' ($F_{1,\,502} = 38.31$, $p < 0.01$) (Fig. 2.2) and remained so for both the granivores ($F_{1,\,502} = 24.69$, $p < 0.01$) and the nectarivores ($F_{1,\,502} = 7.71$, $p < 0.01$) when analysed without the sulphur-crested cockatoo and the rainbow lorikeet respectively (Fig. 2.2). Abundance varied significantly between zones for both the rainbow lorikeet ($F_{1,\,502} = 37.99$, $p < 0.01$) and the sulphur-crested cockatoo when analysed alone ($F_{1,\,502} = 7.78$, $p < 0.05$) (Fig. 2.2). Species presence at sites varied significantly between urban zones for the musk lorikeet ($F_{1,\,502} = 10.68$, $p < 0.01$), red-rumped parrot ($F_{1,\,502} = 16.14$, $p < 0.01$), galah ($F_{1,\,502} = 9.85$, $p < 0.05$) and corellas ($F_{1,\,502} = 10.56$, $p < 0.01$) (Fig. 2.3). (Data for the little corella and long-billed corella were pooled because of uncertainty in separation of the two similar species when they occurred in mixed flocks.)

The outer zone had a significantly higher abundance of 'total granivorous' species than either the city ($p < 0.01$) or the suburban zone ($p < 0.01$) (Fig. 2.2a). When the sulphur-crested cockatoo was removed from analyses, the remaining granivorous species were still found in higher abundance in the outer zone than in either the city ($p < 0.01$, Fishers LSD) or the suburban zone ($p < 0.01$) (Fig. 2.2c). The abundance of the sulphur-crested cockatoo alone was still significantly higher in the outer zone than the city ($p < 0.01$), but abundance no longer varied significantly between the suburban and outer zones (Fig. 2.2e). The outer zone also had significantly more sites with the red-rumped parrots present than in the city ($p < 0.01$) and the suburban zone

($p < 0.01$), significantly more sites with the galah present than the city ($p < 0.01$) and the suburban

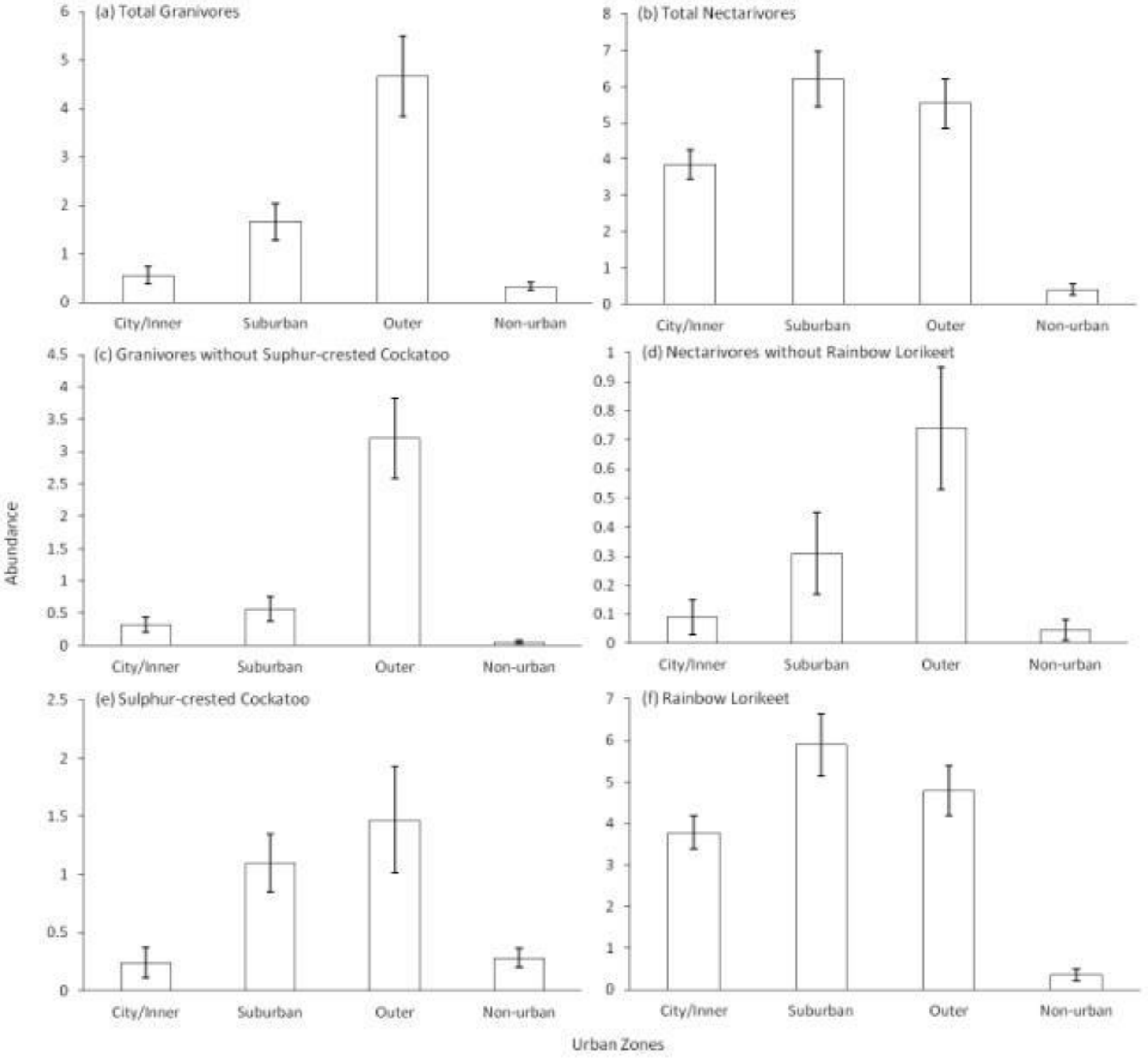

Fig. 2.2 Variation with respect to urban zone in the mean abundance of a) Total Granivores, b) Total Nectarivores, c) Granivores excluding sulphur-crested cockatoos, d) Nectarivores excluding rainbow lorikeets, e) Sulphur-crested Cockatoos and f) Rainbow Lorikeets. Error bars show the standard error of the mean.

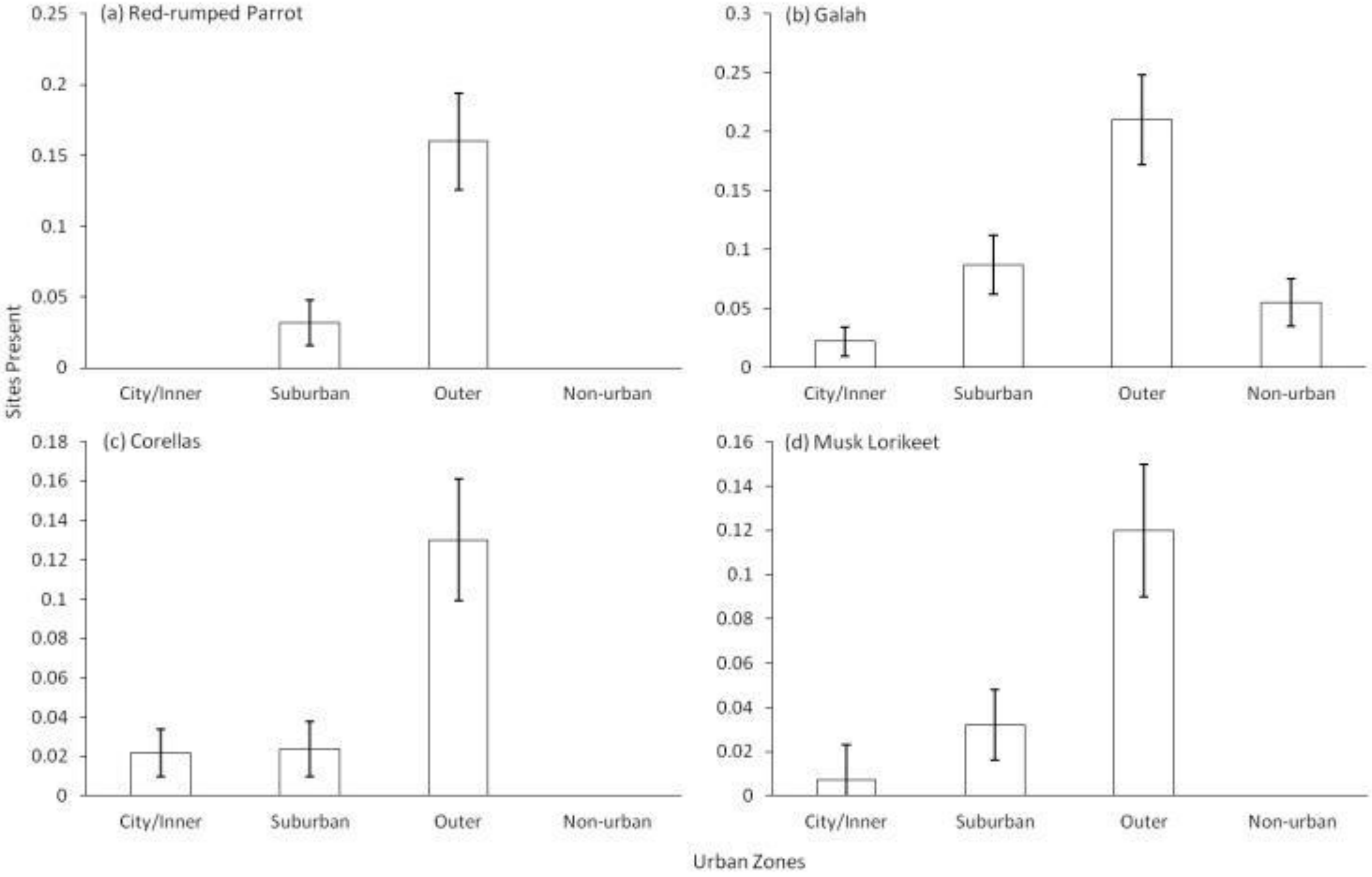

Fig. 2.3 Variation with respect to urban zone in the number of sites at which the a) Red-rumped Parrots, b) Galahs, c) Corellas and d) Musk Lorikeets were present. Error bars show the standard error of the mean.

zone ($p < 0.01$), and significantly more sites with the corellas present than the city ($p < 0.01$) and the suburban zone ($p < 0.01$) (Fig. 2.3a).

No significant differences in abundance between urban zones were detected for 'total nectarivores', however when the rainbow lorikeet was excluded from the 'total nectarivore' group, the abundance of the remaining nectarivores was significantly higher in the outer zone than either the city ($p < 0.01$) or the suburban zone ($p < 0.01$) (Fig. 2.2). The rainbow lorikeet alone did not differ significantly in abundance between the different urban zones. The outer zone also had significantly more sites with musk lorikeets present than either the city ($p < 0.01$) or the suburban zone ($p < 0.01$) (Fig. 2.3).

The non-urban zone had a significantly lower abundance of 'total granivores' than either the suburban zone ($p < 0.01$) or the outer zone ($p < 0.01$) (Fig. 2.2). The non-urban zone also had significantly fewer sulphur-crested cockatoos than either the suburban zone ($p < 0.01$) or the outer zone ($p < 0.01$) and the remaining granivorous species were also in higher abundance in both the suburban ($p < 0.05$) and outer zones ($p < 0.01$), compared to the non-urban zone (Fig. 2.2). The non-urban zone contained no sites with red-rumped parrots or corellas (Fig. 2.3).

The non-urban zone contained fewer 'total nectarivores' than the suburban zone ($p < 0.01$), outer zone ($p < 0.01$) and city ($p < 0.01$) (Fig. 2.2). Likewise, the non-urban zone contained fewer rainbow lorikeets than the city ($p < 0.01$), suburban zone ($p < 0.01$) or the outer zone ($p < 0.01$). For the remaining nectarivorous species, the outer zone was the only zone to have a significantly higher abundance than the non-urban zone ($p < 0.01$) (Fig. 2.2).

2.4.2 Species Diversity

Diversity of parrots in the urban landscape did not vary significantly with either season or habitat but there was a significant difference in diversity between urban zones ($F_{3, 352} = 3.15$, $p < 0.05$). The city was characterised by significantly lower parrot diversity than both the outer zone ($p <0 .01$) and the non-urban zone ($p < 0.05$) (Fig. 2.4).

2.4.3 Species Assemblage

Significant seasonal differences existed between the breeding season and non-breeding season assemblages (Global R = 0.014, $p < 0.05$), however the low R value indicates considerable overlap between the two seasons. The rainbow lorikeet and sulphur-crested cockatoo contributed to over 65% of the dissimilarity in the parrot assemblage between the two seasons.

Within the breeding season, significant differences in assemblages existed between the city and suburban zone (R = 0.089, $p < 0.05$), city and outer zone (R = 0.11, $p < 0.05$) and the suburban and outer zones (R = 0.041, $p < 0.05$). The biggest differences were between the non-urban zone compared to the city (R = 0.43, $p < 0.05$), suburban (R = 0.37, $p < 0.05$) and outer (R = 0.27, $p < 0.05$) zones, with the rainbow lorikeet and the sulphur-crested cockatoo accounting for over 73%, 78% and 61% respectively. (Table 2.2).

Within the non-breeding season, significant differences existed between the city and suburban zone (R = 0.061, $p < 0.05$) outer zone (R = 0.23, $p < 0.05$) and the non-urban zone (R = 0.45, $p < 0.05$) as well as between the suburban and outer zones (R = 0.079, $p < 0.05$). Unlike in the breeding season, differences in assemblage between the non-urban zone and the suburban and outer zones were not significant in the non-breeding season. The rainbow lorikeet and the

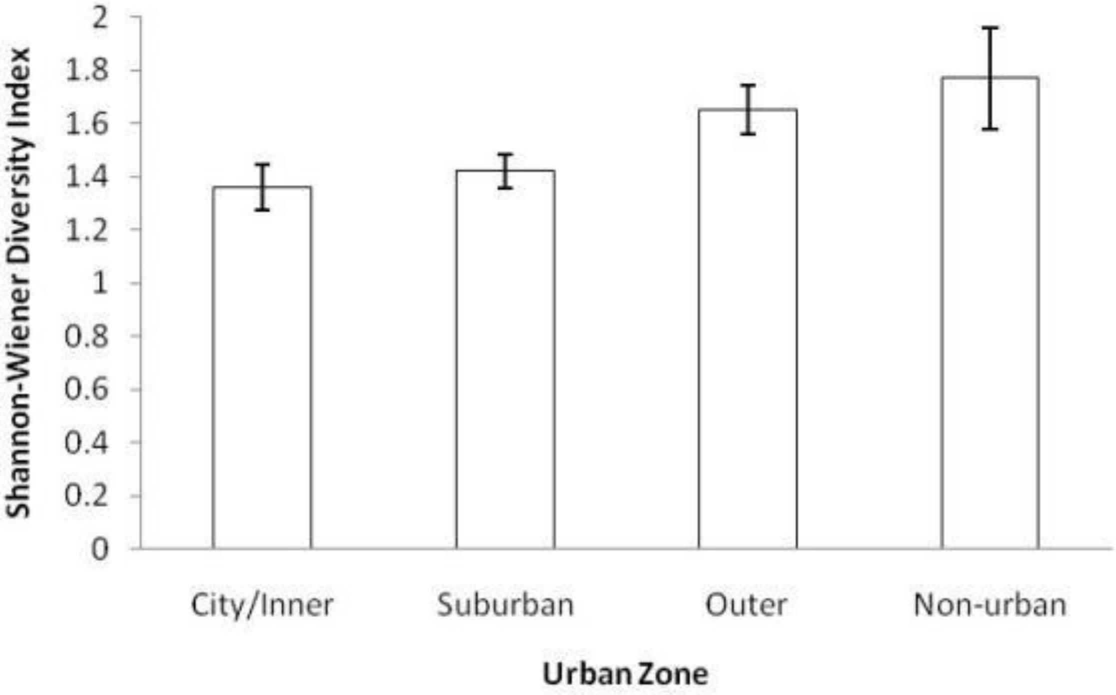

Fig. 2.4 Mean diversity of parrots within the four urban zones, calculated using the Shannon-Wiener Diversity Index.

Table 2.2 Contribution of each species during the breeding season (Br) and the non-breeding season (N-Br) to the percentage dissimilarity between the city, suburban and outer zones. 'C' denotes city, 'S' denotes suburban zone, 'O' denotes outer zone and 'NU' denotes non-urban.

	C-S	C-O	C-NP	S-O	S-NP	O-NP	C-S	C-O	C-NP	S-O	S-NP	O-NP
	Br N-Br	Br N-Br	Br N-Br	Br N-Br	Br N-Br	Br N-Br	Br N-Br	Br N-Br	Br N-Br	Br N-Br	Br N-Br	Br N-Br
Rainbow lorikeet	60	43	56	46	60	43	65	43	43	43	44	30
Sulphur-crested cockatoo	17	17	18	19	18	18	9	9	15	11	14	13
Galah	7	10	7	9	6	9	0	6	0	5	1	5
Eastern rosella	3	7	3	5	2	6	1	6	0	5	1	4
Corellas	0	2	0	2	0	2	6	7	1	8	3	5
Little lorikeet	2	2	0	3	2	2	1	1	0	1	1	0
Musk lorikeet	0	1	0	1	0	1	8	8	1	9	4	6
Scaly-breasted lorikeet	0	0	0	0	0	0	1	3	1	2	0	1
Red-rumped parrot	2	11	0	10	2	10	0	11	0	9	0	8
Crimson rosella	3	4	9	3	7	7	2	2	37	2	30	25
Yellow-tailed black-cockatoo	4	4	7	0	2	2	2	1	1	0	0	0
Australian king parrot	2	1	0	2	2	0	4	3	1	4	2	2

crimson rosella accounted for 80%, 75% and 55% respectively of the dissimilarity between the city, suburban zone and outer zone compared to the non-urban zone, with the sulphur-crested cockatoo contributing less dissimilarity between zones than it did in the breeding season (Table 2.2).

Within the non-breeding season, significant differences existed between the city and suburban zone (R = 0.061, $p < 0.05$) outer zone (R = 0.23, $p < 0.05$) and the non-urban zone (R = 0.45, $p < 0.05$) as well as between the suburban and outer zones (R = 0.079, $p < 0.05$). Unlike in the breeding season, differences in assemblage between the non-urban zone and the suburban and outer zones were not significant in the non-breeding season. The rainbow lorikeet and the crimson rosella accounted for 80%, 75% and 55% respectively of the dissimilarity between the city, suburban zone and outer zone compared to the non-urban zone, with the sulphur-crested cockatoo contributing less dissimilarity between zones than it did in the breeding season (Table 2.2).

A second ANOSIM revealed significant differences in the bird assemblages occupying different habitats, and these differences varied between the breeding and non-breeding season. Within the breeding season, the assemblage of parrots in streets differed from that of parks (R = 0.16, $p < 0.05$), golf courses (R = 0.063, $p < 0.05$) and remnants (R = 0.12, $p < 0.05$). The biggest differences in assemblages were between the non-urban habitat and parks (R = 0.19, p < 0.05), streets (R = 0.48, p < 0.05), golf courses (R = 0.33, p < 0.05) and remnants (R = 0.22, p < 0.05), with the rainbow lorikeet and sulphur-crested cockatoo contributing 56%, 83%, 73% and 73% to the dissimilarities between respective habitats (Table 2.3).

Table 2.3 Contribution of each species during the breeding season (Br) and the non-breeding season (N-Br) to the percentage dissimilarity between parks, streets, golf courses, remnants and the non-urban landscape. 'P' denotes parks, 'St' denotes streets, 'G' denotes golf courses, 'R' denotes remnants and 'NP' denotes national parks.

	P-St		P-G		P-R		P-NP		St-G		St-R		St-NP		G-R		G-NP		R-NP	
	Br	N-Br	Br	N-Br	Br	N-Br	Br	N-Br	Br	N-Br	Br	N-Br	Br	N-Br	Br	N-Br	Br	N-Br	Br	N-Br
Rainbow lorikeet	53	54	42	50	42	53	40	28	59	37	58	57	68	40	47	51	53	41	52	42
Sulphur-crested cockatoo	11	9	17	6	19	8	17	17	19	14	21	13	15	16	25	8	20	9	21	17
Crimson rosella	4	4	2	1	5	5	8	24	2	33	5	5	8	35	3	3	6	23	8	32
Yellow-tailed black-cockatoo	6	2	6	1	5	0	7	4	0	0	2	2	3	2	0	1	2	1	2	3
Galah	9	3	12	5	10	3	11	8	7	2	4	2	4	0	8	5	8	3	6	2
Eastern rosella	7	5	6	5	6	3	7	5	1	2	2	2	4	1	2	3	2	3	2	0
Australian king parrot	1	0	1	1	2	9	1	3	0	0	2	9	0	0	2	6	0	0	2	7
Corellas	1	6	2	13	1	5	1	3	1	4	0	0	0	0	1	10	1	9	0	0
Little lorikeet	2	1	3	0	2	0	2	2	2	0	2	1	2	1	2	0	1	0	1	0
Musk lorikeet	1	10	0	6	0	6	0	1	0	3	4	8	1	5	0	5	0	3	0	2
Scaly-breasted lorikeet	0	3	0	1	0	2	0	2	0	1	0	1	0	1	0	0	0	0	0	2
Red-rumped parrot	5	5	9	11	8	5	4	5	8	3	5	0	0	0	10	8	7	7	5	0

Within the non-breeding season, assemblages differed significantly between golf courses and streets (R = 0.14, $p < 0.05$), parks (R = 0.086, $p < 0.05$) and remnants (R = 0.16, $p < 0.05$) as well as between the non-urban zone and parks (R = 0.17, $p < 0.05$), streets (R = 0.28, $p < 0.05$) and golf courses (R = 0.28, $p < 0.05$). Unlike the breeding season, no significant differences in assemblage between remnants and the non-urban habitat were detected. The rainbow lorikeet and the crimson rosella contributed the most percentage dissimilarity between the parks (70%), streets (74%), golf courses (65%) and remnants (73%) compared to the non-urban zone, with the sulphur-crested cockatoo contributing less to the dissimilarity between habitats than it did during the breeding season (Table 2.3).

2.5 Discussion

This study revealed that there are significant differences in the parrot assemblages that occupy different habitats in the different zones within a large city. Moreover, the nature of the differences varies between seasons and is likely to be related to variation in the distribution of foraging and nesting resources.

2.5.1 Seasonal Differences

The increase in corellas during the post-breeding summer months may be due to the urban landscape offering a more attractive environment than their historical arid range. Seasonal movements of inland cockatoo species have been recorded for the galah as well as Carnaby's black-cockatoo (*Calytorhynchus latirostris*) and long-billed corellas in south western Australia whereby populations migrate to coastal regions during the hot, dry summer months to exploit readily available water and softer foraging ground (Davis et al., 2011; Saunders, 1980; Smith and

Moore, 1992). The urban landscape, however, may not support the large summer flocks of corellas during the breeding season and this, in addition to the corellas' strong affinity for the same annual breeding site, may result in these partly-nomadic parrots returning to their breeding range outside of the urban landscape (Higgins, 1999; Saunders et al., 1982).

Similarly, the increased presence of musk lorikeets in the non-breeding season may be a resource-related movement. Considered nomadic, the musk lorikeet has been reported to increase in abundance in the coastal city of Melbourne, Australia, during summer, which corresponds with the availability of flowering nectar resources, such as species of *Eucalyptus* (Smith and Lill, 2008). Throughout Melbourne and Sydney many non-endemic species of trees have been planted in streets and parks, primarily for their flowering aesthetics, and they have now matured providing an abundant supply of nectar (Fitzsimons et al., 2003; Smith and Lill, 2008; Waterhouse, 1997). Seasonal increases in abundance of parrots have also been reported in Florida, USA, with the non-breeding season characterised by higher numbers of the introduced budgerigar (*Melopscittacus undulates*) (Wenner and Hirth, 1984). In Florida, rather than a resource-related movement however, the higher abundance during the non-breeding season was attributed to both nesting females and fledglings joining the post-breeding flock (Wenner and Hirth, 1984).

The higher abundance of the sulphur-crested cockatoo in the breeding season may suggest that the urban landscape provides more attractive breeding resources than the non-urban landscape. The relatively high percentage of dissimilarity in the overall assemblage in the breeding season between remnants and streets (61%), and the outer zone and the city (68%), compared with the lack of difference in the assemblage between remnants and other urban habitats in the non-breeding season, may further suggest the importance of remnants as urban breeding habitat for parrots. Although urbanisation usually results in both a loss of tree density and a reduction in average tree diameter over time, mature trees in remnants and parks are often maintained for their aesthetic value (French et al., 2005; Strubbe and Matthysen, 2007) and may offer large hollows for breeding sulphur-crested cockatoos in an environment that is characterised by both warmer winter temperatures and a greater availability of food than in the non-urban landscape (Strubbe and Matthysen, 2007). Once these remnants reach carrying capacity, these larger birds may need to disperse into the non-urban habitat, which contains a greater number of suitably sized hollows (Goldingay, 2009; Higgins, 1999; Shukuroglou and McCarthy, 2006; Walker et al., 2005).

2.5.2 Habitat Associations

Whilst there was no significant difference in total parrot abundance between urban habitats, there was significant variation in the parrot assemblage between habitats. Remnants had a significantly different assemblage from the non-urban habitat, during the breeding season, but there was no significant difference during the non-breeding season. Whereas the nomadic and semi-nomadic parrots (corellas and musk lorikeets) may leave the urban landscape during the breeding season, remnants may offer important breeding habitat for sedentary endemic parrots, such as the crimson rosella. The significant difference between remnants and streets may be indicative of the abundance of food available in streets from both native and exotic plantings and, additionally, food resources may be supplemented by bird feeders in gardens, which can result in higher survival rates and subsequent higher breeding densities (Brittingham, 1991; Day, 1995; French et al., 2005; Strubbe and Matthysen, 2007).

2.5.3 Urban Zones

The lower abundance and diversity of parrots that characterised the city compared to other urban zones may be attributed to a reduced amount of vegetation and consequently fewer feeding, roosting and nesting resources. This zone typically consists of terraced houses with small gardens, limited small recreation areas and sparse street- and roadside-vegetation amongst high-density, multi-storey buildings. The rainbow lorikeet was the only parrot for which abundance did not differ between the city and the other urban zones, with a high abundance throughout all of the urban zones. Similarly, the monk parakeet and ring-necked parakeet have successfully colonised major cities throughout North America and Europe and appear to favour built-up areas over natural environments (Butler, 2005; Lambert et al., 2009). Whilst the city may lack large hollows to accommodate larger parrots, such as cockatoos, it may contain many anthropogenic nesting cavities, such as streetlights, palm trees, electricity poles and chimneys that provide breeding cavities for adaptable, smaller-bodied parrots (Garrett, 1997; Higgins, 1999; Wenner and Hirth, 1984).

The increased presence of the granivorous red-rumped parrot, galah and corella species in the outer zone may be due to a greater density of parks and forested remnants. Forested remnants may provide a greater number of nesting and roosting resources than that available in the city, which may further explain difference in assemblages between the city and the suburban and outer zones. Treed urban regions in Belgium also had a greater abundance of the ring-necked parakeet, with its abundance strongly associated with nesting cavity density (Strubbe and Matthysen, 2007).

The ubiquity of the rainbow lorikeet, throughout all urban zones in Sydney, is comparable with that of both the monk parakeet and the ring-necked parakeet, two naturalised species occurring throughout North America and Europe. The abundance of these species has rapidly increased throughout urban regions, raising concerns about a future loss of biodiversity, primarily through competition with native cavity users (Strubbe and Matthysen, 2007; VanBael and PruettJones, 1996). The lower diversity in the city compared to the outer and non-urban zones may be due to a limited amount of suitable habitat containing nesting and feeding resources, with the abundant rainbow lorikeet capable of outcompeting other parrots for these resources. If the density of the rainbow lorikeet continues to increase throughout all urban zones, along with a reduction in suitable habitat due to urbanisation, we may see an increase in the number of competitive interactions between the rainbow lorikeet and other parrots (as well as other hollow-utilising fauna), resulting in a reduction in biodiversity in the suburban and outer urban zones.

Whilst limited evidence has been found for such competition by the ring-necked parakeet in both London and Belgium (Newson et al., 2011; Strubbe and Matthysen, 2007), the rainbow lorikeet differs from both the ring-necked parakeet and the monk parakeet in that it is both native to Australia and a nectarivore, and caution must be used when making inferences across regions and between endemic and naturalised populations. One potential mechanism to explain the success of the rainbow lorikeet is the high availability of nectar that may be present in streets and parks. Hybrid native species of *Banksia* and *Grevillea*, grown for their prolific flowering and long flowering seasons, may provide a continuous nectar resource which could result in a spatial focussing of nectarivore populations in the urban landscape, allowing birds to reach densities far in excess of those present in the non-urban landscape (Ashley et al., 2009; French et al., 2005; McGoldrick and Mac Nally, 1998).

2.5.4 Conclusion

A diverse parrot assemblage comprised of 13 species is present across urban zones and the different habitats that make up Australia’s largest urban centre, Sydney. The suburban and outer suburban zones contain a more diverse assemblage of parrots than the city. Remnant urban vegetation in particular appears to be relied upon heavily during breeding season, becoming less important during the non-breeding season, as parrots utilise other urban zones and habitats.

Seasonal differences, and utilisation of the urban environment, vary between species and further research at a species specific level is required. An area in particular need of research is that of urban hollow usage and the level of competition that may exist for this potentially limited resource, to determine whether any urban parrots or other hollow-utilising fauna are at risk of being out-competed by species such as the rainbow lorikeet and sulphur-crested cockatoo which are becoming highly abundant and currently dominate the parrot assemblage.

Chapter 3: Do Fire and Rainfall Drive Spatial and Temporal Population Shifts in Parrots? A Case Study Using Urban Parrot Populations.

Photo: S Veith

Davis, A., Taylor, C.E. and Major, R.E. (2011). Do fire and rainfall drive spatial and temporal population shifts in parrots? A case study using urban parrot populations. *Landscape and Urban Planning 100*, 295-301

3.1 Abstract

Populations of several species of native parrots have been increasing in many Australian cities since the 1980s, contributing to a shift in the composition of urban avian communities. Anecdotal evidence suggests that some species of parrot may move into the urban landscape during environmental disturbances, such as wild fires or periods of decreased rainfall. This study seeks to determine the extent to which fire and rainfall explain changes in the abundance of parrots in urban Sydney. Multiple regression using the Akaike Information Criterion was used to analyse a 26-year data set, beginning in 1981, to measure the change in abundance of 13 species of parrot in response to wild fire and rainfall. Wild fire, within a radial distance of 100 km, significantly predicted changes in abundance of five species of parrot in urban Sydney. Local and/or inland rainfall significantly predicted changes in abundance of six parrot species in the urban landscape, with decreases in inland rainfall resulting in an increase in abundance in the urban landscape of parrots that traditionally inhabited inland areas.

3.2 Introduction

Urbanisation is one of the most dramatic transformations to shape the natural landscape (Lowry and Lill, 2007), and is considered one of the greatest threats to the conservation of biodiversity (Isaac et al., 2008). While 51 percent of the global population is expected to reside in cities by 2010 (Garden et al., 2006; Isaac et al., 2008), Australia has already surpassed this global average, over 80 percent of the population residing in urban and suburban areas (Isaac et al., 2008). Such a rapid rate of urbanisation has resulted in an abrupt change to the landscape, with continuous tracts of native vegetation transformed into complex spatial mosaics of buildings and bitumen, interspersed with fragmented and discontinuous remnant vegetation, parks and gardens (Catterall, 2004).

Urbanisation results in a profound restructuring of the landscape (Chamberlain et al., 2009) and has been described as catastrophic for some species of birds (Meyer-Gleaves and Jones, 2007), often resulting in the elimination of many indigenous birds from the urban landscape (McKinney, 2002; Shukuroglou and McCarthy, 2006). In Australia, however, there has been a recent increase in abundance of several species of native Australian parrots in suburban areas of Australian cities (Burgin and Saunders, 2007; Lowry and Lill, 2007; Shukuroglou and McCarthy, 2006; Veerman, 1991). In the city of Sydney, New South Wales, prior to 1920, rainbow lorikeets were considered rare (Burgin and Saunders, 2007) however they are now one of the most frequently recorded species in Sydney (Major and Parsons, 2010). During the period between 1981 and 2002, four other species of parrot increased in abundance in urban Sydney (Burgin and Saunders, 2007). Whilst some of these species, such as the sulphur-crested cockatoo, have always been present in the Sydney region, other species such as the long-billed corella and the galah were historically known only from arid areas of inland Australia (Higgins, 1999). There are several factors that may be driving these changes in abundance, one of which is drought.

Drought results in long-term changes to habitat and resources, and Australia regularly experiences drought cycles lasting ten years or more (Hunt, 2009; Ummenhofer et al., 2009). Surface water in the arid zone is normally naturally restricted (Fensham and Fairfax, 2008) and may become locally unavailable during these extended periods of drought, although for highly mobile species such as parrots, available drinking water may not necessarily be a limiting resource, given the widespread distribution of artificial agricultural watering points (Fensham and Fairfax, 2008). Foraging may become increasingly difficult, however, as plant flowering and seeding may be delayed, become dormant throughout the drought or aborted entirely (Ellis and Sedgley, 1992; Law et al., 2000), which may result in a resource-driven movement towards the urban landscape (Saunders, 1980; Smith and Moore, 1992).

Wild fire, which is a frequent occurrence among the sclerophyllous forests and woodlands of the New South Wales coast, is another factor that may account for temporal change in Sydney's parrot community and may result in an increased abundance of local species in the urban landscape immediately following large fires (Recher, 1997). Following a small fire, surrounding vegetation may offer enough food resources so that only local evasive movements by birds are necessary. The effects of large fires (fires that burn in excess of 10 000 ha (Keane et al., 2008)), however, are twofold. There is an immediate effect of the fire itself, where populations of (vertebrate) fauna are often depleted, either as a function of mortality or through dispersal/escape mechanisms (Bradstock, 2008), and a longer term effect that is a function of changed habitat resources, such as food or cover (Whelan, 1995).

It appears that certain species of Australian Psittaciformes may be responding to such environmental events as drought and rainfall, and may be entering the urban landscape in search of shelter or food resources that are limited or unavailable in the surrounding natural vegetation.

This study aims to document changes over a 26 year period in Sydney's parrot community and to determine the extent that drought and wild fire explain annual variation in parrot abundance. The specific aims are to:

1) analyse population dynamics of 13 parrot species in the Sydney region, New South Wales Australia over a 26 year period;

2) determine the extent to which rainfall explains patterns of abundance of urban parrot populations; and

3) determine the extent to which fire explains patterns of abundance of urban parrot populations.

If large wild fires are a driver of changes in parrot abundance in the urban landscape, we predict an increase in abundance of species that have traditionally been present in the Sydney urban landscape (such as the rosellas (*Platycercus* spp.) and Australian king parrot) immediately following large wild fires. If rainfall contributes to changes in abundance in the urban landscape, we predict an increase in the abundance of arid zone species (such as corella species and the galah) in the Sydney urban landscape up to two years following decreases in inland rainfall.

3.3 Materials and Methods

3.3.1 Study Sites

The study site encompassed the Sydney urban region on the east coast of New South Wales, Australia. Sydney extends over an area greater than 12 000 square kilometres and is characterised by a warm, temperate climate. It is an urban island, bounded by the Pacific Ocean to the east and three major national parks to the north, south and west (Fig. 3.1). The area of natural vegetation within these parks surrounding Sydney exceeds 2 700 square kilometres and is predominantly dry sclerophyll woodland or forest, and heath (Keith, 2006). Sydney and its suburbs contain numerous recreational parks and gardens as well as a number of small remnants of native vegetation (shaded in Fig. 3.1), which provide habitat for a range of native bird species (Parsons et al., 2003).

3.3.2 Bird Atlas Data

Bird data were obtained from the "Atlas of New South Wales Wildlife" (NSW National Parks and Wildlife Service), a government database that contains 5808 records of the target species within the study area since 1981. The atlas is limited in that it does not follow a standardised survey technique, but is primarily comprised of incidental sightings. Numbers of birds recorded in the atlas were therefore not consistent, or standardised, for area of search effort, hence only presence/absence information was used. The advantage of this data set, however, is that it contains continuous records from 1980 to the present day, unlike the more systematic Birds Australia Atlas Database (Barrett et al., 2003) that contains records only since 1998. Data were extracted for the years between 1981 and 2007 for ten species of parrot that have traditionally been recorded from Sydney and three species of parrot that have traditionally been associated with the inland (Table 3.1). The ten species of traditional Sydney parrots were the Australian king parrot, crimson rosella, eastern rosella, gang-gang cockatoo (*Callocephalon fimbriatum*), glossy black-cockatoo (*Calyptorhynchus lathami*), musk lorikeet, rainbow lorikeet, scaly-breasted lorikeet, sulphur-crested cockatoo, and yellow-tailed black-cockatoo (*Calyptorhynchus funereus*). The three historically inland parrots were the galah, long-billed corella and the little corella. The little corella and the long-billed corella were pooled into one 'corella' variable as the two species often flock together and are easy to misidentify.

Data for four similarly-sized urban-resident birds, that were not expected to respond to fire and drought, were used as an index of survey effort. The Australian magpie (*Cracticus tibicen*) and the laughing kookaburra (*Dacelo novaeguineae*) are both native carnivorous species, commonly found in both the urban and non-urban landscapes (Higgins, 1999; Slater, 1995). The noisy miner is a native nectarivore that has recently increased in abundance throughout urban landscape (Keast, 1995) and the common myna is an exotic species that is common throughout the urban and rural landscape (Barrett et al., 2003; Martin, 1996). All four reference birds occur throughout the same inland and coastal regions as the 13 selected parrots, are considered sedentary and, except for the laughing kookaburra, are among the top ten most frequently sighted birds within the urban area (Higgins, 1999; Major and Parsons, 2010). The abundance of each species was expressed as the relative percentage of the yearly total of all reported sightings for all 17 species. All records were mapped into a Geographic Information System (ArcMap 9.2) and the report locations were validated to ensure that the majority of records were not collected from only a few locations.

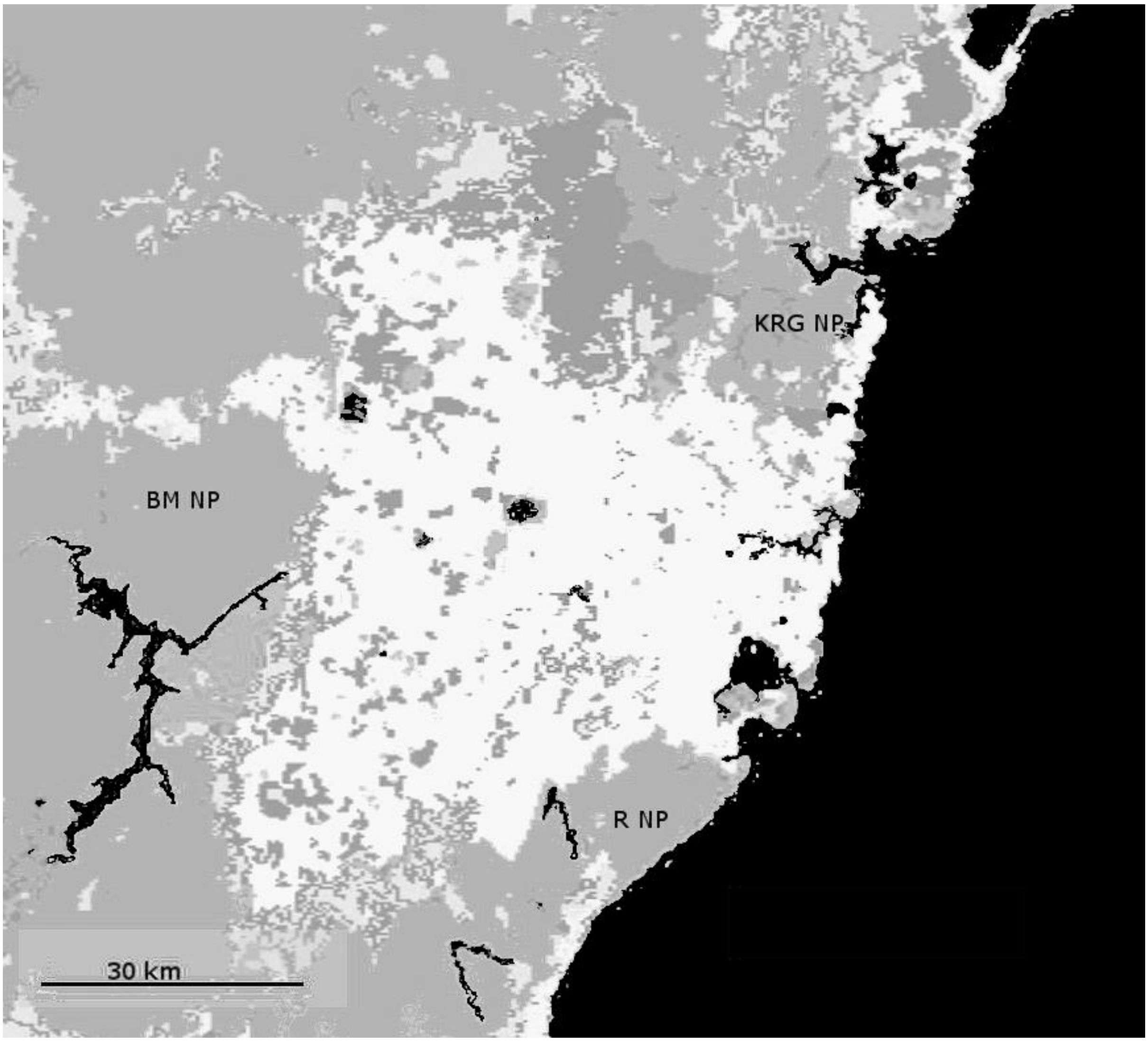

Figure 3.1 Sydney, Australia, showing the Sydney urban landscape (white) and surrounding vegetation (grey) with Royal National Park (Royal NP), Ku-ring-Gai Chase National Park (KRG NP) and the Blue Mountains National Park (BM NP). Water is coloured black.

Table 3.1 Traditional range of each parrot species within the study and the general feeding guild to which each species belongs (Higgins, 1999).

Species	Traditional Association	Main Dietary Classification
Australian king parrot	Coastal/Sydney	Frugivore/Granivore
Crimson rosella	Coastal/Sydney	Granivore
Eastern rosella	Coastal/Sydney	Granivore
Galah	Inland	Granivore
Gang-gang cockatoo	Coastal/Sydney	Granivore
Glossy black-cockatoo	Coastal/Sydney	Granivore
Little corella	Inland	Granivore
Long-billed corella	Inland	Granivore
Musk lorikeet	Coastal/Sydney	Nectarivore
Rainbow lorikeet	Coastal/Sydney	Nectarivore
Scaly-breasted lorikeet	Coastal/Sydney	Nectarivore
Sulphur-crested cockatoo	Coastal/Sydney	Granivore
Yellow-tailed black-cockatoo	Coastal/Sydney	Granivore

3.3.3 Fire Data

Data sets containing information on each wild fire in New South Wales between 1980 and 2007 were obtained from the NSW Department of Environment and Climate Change and mapped into ArcMap 9.2. The number of hectares burnt in each wild fire occurring in national parks within a radial distance of 100 kilometres from the Sydney GPO was calculated. Only wild fires that burnt greater than 100 hectares were included and these were summed to provide the total number of hectares burnt for each year between 1981 and 2007. A variable was also created that lagged data by one year and two years respectively to account for indirect effects of fire.

3.3.4 Rainfall data

Annual rainfall (in mm) records were obtained from the Bureau of Meteorology for both the local coastal area (Observatory Hill: 33.85° S, 151.21 ° E) and inland area (Temora: 34.41 °S, 147.57 °E). Coastal Sydney rainfall was strongly correlated with rainfall in western Sydney and thus the one rainfall record for Sydney sufficed. Drought was defined as any year where rainfall was below the average annual rainfall for the rainfall zone. Lags of one and two years respectively were applied to rainfall data to account for delay in landscape changes and resultant species responses (see Ellis and Sedgley, 1992; Law et al., 2000).

3.3.5 Analysis

All data were tested for homogeneity of variance using Levines test and, where homogeneity was not met, data were log transformed for analysis. Data for any species that still had a small to moderate degree of skewness or kurtosis (values less than 2) were analysed with an alpha equal to 0.01. Data were then analysed using multiple regression.

Curve estimation was undertaken in SPSS 17.0 to determine whether a relationship over time existed for each species. General linear modelling using the *step* function was then undertaken using R (version 2.9.0, 2009) to determine the influence of rainfall and fire on each species. As not all effects were expected to be linear, curvature was assessed for each variable and, when curvature existed, both linear and quadratic terms were entered into the model and the Akaike Information Criterion (AIC) was then employed to select the best models (Manning et al., 2007; Pearce and Ferrier, 2000). ΔAIC values were calculated as the difference between a candidate model's AIC and the lowest AIC value, and AIC weightings (w_i) were calculated for each model to determine the likelihood that each candidate model was the best model (Mazerolle, 2006). ΔAIC values less than 2 indicate substantial support for the model and thus only models with ΔAIC values less than 2 are presented.

3.4 Results

3.4.1 Change over time

Sulphur-crested cockatoo relative abundance increased linearly in the Sydney urban landscape from 1981 to 2007 ($R^2 = .38$, $F_{1,25} = 15.38$, $p = .001$; Fig. 3.2a) whereas relative abundance of the gang-gang cockatoo has declined linearly throughout the same period ($R^2 = .51$, $F_{1,25} = 25.86$, $p < .01$; Fig. 3.2b). A positive quadratic relationship existed for both the combined corella species

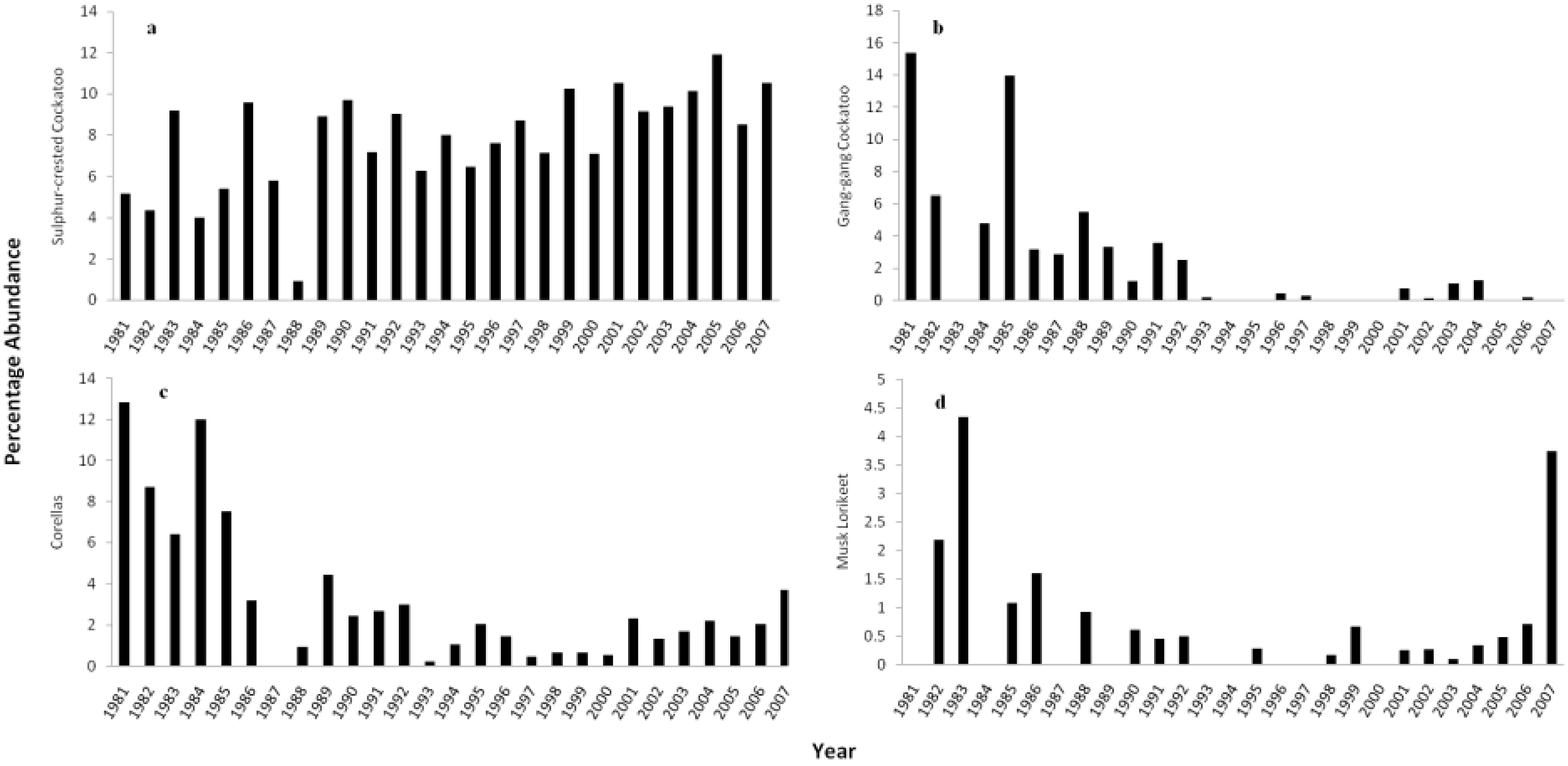

Figure 3.2 Change in the percentage relative abundance in the Sydney region between 1981 and 2007 for the a) sulphur-crested cockatoo sp. b) gang-gang cockatoo c) corella spp. and d) musk lorikeet.

(R^2 = .61, $F_{2,24}$ = 18.99, p < 0.01; Fig. 3.2c) and the musk lorikeet (R^2 = .28, $F_{2,24}$ = 4.58, p < .05; Fig. 3.2d), with both species increasing since 2000. No other species showed significant change in relative abundance through time.

3.4.2 Response to fire and rainfall

Six out of 12 species of parrot showed a relationship with fire and/or rainfall. Models for these species are shown in Table 3.2 along with ΔAIC and w_i values. None of the reference birds showed any significant relationship with fire or rainfall.

The Australian king parrot exhibited a negative response to large wild fires, with the strongest relationship detectable two years following large wild fires (Table 3.2). The galah, rainbow lorikeet and scaly-breasted lorikeet also exhibited a negative response to large wild fires, with the strongest relationship for the galah and rainbow lorikeet detectable in the year immediately following large wild fires and in the second year following large wild fires for the scaly-breasted lorikeet (Table 3.2).

The crimson rosella was the only species that exhibited a positive response to large wild fires, with the strongest relationship detectable in the year immediately following large wild fires. The association continued beyond the first year with significant Sydney rainfall effects detectable both one and two years following increased rainfall (Table 3.2).

The rainbow lorikeet, scaly-breasted lorikeet and sulphur-crested cockatoo exhibited a positive response to local Sydney rainfall (Table 3.2). The rainbow lorikeet exhibited the strongest relationship in the year immediately following local rainfall whereas the scaly-breasted lorikeet

Table 3.2 Candidate best AIC models with ΔAIC < 2.0 and corresponding weights (w_i). A '1' or '2' after the variable denotes a lag of either one or two years. RainSyd indicates annual rainfall in Sydney; RainIn indicates inland annual rainfall. The numerals '0','1' and '2' beside variables indicate the lag period in years. A superscript of '2' denotes the relationship is a quadratic relationship.

Variables in Model	**ΔAIC**	w_i
Australian king parrot		
-Fire2 - RainIn2	0	0.48
-Fire0 - Fire2 - RainIn2	0.43	0.2
Crimson rosella		
Fire1 + RainSyd2^2	0.05	0.23
Fire1 + RainSyd1^2 + RainSyd2^2	1.45	0.12
Galah		
-Fire1 + RainIn2^2	0.47	0.19
Rainbow lorikeet		
-Fire1 + RainSyd1^2 - RainIn1	0	0.3
Scaly-breasted lorikeet		
RainSyd1 - RainSyd2	0	0.3
-Fire2^2 - RainSyd2 + RainSyd1	0.52	0.23
Sulphur-crested cockatoo		
RainSyd2 - RainIn1	0	0.37
RainSyd1 - RainIn2 -RainIn1	1.6	0.17

and sulphur-crested cockatoo displayed the strongest relationship with local Sydney rainfall two years following rainfall (Table 3.2).

The sulphur-crested cockatoo, galah, rainbow lorikeet and the Australian king parrot displayed a negative response to inland rainfall. The relationship was strongest for the rainbow lorikeet and sulphur-crested cockatoo in the year immediately following decreases in inland rainfall whereas the strongest relationship for the Australian king parrot and the galah was apparent two years following decreases in inland rainfall (Table 3.2).

3.5 Discussion

Large wild fires significantly predicted changes in relative abundance of four species of parrot that have traditionally been present in the Sydney urban landscape, with one species increasing in relative abundance in the urban landscape following large wild fires and three other species decreasing. Decreasing inland rainfall resulted in the significant increase in relative abundance of two species of inland parrot in the urban landscape. Three species of parrot also responded to local rainfall, increasing in relative abundance in the urban landscape as local rainfall increased. Three species of parrot increased in relative abundance over time in the urban landscape, independently of wild fires or rainfall, and one species has significantly declined over time.

3.5.1 Change Over Time

The increase in relative abundance of the sulphur-crested cockatoo and the pooled corella species in the Sydney urban landscape is concordant with the results of Burgin and Saunders (1997) who reported a higher encounter probability in 2002 than in 1981, using data from an independent source (Cumberland Bird Observers Club database). Whilst Burgin and Saunders

(1997) demonstrated increases in the abundance of these two species between two discrete years, our study encompasses a continuous 26 year period. Both studies suggest that the sulphur-crested cockatoo and the corellas are increasing in the urban landscape, although it appears from our study that the sulphur-crested cockatoo has increased steadily over the 26 year period, whereas the corellas declined until the year 2000, and have only increased in relative abundance since then.

Similarly, the increase in the musk lorikeet in the Sydney urban landscape is similar to that reported in Melbourne, Australia (Smith and Lill, 2008), where musk lorikeets have increased in abundance since the 1970's. This increase in abundance has been partly attributed to the planting of nectar-producing ornamental street trees (Smith and Lill, 2008), which serve as a prolific and reliable food source.

The decline in the gang-gang cockatoo may be due to loss of habitat throughout the urban landscape. The gang-gang cockatoo is an altitudinal migrant that breeds in the coastal lowlands during winter (Higgins, 1999). Gang-gang cockatoos require large tree hollows to breed and a lack of suitably-sized hollows, due to clearing and wild fire, may be contributing to the decline of this species. However, if loss of large hollows is the cause of decline of gang-gang cockatoos, this is inconsistent with the increase in relative abundance of sulphur-crested cockatoos, which also require large hollows. As would be expected from their opposite temporal trends in relative abundance, post-hoc analysis revealed a significant negative correlation between the sulphur-crested cockatoo and gang-gang cockatoo ($r = -0.578$, $p < 0.01$). It is conceivable that competition for limited nest sites may be contributing to the decline of this species if it is an inferior competitor. Interestingly, we detected no increases in the relative abundance of the rainbow lorikeet or galah, two species which have previously been reported to be increasing in the urban landscape (Burgin and Saunders, 2007). This may be due to the temporal range of the data set used in this study, which encompassed a continuous 26 year period, whereas previous studies have compared abundance between discrete years. This study may include a pattern of fluctuations in populations whereas the previous study may only detect one aspect of that fluctuation.

3.5.2 Response to fire

The crimson rosella was the only species whose post-fire pattern of abundance supported our initial prediction of an increase in the relative abundance of coastal species in the urban landscape following large wild fires. This species nests in hollows of eucalyptus trees surrounded by dense shrubs and trees (Penck, 1992 cited in Higgins, 1999) and, since the urban landscape is generally protected from large wild fires, it may offer nesting and feeding resources that may have become locally limited in surrounding vegetation following wild fires.

Decreases in abundance of birds in the urban landscape following wild fire may be accounted for through mechanisms of either mobility or mortality. Whilst the crimson rosella is a mostly sedentary species (Higgins, 1999), both rainbow lorikeets and galahs are capable of long distance movements (Higgins, 1999; Schodde and Tidemann, 1986; Shukuroglou and McCarthy, 2006). It is possible that they, along with other species of parrots, move between both the urban landscape and the surrounding national parks, frequently or periodically, entering the urban landscape to feed, roost or nest. If these birds are unable to escape the fire front and perish during large wild fires, this may account for the decrease in the abundance of certain species in the urban landscape. Such decreases in parrot abundance following wild fires have been reported, with decreases in abundance of over 70 percent in the area burnt (Loyn, 1999). Three of the fires during the study period burnt more than 374 000 hectares, 173 000 hectares and

360 000 hectares respectively. Whilst emigration to surrounding unburnt areas is possible, given the size of the area burnt, and that multiple fire fronts would have been burning simultaneously, it is more likely that many birds succumbed to either flames or smoke. This appears to have been the case following an extensive wild fire in south eastern Australia, where over 48 percent of avian mortalities recorded post-fire were parrots or other large hollow-nesting birds (Reilly, 1991).

An alternative explanation for decreasing abundance in the urban landscape following wild fires is that birds may make resource-related movements towards the burnt area post fire (Woinarski, 2005). For example the galah, which decreased in relative abundance in this study, is a ground forager (Higgins, 1999) and has been observed feeding in increased numbers in burnt areas (Woinarski, 2005) due to the easier access to seed afforded by the burnt canopy and shrub layer (Espeland et al., 2005; Orians and Milewski, 2007; Woinarski, 2005). The crimson rosella however, whilst still feeding on seeds, consumes a broader diet of fruits and other plant material, and mainly forages in the shrub and tree layer (Penk, 1995; cited in Higgins, 1999) rather than on the ground, and may move to the urban landscape where food resources are more readily available.

3.5.3 Response to rainfall

The response of both the galah and the sulphur-crested cockatoo supported our prediction of an increase in relative abundance of arid zone species in the Sydney urban landscape up to two years following decreases in inland rainfall. The relationship between declining inland rainfall and increasing relative abundance of the galah and the sulphur-crested cockatoo in the urban landscape suggests that these species may move towards the urban landscape in search of more readily available food resources and is concordant with such rainfall related movements reported for Carnaby's cockatoo and corella species in Western Australia (Saunders, 1980; Smith and Moore, 1992). Surprisingly, the rainbow lorikeet and the Australian king parrot exhibited the same relationship even though their foraging is more closely associated with canopy resources in more mesic areas, suggesting that a number of drivers may be correlated with broad scale climatic patterns.

Unlike the studies in Western Australia, the temporal change in the relative abundance of corella species showed no relationship with inland rainfall. The significant increase in relative abundance, particularly since the year 2000 would, however, suggest that factors other than rainfall appear to be driving increases in abundance of corella species.

Whilst decreasing arid rainfall appeared to result in the movement of several arid species into the urban landscape, consistent with our second prediction, changes in local rainfall resulted in fluctuations in the relative abundance of species already present within the urban landscape. The increase in these species of parrot that have traditionally been present in the Sydney urban landscape, up to two years following increases in local rainfall, suggests that feeding resources may be greater in the urban landscape following periods of above average rainfall than in surrounding natural vegetation. Decreases in rainfall can delay or even abort flowering in *Myrtaceous* species (Ellis and Sedgley, 1992; Law et al., 2000) the principle food source of lorikeets (Higgins, 1999) however, the frequent watering and fertilising of parks and gardens (Burgin and Saunders, 2007) as well as prolifically flowering street trees in the urban landscape (Smith and Lill, 2008) provide a buffer against decreases in rainfall. In combination with above average rainfall and elevated temperatures in the urban landscape that often result in prolonged flowering (Lu et al., 2006; Mimet et al., 2009), this results in an increased abundance of food resources that may be greater than that provided in surrounding natural vegetation.

3.5.4 Conclusion

In conclusion, patterns of wild fires surrounding Sydney may explain changes in relative abundance of species of parrot that have traditionally been present in the Sydney urban landscape; however responses to wild fire appear to be complex and are most likely linked to the feeding ecology and mobility of individual species. Decreasing inland rainfall resulted in increases in relative abundance of one inland species within the urban landscape, suggesting that mobile inland birds may make resource-driven movements towards the coastal or urban landscape during drought or following periods of below-average rainfall. Rainfall also appears to drive changes in relative abundance of species of parrot traditionally present in the urban landscape, once again probably as a function of feeding resources, with these birds increasing in relative abundance in the urban landscape following increased periods of local rainfall. The urban landscape appears to not only offer an immediate refuge during wild fires but also offers a more stable environment post fire or during periods of below average rainfall when habitat and food resources may be temporarily limited or unavailable elsewhere.

The utilisation of the urban landscape by native fauna is a consideration that should therefore be taken into account by both urban landscape designers and planners. As the probability of wild fire and drought events is projected to increase with the changing climate, we may see a greater number of species using cities and urban landscapes as a stable resource which provides refuge amongst the dynamic and unpredictable natural environment. As urban areas continue to expand globally, it is important to ensure that future urban planning protocols provide resources for native species through maintenance of existing remnant vegetation and incorporation of park, street side and garden landscaping within newly-developed estates. There is also scope in older cities and their suburbs, particularly those cities in regions prone to wild fire or cities in drier climates, for planners to encourage the proliferation of resources such as native gardens, nesting boxes or suitable water sources in public parks and reserves to ensure available resources for species that use cities as an urban refuge.

Part 2

The Availability and Usage of Nectar Resources by Nectarivorous Parrots within the Urban Landscape.

Photo: A Davis

Chapter 4: Does Nectar Availability Explain Variation in Nectarivore Abundance Between Urban and Natural Environments?

Photo: A Davis

Davis, A., Major, R.E. and Taylor, C.E. Does nectar availability explain variation in nectarivore abundance between urban and natural environments. In prep.

4.1 Abstract

In some Australian and South American cities, nectarivores have become a conspicuous component of the avifaunal community. One mechanism that has been proposed to explain their success is an increased availability of nectar that is provided by suburban gardens and other ornamental plantings. To determine whether the amount of nectar within the suburban landscape is comparable to that of the non-urban landscape we measured floral abundance and nectar concentrations in 24 sites in Sydney, Australia. We also measured the abundance of four species of nectarivores and available nectar energy over a period 18 months within streets, remnant vegetation, forest and heathland, to determine whether nectar availability explains nectarivore abundance. Two species of nectarivorous parrot, the rainbow lorikeet and musk lorikeets were more abundant within the suburban landscape compared to the non-urban landscape and streets provided significantly more nectar than the natural environment during spring and winter. Both rainbow lorikeets and musk lorikeets were associated with flowering of *Eucalyptus* spp and red wattlebirds with the flowering of *Grevillea* and *Callistemon* spp. within streets. Streets appear to provide a constant supply of nectar for large-bodied nectarivores and provide for more efficient foraging, perhaps explaining the success of these species in urban environments.

4.2. Introduction

Avifaunal assemblages within cities of the northern hemisphere are typically comprised of generalist omnivorous and granivorous species, often termed 'urban adaptors' or 'urban exploiters' (Carbo-Ramirez and Zuria, 2011; Evans et al., 2009; Khera et al., 2009; Ortega-Alvarez and MacGregor-Fors, 2009; Smith and Lill, 2008). Such species are capable of subsistence entirely within the urban matrix and may be predisposed to capitalise upon a novel suite of resources within newly created habitat in the urban matrix (Conole and Kirkpatrick, 2011; Parsons et al., 2006; Smith and Lill, 2008). These species are capable of reaching higher densities in urban habitats than within their traditional habitat, and thus cities are often typified by a high abundance of a few generalist species (Blair and Johnson, 2008; Chace and Walsh, 2006; Davis et al., 2012a; French et al., 2005; Major and Parsons, 2010; Ortega-Alvarez and MacGregor-Fors, 2009).

The avifaunal community of cities in the southern hemisphere, however, often differs from cities in the northern hemisphere, due to the dominance of several species of nectarivores (Biamonte et al., 2011; Clergeau et al., 2006; Davis et al., 2012a; Major and Parsons, 2010; McKinney, 2006; Parsons et al., 2006; Smith and Lill, 2008; Young et al., 2007). In cities throughout South America, hummingbirds (Trochilidae) and some species of sunbird (Nectarinidae) are often a conspicuous component of the avifauna, and some species of nectarivores, particularly large-bodied honeyeaters of the family Meliphagidae and Psittacidae, are abundant throughout many Australian cities (Arizmendi et al., 2007; Catterall, 2004; Catterall et al., 2010; Davis et al., 2012a; de Toledo et al., 2012; Major and Parsons, 2010; Young et al., 2007).

Nectarivore abundance has previously been positively associated with the amount of nectar provided by nectar-bearing plants, within both forested areas and the urban landscape (Ashley et al., 2009; Collins and Newland, 1986; Cotton, 2007; Franklin and Noske, 1999; French et al., 2005; Pauw and Louw, 2012; Pyke et al., 1993; Ramsay, 1989; Symes et al., 2008). Within Australia, species of *Eucalyptus* and *Grevillea*, particularly large hybrid *Grevillea* spp. that are popular in garden plantings, are recognised as important nectar providing resources within suburban regions of the urban landscape, particularly as they produce more nectar than some non-natives (Ashley et al., 2009; Catterall et al., 1998; French et al., 2005; Sewell and Catterall, 1998). The composition and diversity of flowering vegetation within the suburban landscape has the potential to result in either a prolonged period of nectar availability or a continuous supply of nectar when nectar within non-urban habitat is scarce (Ashley et al., 2009; Catterall et al., 1998; French et al., 2005; Sewell and Catterall, 1998; Smith and Lill, 2008).

The composition and abundance of nectar-providing plants within suburban landscapes may thus be capable of influencing the density and composition of nectar-feeding birds within suburban landscape compared to the non-urban landscape. The aim of this study is to determine whether nectar availability can explain variations in nectarivore abundance between suburban and natural environments. Specifically, we aimed to

1) determine if the amount of energy available from nectar is higher within streets than in surrounding natural habitats,
2) determine if the association between four species of nectarivorous birds is positively associated with the amount of available energy supplied by nectar within suburban and non-urban habitats, and
3) determine whether the abundance of the most common nectarivorous birds is higher within suburban habitats (streets and patches of remnant vegetation) compared to non-urban habitats (forest and heathland.

4.3 Methods

4.3.1 Study sites

The study was undertaken in the Sydney region on the east coast of Australia (Fig. 4.1), a temperate region with a warm summer (average temperature 24 degrees C), mild winter (average July temperature 12 degrees C) and an average annual rainfall of 1200 mm (Commonwealth Bureau of Meteorology, 2011a, b).

Six 2 ha plots were established in each of four "habitats": streets, small patches of remnant forest (remnants), continuous forest (forest) and (Davis et al., 2012a) continuous heathland (heath). Plots measured 100 m by 200 m in remnants, forest and heath, but in streets they varied between 25 m and 50 m in width, and between 400 m and 800 m in length, depending on the width of the street (Davis et al., 2012; Lowe et al., 2011). The width of street plots was measured (using Google Earth) (Davis et al., 2012a) from the residential boundaries on one side of the street to the residential boundaries on the opposite side, with the length adjusted to produce a plot with an area of 2 ha. Street plots thus included footpaths and roads, but not residential gardens and the portion of any tree or shrub that over-hanged the boundary was included in the assessment of flower density. Each plot was at least 1 km away from any other site to ensure independence of replicates (Davis et al., 2012a; Lowe et al., 2011).

Plots in remnants were all comprised of Sydney Coastal or Sydney Hinterland Dry Sclerophyll or Sydney Forest (Keith, 2006) growing on soils derived from the Hawkesbury sandstone complex (Benson and Howell, 1995; Threlfall et al., 2011) and were typically surrounded by suburban development. Plots in forests sites were comprised of the same vegetation class as that within remnants, and were situated within the Royal National Park to the south of Sydney and Ku-ring-gai Chase National Park in the north of Sydney. Heath plots were situated within the same

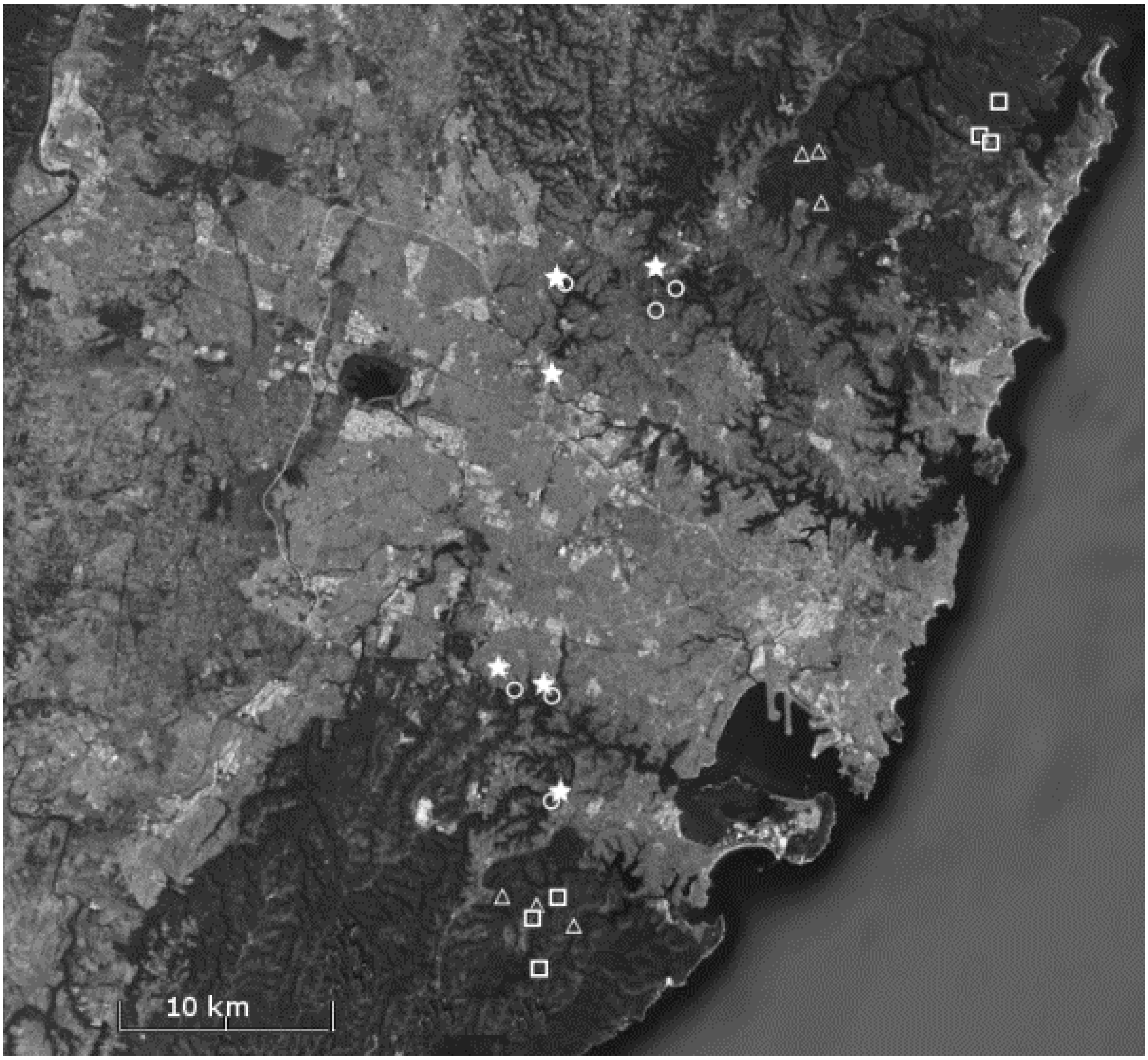

Fig. 4.1 Map of Sydney, Australia showing location of suburban plots within streets (stars) (n = 6), remnant vegetation (circles) (n = 6), forest (triangles) (n = 6) and heathland (squares) (n = 6).

national parks and were comprised of Sydney Coastal Heath (Keith, 2006).

4.3.2 Nectar extraction and calculation of energy content

To determine the available energy content of the standing crop of nectar contained within a flower or inflorescence (here after referred to as 'energy'), we extracted nectar from flowers of the genera *Eucalyptus, Corymbia, Banksia, Melaleuca, Camellia, Callistemon* and *Grevillea* (Table 4.1). These flowering plants comprised the dominant flowering vegetation in the four habitats and were expected to provide the majority of available nectar for consumption by large nectarivorous birds. We did not sample smaller (shrubs less than 1 m in height) native vegetation (e.g. *Philotheca buxifolia*) as it was not recorded as part of the primary diet of the four large study species (Higgins, 1999; Higgins et al., 2001)

To sample flowers from *Eucalyptus, Corymbia* and *Camellia*, we selected three individuals of each species within streets that had flowers accessible from the ground. A branch (or branches) from each of the three individual plants was covered with a white nylon mesh bag that was tied to the branch for a period of 24 hours (French et al., 2005). This ensured the exclusion of nectar-feeding birds, mammals and insects whilst still allowing airflow. Bags were removed before 9am the following day and the branch or stems of the flowers/inflorescences were cut from the tree. Seven flowers from each of the three branches (N = 21) were sampled within 30 minutes of being removed from the tree. Nectar was passively extracted by inserting a 45 μl capillary tube into the flower (Armstrong, 1991). If nectar filled the entire tube, a second capillary tube was used to extract the remaining nectar. The volume of nectar obtained from the flower was then determined. A refractometer was used to determine the amount of dissolved sucrose as a percentage by weight (measured in °Bx) of the nectar (Armstrong, 1991; Law, 1992, 1994).

Table 4.1 Species of plant from which nectar was extracted, the habitat in which the plants were sampled, and the average number of kilojoules that obtained nectar yielded and the number flowers/inflorescences that were sampled (n).

Species	Habitat	Mean Energy (kj/flower)	Mean Concentration (% w/w) of Sugars	n
Banksia serrata	Forest, Heath	6.03 ± 1.76	7.65 ± 2.55	9
Banksia ericifolia	Forest, Heath	10.33 ± 2.54	41 ± 2.03	9
Banksia marginata	Forest, Heath	3.46 ± 1.76	27 ± 4.80	9
Eucalyptus sideroxylon	Street	0.095 ± 0.16	18.86 ± 1.64	21
Corymbia gummifera	Street, Remnant, Forest, Heath	0.037 ± 0.041	18.11 ± 2.92	21
Eucalyptus citriodora	Street, Remnant, Forest, Heath	0.065 ± 0.013	12.45 ± 0.47	21
Melaleuca quinquenervia	Street	0.49 ± 0.075	13.89 ± 3.74	9
Camellia sasanqua	Street	0.07 ± 0.017	15.44 ± 1.056	9
Grevillea whiteana	Street	1.85 ± 0.47	11.22 ± 0.81	9
Callistemon citrinus	Street	0.47 ± 0.14	11.33 ± 1.94	9

Once the sugar content and volume of the nectar from each flower was obtained, the number of kilojoules contained within the nectar from each flower was calculated (Armstrong, 1991; Bolton et al., 1979; Law, 1994). We then calculated the average kilojoules per flower for each species (Armstrong, 1991).

To sample flowers from the larger inflorescences of *Banksia serrata*, *B. ericifolia, B. marginata, Calistemon citrinus, Grevillea whiteana* and *Melaleuca quinquenervia,* we selected three shrubs of each species and bagged nine inflorescences for a period of 24 hours (Law, 1994). *Banksia serrata* flowers were sampled from remnant vegetation and *B. ericifolia* and *B. marginata* were sampled from heath and forest respectively. *Callistemon, Grevillea* and *Melaleuca* flowers were sampled from streets. Inflorescences were centrifuged in a zip-lock bag for 40 seconds (Armstrong and Paton, 1990; Law, 1994). Extracted nectar was then removed from the bag with a Pasteur pipette. Remaining drops of nectar inside the plastic bag were removed with a capillary tube. The number of kilojoules yielded by the nectar from each inflorescence was calculated (Bolton et al., 1979), and a correction factor of 1.4 was applied to account for nectar that remained on the inflorescence due to drag whilst being centrifuged (Armstrong and Paton, 1990; Law, 1994). The average kilojoules per inflorescence for each species was then calculated.

4.3.3 Flowering activity between habitats

To determine the level of flowering activity, and subsequent energy available in each habitat, we surveyed each site monthly for 18 months from October 2010 to April 2012. During each survey, we searched the 2 ha plot and counted the number of flowers or inflorescences per shrub or tree on any species of the genera *Eucalyptus, Corymbia, Angophora, Callistemon, Melaleuca, Banksia*, *Camellia and Grevillea* (excluding smaller flowering *Grevillea* spp. such as *G. sericea* and *G. diffusa*, as small-flowering species did not feature prominently in the diet of large-bodied nectar-feeding birds (Higgins 1999; Higgins et al., 2001)). Plots were systematically searched, starting from one corner of the plot and walking the width of the plot. Once the width of the plot was walked, we moved 10 m down the length of the plot and walked the width of the plot in the opposite direction. This ensured that no obscured flowering plants were missed and allowed us to remain aware of shrubs we had passed to ensure that no flowers were double counted. Where flowers or inflorescences were either too numerous to count or not possible to count from the ground (e.g. trees), we photographed the flowering canopy with an Olympus SP-565UZ camera capable of 20 x optical zoom and then counted the flowers visible from the magnified photo. The number of photos taken of the canopy depended on the size of the canopy and the amount of magnification required to provide definition for individual flowers. Multiple photos were taken from all 'accessible' sides of the tree to ensure all sections of the canopy were photographed. Multiple photographs were aligned to ensure the same section of tree was not included in multiple photographs. When access to all sides of the tree was not available, the number of flowers on the non-accessible side of the tree was estimated by extrapolating from the number of flowers on the accessible side of the tree relative to the proportion of the canopy that was not visible. The number of flowers was determined by increasing the magnification of each photo and manually counting the number of flowers present. Where individual flowers were not clearly visible (for example in a cluster of flowers), the number of open flowers present on a cluster was estimated from the anatomical morphology of each species' floral bud arrangement (Robinson, 2003). Once the total number of flowers within each site was determined, we then used the kilojoule values calculated from the nectar extraction to determine the total number of kilojoules per site available on the day of each monthly count. As it was not logistically feasible to extract nectar from every plant species, some energy values were estimated from the means of closely related species. The average amount of energy from all *Eucalyptus* and *Corymbia* flowers that we sampled was used for any species of *Eucalyptus*, *Corymbia* and *Angophora* that we had not extracted nectar from. The amount of energy obtained for *Callistemon citrinus* (Table 1) was used for both species of *Callistemon* that occurred within streets. Likewise, the amount of energy obtained from *Grevillea whiteana* "Moonlight" cultivar (Table 1) was used for all species of *Grevillea* cultivars. Plant species for which no feeding records had been recorded for any of the four birds species (e.g. *Eucalyptus haemastoma*) was not included in the study (Higgins, 1999; Higgins et al., 2001).

4.3.4 Bird Surveys

To determine the density of rainbow lorikeets, musk lorikeets, red wattlebirds and little wattlebirds (*Anthochaera chrysoptera*) in each habitat, during each monthly survey, we searched each 2 ha plot within streets, remnants, forest and heath for 20 minutes (Barrett et al., 2003; Davis et al., 2012). Plots in remnants, forest and heath were searched by systematically searching the plot (see section 4.3.3) and plots in streets were searched by first walking one side of the street and then walking back up the street on the other side of the road. Birds were counted if they were seen or heard feeding or perching within the site (Davis et al., 2012; White et al., 2005), but not if they were flying overhead. Groups, pairs or individual birds were not recorded again if they appeared in the same specific location (Gibbons et al., 1996). All surveys were carried out in the period an hour after sunrise and before 10am in fine weather with low winds. Given that the four focal species are large (> 50 g), and produce loud conspicuous calls during both flight and feeding that are audible from a distance (Higgins et al., 1999; 2001), we do not believe there to be any detection bias between habitats.

4.3.5 Analysis

To determine if there was a difference in the amount of energy produced per standing crop or the abundance of birds between habitats and seasons, and the amount of nectar produced by different genera of plants, we used Linear Mixed Models in (SPSS v. 17.0). 'Month' was used as the random factor and 'habitat', 'genus' and 'season' as fixed factors. 'Season' comprised the austral calendar seasons and 'genus' comprised the genera *Eucalyptus* (which included species from the genera *Eucalyptus*, *Corymbia* and *Angophora*), *Banksia*, *Callistemon* (which included the genus *Melaleuca*), *Grevillea* and *Camellia*. Main effects and interactions were tested and Bonferroni-adjusted multiple comparisons were used to compare simple effects.

To determine whether the abundance of birds in streets, remnants, forest or heath was associated with the number of kilojoules provided by *Eucalyptus, Callistemon, Banksias*, *Grevillea* and *Camellia*, we used a stepwise regression analysis with the amount of energy provided by each genera as variables and the abundance of each bird as a separate dependent variable. Models for the rainbow lorikeet, musk lorikeet, red wattlebird and little wattlebird in each habitat were tested.

4.4 Results

4.4.1 Variation in nectar energy between habitats

Callistemon, *Grevillea* (hybrid) and *Camellia* were only present in streets. *Banksia* and *Eucalyptus* were present in all habitats. The amount of available energy within each habitat varied (Fig. 4.2), with a significant interaction between habitat and season ($F_{9, 396} = 17.31, p < 0.01$). Streets produced significantly more energy per unit area compared to remnants, forest and heath in spring ($p < 0.05$), significantly more energy than remnants and forest in winter ($p < 0.05$) and significantly more energy compared to remnants in summer and autumn ($p < 0.05$) (Fig.2). Forest produced a significantly greater amount of energy than remnants in summer and autumn ($p < 0.05$) (Fig. 4.2). Heath produced more energy than all habitats during autumn ($p < 0.05$).

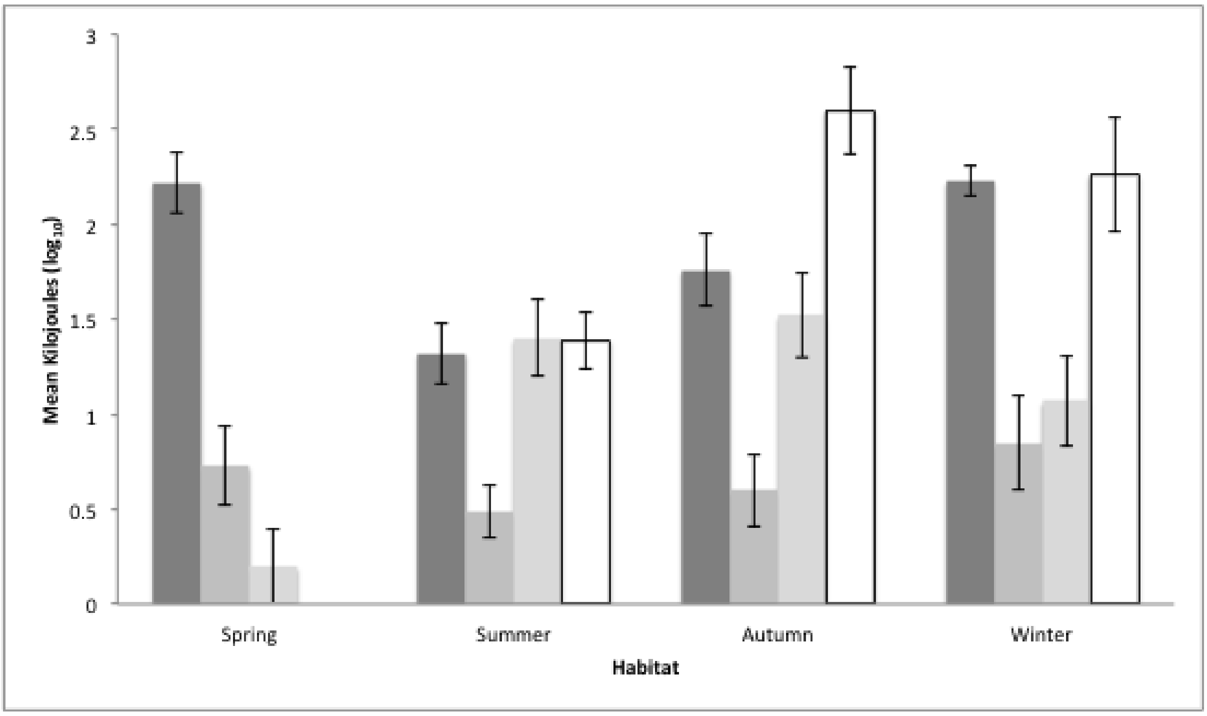

Fig. 4.2 Mean amount of energy provided by standing crop of nectar (kj) per 2 ha in streets (dark grey), remnants (mid-grey), forest (light grey) and heath (open) during each calendar season. Error bars denote standard error.

4.4.2 Variation in nectar energy between genera

There was a significant interaction between the amount of energy provided by plants and habitat ($F_{12, 100} = 12.79, p < 0.01$). Within streets, *Eucalyptus* produced more energy than both *Banksia* and *Camellia* ($p < 0.01$), with *Callistemon* producing more energy than *Grevillea*, *Banksia* and *Camellia* ($p < 0.01$) and *Grevillea* produced more energy than both *Banksia* and *Camellia* ($p < 0.01$) (Fig. 4.3). *Banksia* produced more kilojoules than *Eucalyptus* in both forest and heath ($p < 0.01$) (Fig. 4.3). *Callistemon*, *Grevillea* (hybrid) and *Camellia* were only present in streets.

4.4.3 Nectarivore abundance

There was a significant interaction between habitat and season in the abundance of the rainbow lorikeet ($F_{9, 396} = 2.44, p < 0.05$), musk lorikeet ($F_{9, 396} = 3.80, p < 0.05$) and little wattlebird ($F_{9, 396} = 11.11, p < 0.01$). Streets and remnants contained significantly more rainbow lorikeets than both forest and heath during all seasons ($p < 0.05$). During summer, heath contained a higher abundance of rainbow lorikeets than forest ($p < 0.05$) (Fig. 4.4). Streets contained significantly fewer musk lorikeets compared to remnants during spring, however remnants contained a higher abundance of musk lorikeets compared to both forest and heath across all seasons ($p < 0.05$). Whilst remnants contained fewer little wattlebirds during summer and autumn compared with heath ($p < 0.05$), heath was characterised by a significantly higher abundance of little wattlebirds compared to streets during all seasons ($p < 0.05$), a significantly higher abundance of little wattlebirds compared to remnants during summer and autumn and a significantly higher abundance of little wattlebirds compared to forest during summer, autumn and winter ($p < 0.05$) (Fig. 4.4). Whilst not significant, streets and remnants appeared to have a higher abundance of red wattlebirds compared to forest and heath (Fig. 4.4c). There were no significant differences in abundance of the red wattlebird between seasons.

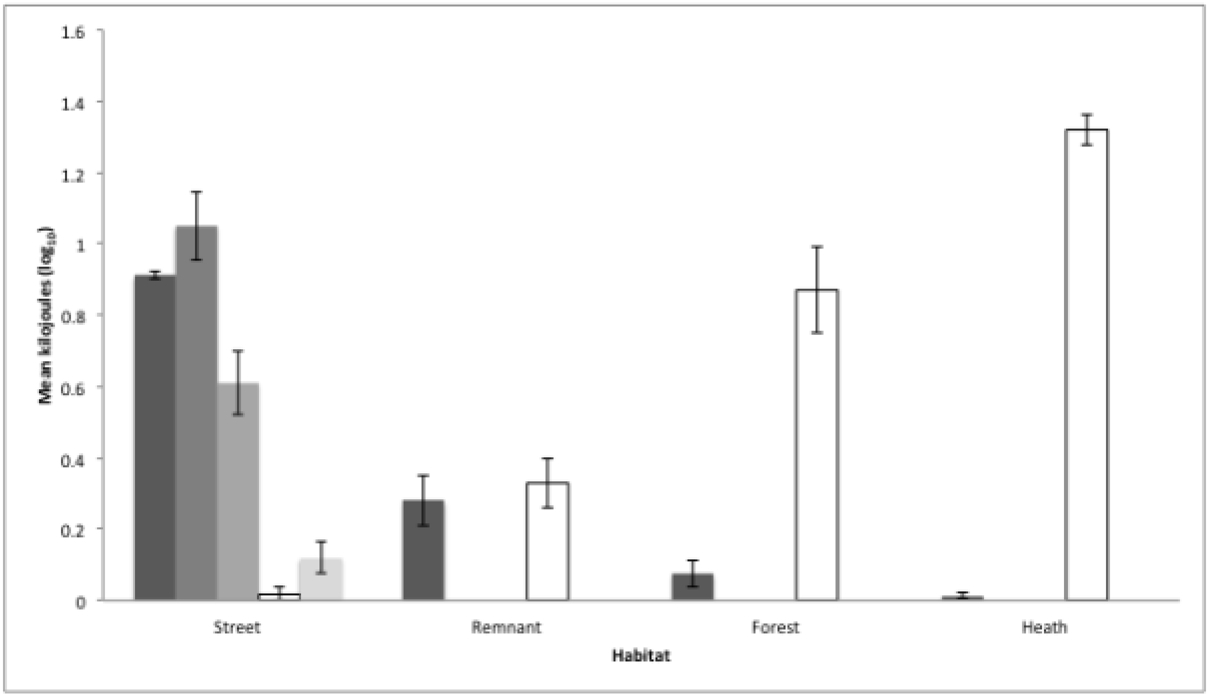

Fig. 4.3 Mean amount of energy provided by standing crop of nectar for *Eucalyptus* (darkest grey), *Callistemon* (dark grey), *Grevillea* (mid-grey), *Banksia* (open) and *Camellia* (light grey) per 2 ha in each of the four habitats. Error bars denote standard error.

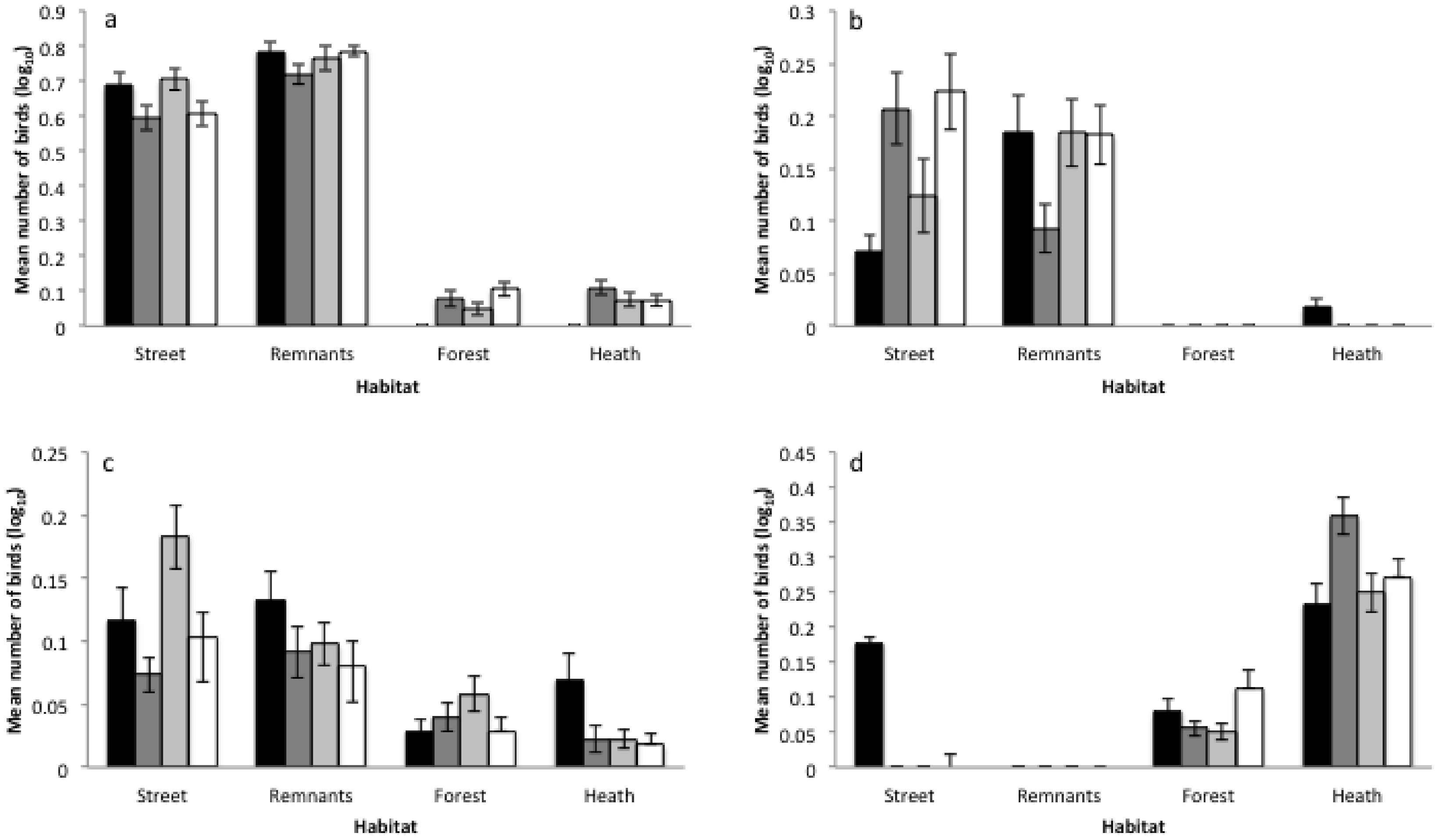

Fig. 4.4 Mean abundance of the a) rainbow lorikeet, b) musk lorikeet, c) red wattlebird and d) little wattlebird during spring (dark grey), summer (mid-grey), autumn (light grey) and winter (open) in streets, remnants, forest and heath. Error bars denote standard error.

4.4.4 Association between nectarivore presence and nectar energy availability.

Heath was the only habitat with a significant and positive association between the total number of birds, pooled for all species, and the total amount of nectar energy, pooled for all plant species ($F_{1, 105} = 37.45, p < 0.01, R^2 = 0.26$). There was no significant difference detected between the total number of birds, pooled for all species, and the total amount of nectar energy, pooled for all plant species, in streets ($F_{1, 105} = 0.71, p > 0.05, R^2 = 0.001$), remnants ($F_{1, 105} = 2.88, p > 0.01, R^2 = 0.026$) or forest ($F_{1, 105} = 0.18, p > 0.05, R^2 < 0.001$).

Significant associations existed between individual species of birds and the total amount of nectar, pooled for all plant species. Within remnants, musk lorikeets were the only species of nectarivore with a significant positive, though weak, association with the total amount of nectar ($F_{1, 107} = 5.49, p < 0.05, R^2 < 0.049$). The strongest associations between total nectar, pooled for all plant species, and nectarivorous birds occurred in heath, with the red wattlebird ($F_{1, 105} = 9.81, p < 0.01, R^2 < 0.084$) and the little wattlebird ($F_{1, 105} = 17.78, p < 0.01, R^2 < 0.14$) positively associated with total nectar availability. The rainbow lorikeet had the strongest association in heath, increasing in abundance as the total available amount of nectar increased ($F_{1, 105} = 24.57, p < 0.01, R^2 < 0.19$).

Significant associations, though weak, also existed between individual species of nectarivore and the amount of available nectar provided by individual species of plants. Within streets, the abundance of rainbow lorikeets ($F_{1, 105} = 8.98, p < 0.01, R^2 = .079$) and musk lorikeets ($F_{1, 105} = 13.06, p < 0.01, R^2 = .10$) were positively associated with the amount of energy provided by *Eucalyptus*. Red wattlebirds were positively associated with the amount of energy provided by both *Grevillia* and *Callistemon* ($F_{1, 105} = 7.80, p < 0.01, R^2 = .096$) in streets. Within remnants, rainbow lorikeets ($F_{1, 105} = 5.57\ p < 0.05, R^2 = .041$) and musk lorikeets

($F_{1,105} = 11.46, p < 0.05, R^2 = .089$) were positively associated with the amount of energy provided by *Eucalyptus*, and red wattlebirds with the amount of energy provided by *Banksia* ($F_{1,105} = 4.50, p < 0.05, R^2 = .032$). Within forest, the rainbow lorikeet was significantly and positively associated with *Eucalyptus* ($F_{1,105} = 6.05, p < 0.05, R^2 = .045$) and within heath, the rainbow lorikeet ($F_{1,105} = 11.40, p < 0.05, R^2 = .089$) and red wattlebird ($F_{1,105} = 31.13, p < 0.01, R^2 = 0.22$) were significantly and positively associated with the amount of energy provided by *Banksia.* The strongest association existed between the little wattlebird and the amount of energy provided by *Banksia* within heath ($F_{1,105} = 95.49, p < 0.01, R^2 = .48$).

4.5 Discussion

4.5.1 Energy availability within habitats.

Vegetation within streets produced, on average, two and a half times the energy per unit area within remnants and one and a half times the energy per unit area within forest. This was due to both a higher number of eucalypt trees that flowered and the presence of non-endemic and ornamental *Callistemon* and *Grevillea* spp. that are absent from remnants, forest and heath. Similar amounts of nectar energy were produced in streets as in heath, due to the high number of *Banksia* sp. in heath. In addition to planted native trees and pre-existing remnant trees within streets, many non-endemic trees (e.g. *Eucalyptus sideroxylon* and *Eucalyptus citriodora*) were planted 40-50 years ago for their flowering aesthetics. As well as having conspicuous colouration and flower size, they may provide large amounts of nectar for prolonged periods, which is fed upon by musk lorikeets (Fitzsimons et al., 2003; Smith and Lill, 2008). As in this study, Smith and Lill (2008) found that musk lorikeets were associated, with the nectar provided by eucalypts. Additionally, these non-endemic trees may flower at different times of the year to endemic trees (Fitzsimons et al., 2003; Smith and Lill, 2008). This diversity in species and subsequent flowering periods means that there may be nectar available to nectarivores from flowering trees within streets when trees within remnants and forest are not in flower. Additionally, the diversity of non-native trees (e.g. *Jacaranda* spp.) and shrubs (e.g. *Camellia sasanqua*) provide additional nectar, resulting in a constant and relatively stable supply of nectar and consequently, energy (French et al., 2005).

4.5.2 Abundance of birds within habitats

Both streets and remnants were characterised by a higher abundance of rainbow lorikeets and musk lorikeets, compared to forest and heath. The lack of variation in abundance between streets and remnants is most likely to be due to differences in habitat utilisation, with rainbow lorikeet and musk lorikeets foraging in nearby streets and roosting, loafing and nesting within remnants. Rainbow lorikeets and musk lorikeets have been documented both roosting and loafing in tall trees up to several kilometres away from foraging sites (Higgins, 1999). Rainbow lorikeets were the most common bird within remnants in Brisbane, Queensland (Catterall et al., 1998) and in Argentina the New Caledonian rainbow lorikeet (*Trichoglossus haematodus deplanchii*) and vinaceous parrot (*Amazona vinacea*) are abundant in areas of human habitation and frequently utilise remnant vegetation (Cockle et al., 2007; Legault et al., 2012). Remnants close to foraging sites may also be particularly important to both rainbow lorikeets and musk lorikeets, given that they are both obligate cavity nesters, which may explain the significantly higher abundance of musk lorikeets in remnants compared to streets in spring.

4.5.3 Association of nectarivores with available energy.

Both the musk lorikeet and the rainbow lorikeet were weakly associated with the amount of energy provided by flowering eucalypts within streets. The required energy intake of captive rainbow lorikeets has been estimated at between 99 - 260 kj per day (Cannon, 1979; Wolf et al., 2007). Wild rainbow lorikeets presumably require a higher number of kilojoules per day, with recorded flights of up to 100 km per day (Schodde and Tidemann, 1986). *Eucalyptus* provided between 0.037 and 0.095 kj per flower (see Table 4.2) which means that, given an average requirement of 180 kj per day, a rainbow lorikeet would need to visit between 1800 and 4800 flowers per day. Rainbow lorikeets have been estimated to visit, on average, 35 *Eucalyptus* flowers per minute (Cannon, 1979), which means they must spend between 50 min to 2.5 hours foraging per day to satisfy energy requirements. Though no significant association was detected between rainbow lorikeets and Callistemon and Grevillea in streets, rainbow lorikeets were observed feeding upon both *Callistemon* and *Grevillea* flowers, which may act as an alternate food source. It has previously been suggested that rainbow lorikeets are capable of tracking nectar at small spatial scales, such as individual trees (Franklin and Noske, 1999) and the weak association for both musk and rainbow lorikeets with nectar energy may support this. The diversity of *Eucalyptus* species within streets provides both a large amount of nectar and an almost continual supply of nectar which, along with additional ornamental shrubs, means that nectarivorous birds may not need to travel far to forage within the urban landscape compared to other habitats, instead foraging at a more local scale.

The little wattlebird was the only species that was more abundant in its natural habitat than in the urban landscape and, in heath, its abundance was positively associated with increases in energy. There was also a small but significant change in the abundance of the rainbow lorikeet within forest and heath, during spring and winter, which also appeared to change as nectar availability changed.

The large volume of available nectar within the planted street may be responsible for the high abundance of many nectarivores within cities throughout the southern hemisphere, particularly the rainbow lorikeet within Australia and several species of hummingbirds in South America.

The consistent availability of nectar within the urban region, compared to forest or heath, appears to support larger populations than those outside the urban landscape (Anderies et al., 2007; Catterall et al., 1998; Shochat et al., 2004). An understanding of urban landscaping and the effects that modification to resource-providing vegetation may have upon urban wildlife is important to consider in future planning. The high amount of available nectar appears to support large-bodied nectarivores, however the comparatively lower amount of energy provided by remnants may have implications for smaller-bodied nectarivores which are not able to penetrate as far into the urban landscape as the rainbow lorikeet or the red wattlebird. The comparatively lower amount of available nectar provided by remnants may have further implications for how vegetation corridors are used by species within the urban landscape. Knowledge of how certain species respond to different types and amount of vegetation may help reduce undesirable changes in community structure, such as dominance by a few species.

Chapter 5: Do Trees Flower Longer in the City? A Comparison of Flowering Eucalyptus Trees in Streets, Remnants and Continuous Forest and their Association with Nectarivorous Birds.

Photo: A Davis

Davis, A., Major, R.E. and Taylor, C.E. Do trees flower longer in the city? A comparison of flowering Eucalyptus trees in streets, remnants and continuous forest and their association with nectarivorous birds. *Landscape and Urban Planning*. In review.

5.1 Abstract

Human dominated environments are often subjected to increased nutrient and moisture regimes which have the potential to influence the flowering phenology of plants. Protracted flowering periods within urban landscapes may result in increased availability of food resources, such as nectar, over extended periods, and this may support a higher abundance of nectarivorous birds within cities. In order to determine whether there is a difference in the productivity and flowering period associated with urbanisation, we compared the numbers of flowers produced and duration of flowering for three species of native tree in streets, remnant vegetation and continuous forest. We also recorded the numbers of nectarivorous parrots present on flowering trees to determine if the presence of nectarivores was associated with flower production. All three species in streets produced more flowers and flowered for longer than those in remnants and natural forest. The number of flowers per tree significantly predicted the presence of nectarivorous parrots. This study demonstrates that the flowering phenology of plants within streets can differ from natural forest, with remnants appearing to be intermediate. This increased flower production and consequent resource availability, within urban landscapes, may be partially responsible for the increasing abundance of nectarivorous parrots within some cities.

5.2 Introduction

Urbanisation results in both the fragmentation of existing vegetation as well as the creation of novel 'green space' habitats comprised of gardens and recreational parks (Jokimäki, 1999; White et al., 2005). Suburban street vegetation is an example of urban green space that is common to cities around the world, comprising sparse or newly established vegetation through to heavily vegetated areas with large mature trees that have either been planted or retained along roadsides (White et al., 2005).

The flowering patterns of vegetation within the urban landscape have gained increasing attention in the last decade, particularly in Europe and North America, due to differences in their phenology, compared with equivalent plant communities outside the urban landscape (Altermatt, 2012; Neil and Wu, 2006; Neil et al., 2010). Indirect effects of urbanisation, such as changed climate, altered hydrology and nutrient enrichment, can result in extended or more frequent periods of flowering (Jochner et al., 2012; Kowarik, 2011; Luo et al., 2007; Parris and Hazell, 2005), and such altered phenological regimes may subsequently affect the availability of food resources for fauna inhabiting the urban matrix (Kowarik, 2011).

There is the potential for phenological regimes within the urban landscape to shift such that food resources from urban vegetation, in the form of nectar and pollen, may be available in both greater quantities and for longer periods of time, as compared to that in vegetation outside the urban landscape. This increased resource availability may support a high density of fauna within cities and particular species may dominate urban faunal communities if they are highly efficient at exploiting such resources (Marzluff, 2001; McIntyre, 2000; Shochat, 2004; Shochat et al., 2006).

Nectarivorous birds are a conspicuous component of Australian cities, with some species having increased in density, over the last 40 years, to the point where they are now present in higher densities in urban regions than in their original natural habitat (Davis et al., 2012a; Hasebe and Franklin, 2004). Nectarivore densities have been closely correlated with flowering patterns of *Eucalyptus* trees and the consequent availability of nectar and pollen (Hasebe and Franklin, 2004; McGoldrick and Mac Nally, 1998). Street trees within Australian cities, both planted and pre-existing prior to development, are often native species and typically of the genera *Eucalyptus* or *Corymbia.* They are frequently a mix of locally endemic (e.g. *Angophora costata*) and non-endemic (e.g. *E. sideroxylon*) trees, the latter which are often specifically planted for their prolific flowering, and in all of which the intensity, frequency and duration of flowering increases as they mature (Nagendra and Gopal, 2010; Smith and Lill, 2008; Tzilkowski et al., 1986; White et al., 2005; Williams et al., 2006). Total amounts of nectar from ornamental urban plantings has been anecdotally hypothesised to explain increases in nectarivore density (McCaffrey and Mannan, 2012) however, to date, few studies have addressed the contribution of nectar from ornamental plantings (see Ashley et al., 2009; Sewell and Catterall, 1998). Additionally, it has been suggested that remnant vegetation, patches of natural vegetation retained within the urban landscape, may form an intermediate between the climate within the urban environment and the climate within the non-urban environment (Carreiro and Tripler, 2005). Flowering patterns of trees within remnant vegetation may differ compared to the flowering patterns of trees within streets.

The aim of this study is to compare the flowering phenology of the same species of tree growing in urban (streets), small patches of remnant vegetation within the urban matrix and "natural" forest locations to determine whether altered production of nectar may account for the elevated population densities of nectarivorous birds in suburban landscapes. To date, no study has compared the productivity of *Eucalyptus* species between urban and non-urban habitats nor has the comparison been made between the urban and non-urban habitat as well as within remnant vegetation for the same species. Specifically we investigate whether 1) flowering intensity and duration of flowering differ between trees in the urban and non-urban landscape, and 2) whether flowering intensity and nectarivore abundance are correlated. Using the same three species of tree growing in urban streets, remnant forest and continuous forest, we expect

1) a greater number of flowers to be produced on trees in streets than in remnants and natural forest,
2) a greater number of flowers to be produced on trees in remnants than in natural forest,
3) the flowering period to be longer in streets than in remnant and natural forest, and
4) the abundance of nectarivorous parrots to be positively associated with the flowering intensity of urban trees.

5.3 Methods

5.3.1 Study site

This study was conducted in the suburbs of Sydney, Australia and in natural forest to the south of the city. Streets (n = 38) were chosen based on the presence of a suitable target tree (see section 5.3.2) and remnant vegetation (n = 17) was selected via Google Earth. Both street and remnant sites were all selected from within suburban Sydney (Fig. 5.1). The suburban region of Sydney was defined by local government divisions and distance from the city central business district, and typically contained 5 or less dwellings ha^{-1} with 5-40% vegetation cover (Davis et al., 2012a; Threlfall et al., 2011). Trees within streets are generally surrounded by mown grass and may also be situated in close proximity to a concrete footpath or bitumen road. Remnants were predominantly comprised of Sydney Coastal or Sydney Hinterland Dry Sclerophyll or Sydney

Forest (Keith, 2006) growing on soils derived from the Hawkesbury sandstone complex, which is typically of low fertility (Benson and Howell, 1995; Threlfall et al., 2011). Natural forest sites (n = 13) (hereafter referred to as 'forest') were located in the same vegetation communities within the Royal National Park, a large continuous forested national park of 15 068 ha to the south of Sydney (Fig. 5.1). All sites occurred on sandstone geology and are located within the same temperate region with a warm summer (average temperature 24 degrees C), cold winter (average July temperature 12 degrees C) and an average annual rainfall of 1200 mm (Commonwealth Bureau of Meteorology, 2011a, b).

5.3.2 Tree Selection and Measurement of Flower Abundance

To determine flower productivity between habitats, individuals of three species of nectar-rich tree, that occur in both urban and natural locations, were monitored. Species from the family Myrtaceae, (*Angophora costata* (Sydney red gum)*, Eucalyptus pilularis* (blackbutt) and *Corymbia gummifera* (red bloodwood)) were chosen for the study and occur naturally in all three habitats. *Angophora costata* grows up to 25 m in height and typically flowers from October to January and is distributed locally within the Sydney region up to the NSW central coast (Brooker, 1998). *Eucalyptus pilularis* grows up to 70 m tall, flowering from December to January and is distributed between the NSW south coast and Queensland (Brooker and Kleinig, 2012; Robinson, 2003). *Corymbia gummifera*, reaches heights up to 30 m and flowers from late January to March and is distributed along the east coast between Victoria and Queensland (Brooker and Kleinig, 2012; Robinson, 2003). Flowers of all three genera are fed upon by native nectarivorous bird species (Higgins, 1999).

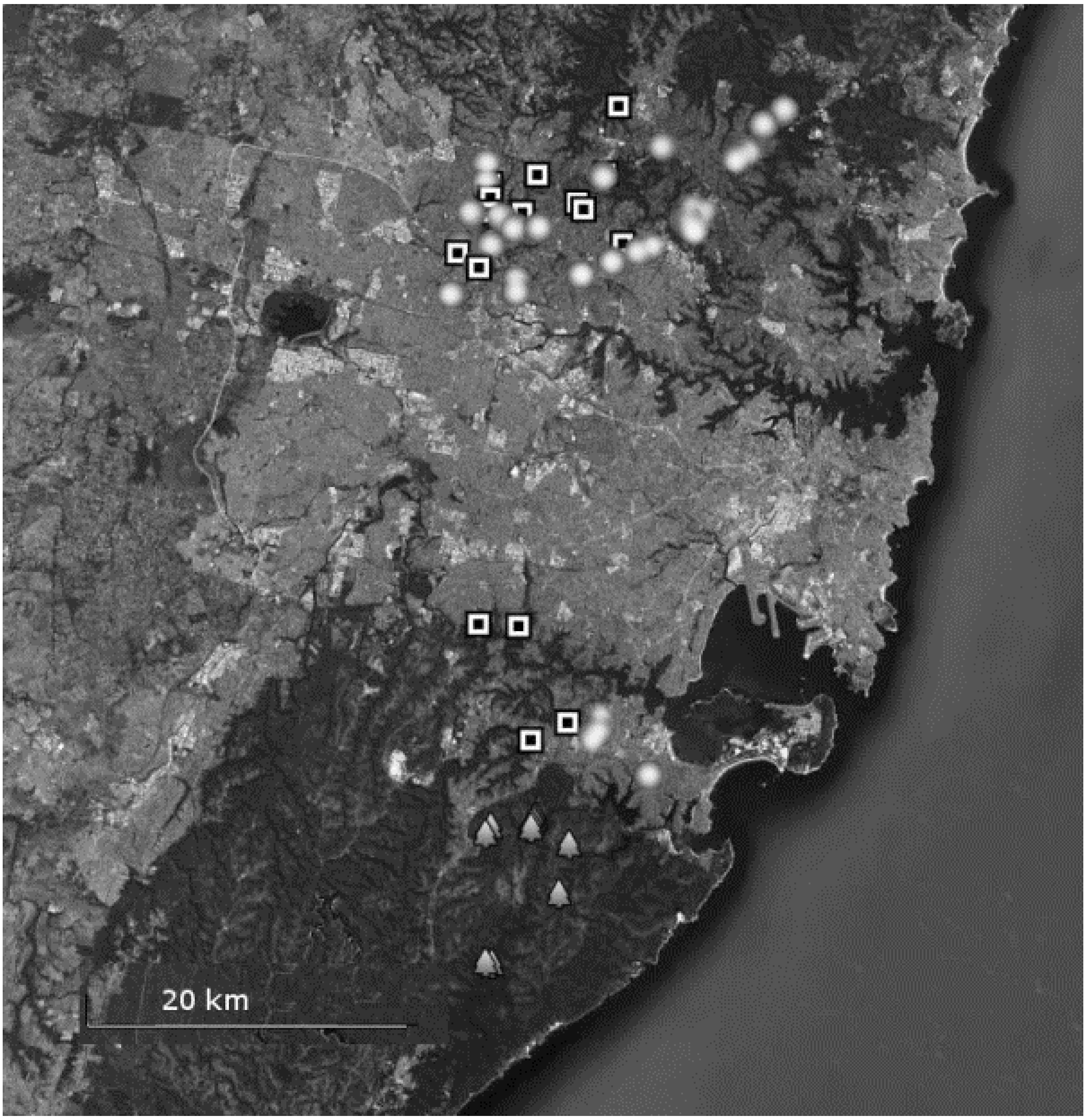

Fig. 5.1 Photograph of Sydney Australia showing the location of focal trees within streets (circles), remnants (squares) and forest (trees) to the south of Sydney (edited from Google Earth).

Twenty trees of each species were randomly selected in each habitat giving a total sample of 180 trees. Multiple trees within remnants and forest sites may have been selected (depending on the size of the site) providing that each tree was at least 500 m apart from the nearest study tree of the same species. In remnants and forest, we located a tree that was one of the three target species. The three closest trees (one of each of the three target species) to this tree were then selected as the study trees. As floral production may be influenced by the size of the tree, the diameter at breast height (DBH) of each tree was measured with a diameter tape. Trees with a DBH of less than 20 cm were discarded and the next closest tree was selected. Each tree was visited monthly and once bud burst was detected on one tree, all individuals of that species in all three habitats were monitored weekly until cessation of flowering on the last flowering tree occurred. The presence of any nectarivorous parrots in the tree during each inspection was recorded throughout the flowering period.

Flowers on each tree were photographed weekly using an Olympus SP-565UZ digital camera capable of 20 x optical zoom. The number of photos taken depended on the size of the canopy and the amount of zoom required to provide definition for individual flowers. Multiple photos were taken from all 'accessible' sides of the tree to ensure all sections of the canopy were photographed. Care was taken to ensure the same section of tree was not included in multiple photographs. When access to all sides of the tree was not available, the number of flowers on the non-accessible side of the tree was estimated by extrapolating from the number of flowers on the accessible side of the tree relative to the proportion of the canopy that was not visible. Photos were adjusted in Microsoft Office Picture Manager (version 12.0) by manipulating the brightness, contrast and mid tones to ensure flowers were clearly visible. The number of flowers was determined by increasing the magnification of each photo and manually counting the number of flowers present. Where individual flowers were not clearly visible (for example in a cluster of flowers), the number of open flowers present on a cluster was estimated from the anatomical morphology of each species' floral bud arrangement (Robinson, 2003). Flowers that were not visible due to occlusion by leaves or branches were not counted. Some occlusion of flowers occurred at all trees, regardless of species or site, and this was not considered to influence the relative abundance of flowers between habitats.

5.3.3 Analysis

5.3.3.1 Flower production

To determine whether there was a relationship between DBH and both floral production and flowering period, the Pearson correlation coefficient was calculated. To determine differences in the total number of flowers produced per tree between habitats, Linear Mixed Models were used with 'habitat' as a fixed factor and 'visit number' (the first visit and each subsequent visit after) as a repeated measure. The number of visits was calculated for each species based on the maximum number of weeks that the species flowered (*A. costata* = 5 weeks, *E. pilularis* = 7 weeks, *C. gummifera* = 6 weeks). Differences between habitats in number of flowers produced per tree were compared using Bonferroni-adjusted pairwise comparisons (mean difference). *Angophora costata* was excluded from this analysis as, although present in all habitats, it only flowered in streets during this study.

Differences in the number of flowers produced per tree between species were determined in streets only, because of the lack of flowering of *A. costata* in the other habitats. Linear Mixed Models were used with 'species' as the fixed factor and 'visit number' as the repeated factor. Pairwise comparisons were made as described above. DBH did not correlate significantly with the number of flowers produced per tree and so was not included as a covariate.

5.3.3.2 Length of Flowering Period

To identify differences in the length of the flowering season between habitats, Linear Mixed Models were used, including only the fixed factor 'habitat', and Bonferroni-adjusted pairwise comparisons (mean difference) were made between habitats. The dependent variable 'length of flowering' was the total number of days that each tree flowered and therefore there was no repeated measure. *Angophora costata* was again excluded from this analysis as it only flowered in streets.

To determine if there were differences between species in the total number of days that each tree flowered within streets, Linear Mixed Models were used with species as the fixed factor, and pairwise comparisons were made between species.

5.3.3.3 Presence of Nectarivores

To determine whether the presence of nectarivorous parrots on each tree was related to the number of available flowers present on the tree, nectarivore data were transformed into presence/absence data and analysed with logistic regression. To check the goodness of fit of the model, we used the Hosmer and Lemeshow test, and to assess model accuracy, we calculated the area under the curve (AUC). An AUC greater than 70 is considered acceptable for model accuracy, greater than 80 is considered excellent and greater than 90 is considered outstanding (Lemeshow and Legall, 1994).

5.4 Results

5.4.1 Flower Production

Flowering was observed in at least some individuals of each of the three species, but it did not occur for all individuals in all habitats (Fig. 5.2). No *Corymbia gummifera* trees within forest flowered during the study period and streets were the only habitat within which *Angophora costata* trees flowered, thus *A. costasta* was not included in the analysis.

Flower production per tree differed significantly between habitats for both *Eucalyptus pilularis* ($F_{2,57} = 25.53$, $p < 0.01$) and *C. gummifera* ($F_{2,57} = 17.77$, $p < 0.01$), with flower production significantly greater for trees in streets than in remnants for both *E. pilularis* ($p < 0.01$) and *C. gummifera* ($\mathrm{p} < 0.01$) (Fig. 5.3). More flowers per tree were produced by *E. pilularis* within streets than by trees within forest ($p < 0.01$) (Fig 5.3). There was no significant difference in the number of flowers produced by *E. pilularis* trees in remnants compared with trees in forest (Fig. 5.3). No significant difference in the number of flowers produced between species was detected ($F_{2,57} = 2.26$, $p > 0.05$). Comparisons between tree species could only be made in streets due to a lack of flowering of some species in remnants and continuous forest.

5.4.2 Flowering Period

The length of the flowering period differed significantly amongst habitats for both *Eucalyptus pilularis* ($F_{2,57} = 28.85$, $p < 0.01$) and *Corymbia gummifera* ($F_{1,59} = 24.73$, $p < 0.01$). Flowering period was significantly longer in streets than in remnants for both *E. pilularis* ($p < 0.05$) and *C. gummifera* ($p < 0.05$) (Fig. 5.4). The flowering period of *E. pilularis* in streets was significantly longer than that of *E. pilularis* in forest ($p < 0.05$) (Fig. 5.4), but the flowering period of *E. pilularis* within forest did not differ from that of *E. pilularis* within remnants (Fig. 5.4).

	June	July	August	September	October	November	December	January	February	March	April	May
A. costata												
Streets					■	■	■					
Remnants												
Forest												
E. pilularis												
Streets					▨	▨	■	■				
Remnants							■	■				
Forest								■				
C. gummifera												
Streets								▨	■	■	▨	
Remnants									■	■		
Forest												

Fig. 5.2 Flowering season of *A. costata, E. pilularis* and *C. gummifera* in streets, remnants and forest. Black represents the main flowering period, where greater than 20% of trees were flowering. Grey represents months in which some flowering (but less than 20% of trees) was observed

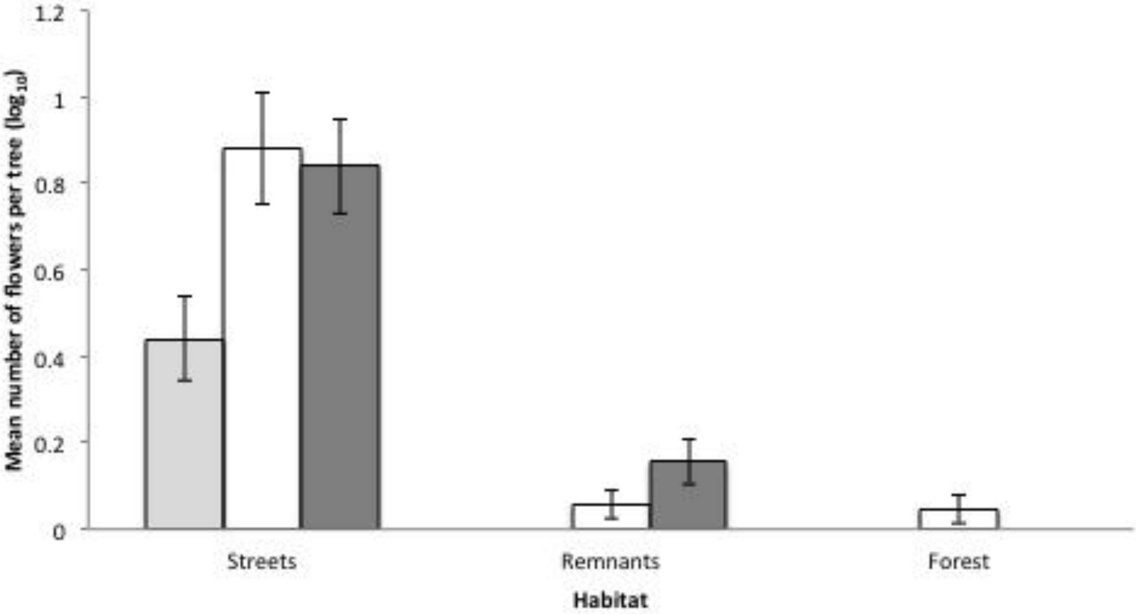

Fig. 5.3 The mean number of flowers per tree ($\log_{10}$ transformed) in streets, remnants and forest. Light grey bars represent *Angophora costata*, open bars represent *Eucalyptus pilularis* and dark grey bars represent *Corymbia gummifera*. Error bars denote standard error.

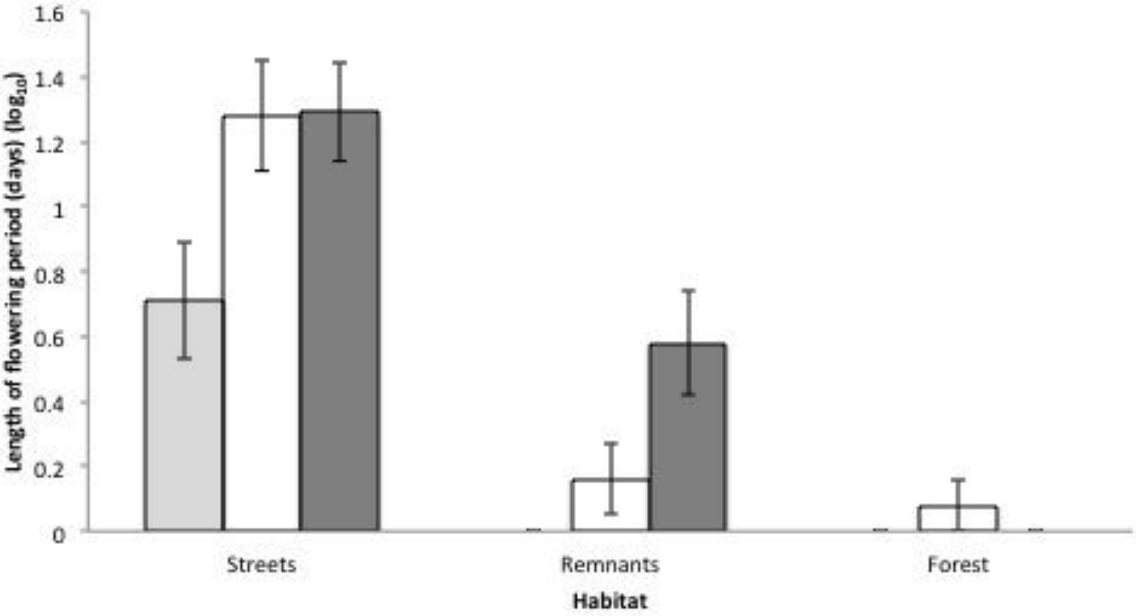

Fig. 5.4 The mean length of flowering period (days) ($\log_{10}$ transformed) for each species of tree in streets, remnants and continuous forest. Light grey bars represent *Angophora costata*, open bars represent *Eucalyptus pilularis* and dark grey bars represent *Corymbia gummifera*. Error bars denote standard errors.

There was a significant difference in the length of the flowering period between species of street tree ($F_{2,57} = 3.93$, $p < 0.05$). *Angophora costata* flowered for significantly fewer days than both *E. pilularis* ($p < 0.05$) and *C. gummifera* ($p < 0.05$) (Fig. 5.4). The number of days that *E. pilularis* and *C. gummifera* flowered did not differ significantly. Comparisons between tree species could, again, only be made in streets due to a lack of flowering of some species in remnants and continuous forest.

5.4.3 Parrot Abundance

Both rainbow lorikeets and musk lorikeets were observed feeding on both flowering *E. pillularis* and *C. gummifera* trees within streets. The number of flowers on each tree significantly predicted the combined presence of the two nectarivorous parrots in streets (-2 log likelihood = 71.56, *d.f.* = 1, $p < 0.01$) explaining 55 % of the variance (Negelkerke $R^2 = 0.55$). The Hosmer and Lemeshow test was non-significant ($\chi^2 = .32$, $p > 0.05$), indicating adequate goodness of fit, and model accuracy was considered outstanding (AUC = 0.96) (Fig. 5.5).

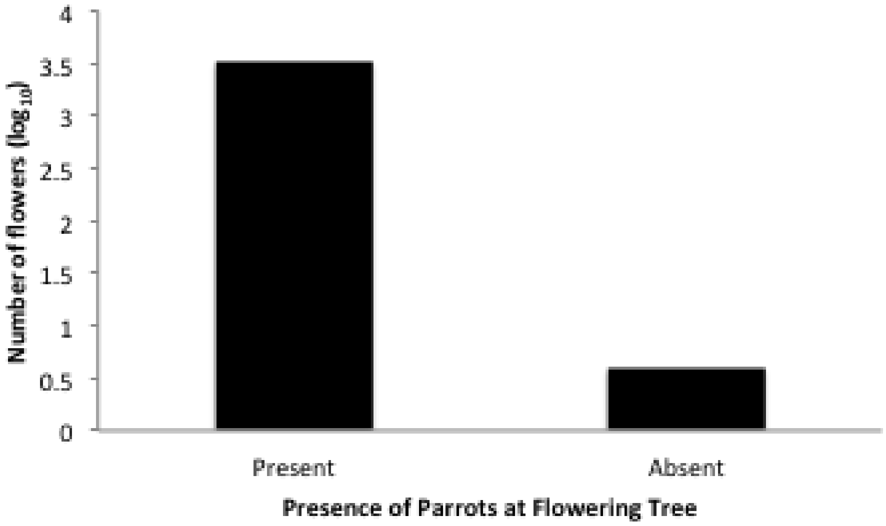

Fig. 5.5 The mean number of flowers that were present on trees within streets where one or more nectarivorous parrots were present compared to when they were absent.

5.5 Discussion

Trees within streets produced significantly more flowers and flowered significantly longer than the same species of tree growing in remnants and continuous forest. Earlier flowering and growing periods in urban habitats have also been reported in the northern hemisphere, with urban plants commencing flowering from a few days to a few weeks earlier than their non-urban conspecifics (Neil and Wu, 2006). Rag weed (*Ambrosia artemisiifolia*) in Baltimore, United States, grew faster, flowered earlier and senesced earlier than the same species in rural sites (Ziska et al., 2003) and flowering of deciduous cherry blossoms (*Prunus yedoensis*) in Japan commenced earlier in the city (Ohashi et al., 2012) than in the surrounding mountain regions.

Flowering within a species was more reliable in urban sites, with *Corymbia gummifera* failing to flower in forest sites, and *Angophora costata* failing to flower in remnant and forest sites in the year of this study. Flowering of eucalypt species is known to be highly variable and irregular, and the onset and end of flowering can vary at different spatial scales, even within the same species (Franklin and Noske, 1999; Law et al., 2000; McGoldrick and Mac Nally, 1998). Differential flowering over large spatial scales has been observed with *C. variegata* trees flowering sporadically in southern New South Wales, whilst a mass flowering of the same species occurred in northern New South Wales within the same year (Law et al., 2000). In contrast, the present study detected variation over small spatial scales within the same region: individuals of the same species did not flower in continuous forest whilst their conspecifics in streets did. There are four possible explanations of these patterns of flowering: the urban heat island effect (UHI), variation in solar/infrared radiation, differential water runoff and increased soil fertility from anthropogenic input.

Elevated urban temperatures, arsing from domestic heating and reduced ambient cooling, are common to almost all cities, with some cities (e.g. Japan) having an UHI effect of as much as 12 degrees Celsius (Altermatt, 2012; Chung et al., 2009; Jochner et al., 2012; Luo et al., 2007; Neil and Wu, 2006). Such an elevation in temperature can effect phenology in urban regions differently to that in non-urban regions (Altermatt, 2012; Jochner et al., 2012; Luo et al., 2007; Parris and Hazell, 2005). Our study differed to other studies (Landsberg, 1981; Neil and Wu, 2006; Ohashi et al., 2012; Ziska et al., 2003) in that, rather than monitoring plants within the city centre, we monitored trees within the suburbs. It is likely that the UHI effect is stronger closer to the city centre and plants have been recorded blooming earlier as distance from the city centre decreases (Ziska et al., 2003). Temperatures within the outer suburbs of cities such as Sydney, however, can still be up to 0.6 °C warmer than the natural environment, due to factors such as multiple central business districts (CBD), industrial complexes and newly developed housing estates with no mature trees (Gero et al., 2006).

Urban remnants are capable of creating their own cooler microclimates, however they are still situated within the UHI and so, whilst they may have cooler temperatures then urban streets, (due to vegetative shading and a lack of bitumen and concrete that reflects heat) they are likely to still have an elevated temperature compared to continuous forest (Bonan, 2002), with soil temperatures in urban remnants up to 5° C warmer than forest (Pouyat et al., 1995). Remnants, in this study, were an 'intermediate' habitat, with trees producing fewer flowers then in streets, yet more flowers than in forest, and may be an 'intermediate' system with a temperature profile between that of urban streets and continuous forest (Carreiro and Tripler, 2005).

The amount of solar/infrared radiation may also influence behaviour of street trees. Solar and infrared radiation on the tree or buds themselves has been shown to be particularly important in the flowering of cherry blossoms in Japan (Ohashi et al., 2012) and coffee plants (*Coffea arabica*) in America (Rodriguez et al., 2011). Trees situated within streets may receive more direct solar/infra red radiation than trees within both remnants and forest, due to a lack of nearby trees or canopy to limit light. This is an alternative explanation to the UHI which may explain both the greater number of flowers and the longer duration of flowering of trees in streets.

Soil moisture and rainfall have been shown to influence flowering, with greater flowering in species of Myrtaceae occurring nine months after rainfall and the abortion of buds following periods of drought (Law et al., 2000; Neil and Wu, 2006). Trees within streets may also experience a higher soil moisture level than trees within both remnants and forests. Domestic watering of lawns and gardens as well as commercial irrigation and runoff, particularly throughout summer, may contribute towards elevated soil moisture levels in streets and parks/ovals (Neil and Wu, 2006).

Increased nutrient loading of soils within the urban landscape may result in greater production of flowers within streets and remnants compared to forest. Anthropogenic input of nutrients from stormwater runoff, sewerage pipes, garden rubbish and soil-fill typically results in elevated levels of phosphorous and other nutrients (Lake and Leishman, 2004; Leishman et al., 2004; Rose, 1997). Within Australian soils, phosphorous is a usually a limiting nutrient, but within the urban landscape, levels of phosphorous within soils near roads and storm water outlets may be up to six times higher than in adjacent uphill sites (Beadle, 1962; Leishman et al., 2004; Specht, 1963). High levels of soil nutrients within urban regions have been associated with the increased growth of *Pittosporum undulatum* (Rose, 1997) and may also contribute to the greater floral productivity of urban trees.

5.5.1 Nectarivore Abundance

Flowering of street trees significantly predicted the presence of nectarivores, supporting previous observations of a strong correlation between flowering intensity and duration and nectarivore density (McGoldrick and Mac Nally, 1998). The abundance of large honeyeaters, such as the red wattlebird, closely mirrored the intensity of flowering of *Banksia menziesii* in Western Australian heathland (Ramsay, 1989), cape sugar birds (*Promerops cafer*) increased in abundance when *Protea* spp. flowered (Fraser and McMahon, 1992) and the abundance of hummingbirds (Trochilidae spp.) has also been positively associated with flowering in urban remnants (Harrison et al., 1997).

Nectarivorous birds may vary in their nectar foraging strategies based on their degree of mobility. More sedentary honeyeaters switch to alternative non-nectar sources of carbohydrate (e.g. lerps) during periods when localised nectar sources are not available (Ashley et al., 2009). Rainbow lorikeets, however, are highly mobile and can spend up to 94% of their time foraging at flowers (Ashley et al., 2009; Hasebe and Franklin, 2004; Higgins, 1999). They appear to track flowering of *Eucalyptus* trees at varying spatial scales, including at the level of the individual tree (Franklin and Noske, 1999). This may allow them to exploit nectar from street trees during both mass flowering events or during patchy asynchronous flowering, despite individual trees being separated both spatially and temporally throughout the city landscape.

Street trees may provide a steady supply of nectar resources for mobile species that are able to track flowering of individual trees. *Eucalyptus* trees and other Australian plants are widely recognised for their high energy floral resources (Wilson and Bennett, 1999) with Australian nectar-bearing plants producing more nectar per floral unit per plant and more sugar per floral unit than non-native plants (French et al., 2005). Many native *Eucalyptus* trees that line streets were planted pre-1970 and have since matured (Williams et al., 2006). Additionally, non-endemic eucalypts are often planted for their flowering aesthetics and produce a greater supply of nectar than locally endemic eucalypts (Smith and Lill, 2008; Williams et al., 2006). Over half the feeding records of musk lorikeets in Melbourne were from non-endemic eucalypt species (Smith and Lill, 2008).

Whilst street trees provide an abundant source of nectar, they contain fewer hollows than trees within remnants. Remnants provide a critical resource in the form of nesting hollows for nectarivorous parrots, and whilst trees within remnants produced more flowers than trees within the non-urban landscape, they produced fewer flowers than trees within streets. Streets and remnants appear to compliment each other in terms of resources provided for nectarivorous parrots.

5.5.2 Conclusion

The greater floral productivity of trees within the urban landscape, compared to those in forest, results in the wider availability of a rich resource for several species of nectarivorous parrot. Given the rich feeding resources that trees in streets provide, they are capable of influencing the structure and composition of avian communities both spatially and temporally (Ashley et al., 2009; Symes et al., 2008). Within the urban landscape, trees within both streets and remnants provide important resources for nectarivorous parrots. As the composition of street trees change, through planting of different species, clearing for development or through natural senescence, the amount of available nectar may change and alter the carrying capacity for nectarivorous parrots. Further knowledge of how the vegetation within streets influences parrots and the interrelationship between vegetation and nectar supply in streets and remnants is needed to understand how parrots utilise the urban landscape.

Part 3

The Distribution and Availability of Tree Hollow Resources in an Urban Environment.

Photo: A Davis

Chapter 6: Housing Shortages in Urban Regions: Aggressive Interactions at Tree Hollows in Forest Remnants.

Photo: A Davis

Davis, A., Major, R.E. and Taylor, C.E. (2013). Housing shortages in urban regions: aggressive interactions at tree hollows in forest remnants. *PLoS ONE 8 (3):* e59332. doi: 10.1371/journal.pone.0059332

6.1 Abstract

Urbanisation typically results in a reduction of hollow-bearing trees and an increase in the density of particular species, potentially resulting in an increased level of competition as cavity-nesting species compete for a limited resource. To improve understanding of hollow usage between urban cavity-nesting species in Australia, particularly parrots, we investigated how the hollow-using assemblage, visitation rate, diversity and number of interactions varied between hollows within urban remnant forest and continuous forest. Motion-activated video cameras were installed, via roped access to the canopy, and hollow usage was monitored at 61 hollows over a two-year period. Tree hollows within urban remnants had a significantly different assemblage of visitors compared to those in continuous forest as well as a higher rate of visitation compared to hollows within continuous forest, with the rainbow lorikeet making significantly more visitations than any other taxa. Hollows within urban remnants were characterised by significantly higher usage rates and significantly more aggressive interactions than hollows within continuous forest, with parrots responsible for almost all interactions. Within urban remnants, high rates of hollow visitation and both interspecific and intraspecific interactions observed at tree hollows suggest the number of available optimal hollows may be limiting. Understanding the usage of urban remnant hollows by wildlife, as well as the role of parrots as a potential flagship for the conservation of tree-hollows, is vital to prevent a decrease in the diversity of urban fauna, particularly as other less competitive species risk being outcompeted by abundant native species.

6.2 Introduction

Urbanisation typically results in heavy fragmentation of the landscape, creating a complex matrix of remnant vegetation, housing and industrial estates surrounded by continuous native forest (Crooks et al., 2004; Møller, et al., 2012). This re-structuring of the landscape can result in changes to the composition and richness of biotic communities and changes in species' distributions (Burgin and Saunders, 2007; Dixon, 2012). Birds, in particular, have been a major focus of urban ecological research (Magle et al., 2012) and it is well documented that some urban bird populations have greater densities than populations in their original habitat (Davis et al., 2012a; Major and Parsons, 2010; Martin et al., 2007). In Australia, avian communities within some urban regions are now comprised of both a higher abundance and a more diverse assemblage of some parrot species compared to that which was historically present (Burgin and Saunders, 2007; Major and Parsons, 2010). Few studies, however, have focused on the impact of urbanisation on birds with specific nesting requirements, such as cavity-nesting species.

As parrots are cavity-nesters, tree hollows may become a critical resource that may strongly influence the ability of some species to sustain urban populations. Not all cavities are suitable for some species to utilise (Cockle et al., 2010) and when these cavity types are limited, intense interspecific competition may occur as different species compete for the same type of resource (Heinsohn et al., 2003; Murphy et al., 2003; Salinas-Melgoza et al., 2009; Waltman and Beissinger, 1992). High levels of aggression have been observed at tree hollows amongst conspecifics and interspecifics (Beissinger and Osborne, 1982; Heinsohn et al., 2003; Krebs, 1998; Renton, 2004). Guarding of tree hollows and other aggressive interactions, including the killing of interspecific chicks, has been observed both at the hollow and within buffer zones established around the hollow-bearing tree (Heinsohn et al., 2003; Krebs, 1998; Renton, 2004).

Remnant vegetation within urban landscapes has been shown to contain half the density of hollow bearing trees as continuous forest. The continued loss of hollow-bearing trees due to land clearing, senescence, and suppression of abiotic processes (such as wild fire) that promote natural hollow development, may lead to a potential shortage of hollows in urban landscapes, particularly in areas where hollow development is slow (Harper et al., 2005a; Manning and Lindenmayer, 2009). Unlike in Europe, and North and South America, where primary hollow development frequently occurs through active excavation by woodpeckers, hollow development in Australia is a secondary process and dependent on insect damage and/or fungal decay following damage to the tree (Aitken and Martin, 2007; Harper et al., 2005b; Koch et al., 2008b; Saunders, 1979; Smith, 2006; Strubbe and Matthysen, 2007). Consequently, hollow creation is slow, and in urban environments may be further limited by the removal of decaying tree limbs in the interests of public safety (Harper et al., 2005a; Ranius et al., 2009; Terho and Hallaksela, 2008) and a reduction in fire frequency (Collins et al., 2012; Gill and Williams, 1996; Inions et al., 1989). Thus the loss of critical resources (hollows) for breeding has the potential to strongly influence the abundance of cavity-nesting species in urban areas.

Despite the theoretical importance of hollow loss in urban areas (Burgin and Saunders, 2007; van der Ree and McCarthy, 2005) there has been no study to date that has investigated the ecological impact on fauna. As a result, the link between urbanisation processes and changes in faunal community structure is not well understood. We used motion-triggered cameras during the breeding season to investigate hollow usage in urban remnants compared with that in undisturbed forest. We were particularly interested in differences in the assemblage of species using hollows, differences in visitation frequency and differences in the level of interference competition.

We predicted that

1) visitation rates at hollows within suburban forest remnants will be higher than at hollows within undisturbed forest,
2) a greater diversity of parrots will visit individual hollows within suburban forest remnants than hollows within undisturbed forest and
3) there will be a greater level of interference interactions at hollows within suburban forest remnants than at hollows within undisturbed forest.

6.3 Materials and Methods

6.3.1 Study Sites

The study area encompassed the Sydney urbanised landscape on the east coast of New South Wales, Australia (Fig. 6.1a), bounded by the Pacific Ocean to the east and three major national parks to the north, south and west. It extends over an area greater than 12 000 square kilometres and is characterised by a warm, temperate climate.

Study sites in suburban remnant forest vegetation (hereafter referred to as 'remnants') (Fig. 6.1d, 6.1e) were selected from the suburban region of Sydney (Davis et al., 2012a). Candidate remnants were initially selected via satellite imagery and were required to meet the following criteria: 1) have an area greater than 2 ha (mean = 87.9 ha, se = ± 29.74, min = 2.78, max = 475), 2) be at least 0.5 km apart from each other (mean = 1.32 km, se = ± 0.26, min = 0.26, max = 4.83) and 3) be surrounded by housing. A sample of 22 remnants was randomly selected from the 44 that satisfied these criteria. Remnants differed in distance to undisturbed forest (mean = 20.77 km, se = ± 2.60, min = 5.21, max = 39.68) and southern undisturbed forest (mean = 26.89 km, se = ± 2.7, min = 6.22, max = 41.19). Sites in undisturbed forest (hereafter referred to as 'forest' (Fig. 6.1b, 6.1c) were selected from within Ku-ring-gai Chase National Park (13 500 ha) and Royal National Park (15 068 ha) to the north and south of

Sydney respectively. They were chosen because they 1) were situated at similar distances from the coast as the remnant sites, 2) shared similar soil type and geology as the remnant sites, and 3) predominantly comprised Sydney Coastal or Sydney Hinterland Dry Sclerophyll or Sydney Forest (Keith, 2006).

6.3.2 Tree selection and camera installation

Hollow-bearing trees were selected from the genera *Angophora*, *Eucalyptus* and *Corymbia*, which comprise both the dominant canopy vegetation, and the main species of hollow-forming trees in the Sydney region. For a tree to be eligible for inclusion in the study, it had to meet five criteria. The tree must have contained a hollow visible from the ground that 1) was at least 3 m above the ground, 2) was in a part of the tree that was safe to access with climbing ropes, 3) was in a position where a camera could be fixed to view the hollow (see below for details), 4) had a minimum opening diameter of 3 cm and a minimum depth of 15 cm and 5) showed no signs of current occupation (presence of eggs, feathers or fur). These criteria for opening height, opening diameter and hollow depth were chosen based on minimum criteria that parrots have been observed to utilise (Goldingay, 2009; Higgins, 1999), and occupied hollows were avoided to ensure that we were not distracted by parental activity that might bias our otherwise random selection. The first hollow-bearing tree at each site, that met these criteria, was selected and hollows were accessed using "Single Rope Technique", by which a slingshot was used to launch a temporary climbing rope into the tree that could then be ascended using climbing equipment. If, upon inspection, the hollow did not meet minimum width and depth criteria, the next tree that met these criteria was used. Thirty-two hollow-bearing trees from 22 remnants and 29 hollow-bearing trees in forest were selected. In some large remnants, several trees were selected, providing they were at least 0.5km apart. Eighteen hollows were monitored for six months throughout June to November in 2009 and another sample of 43 hollows was monitored during

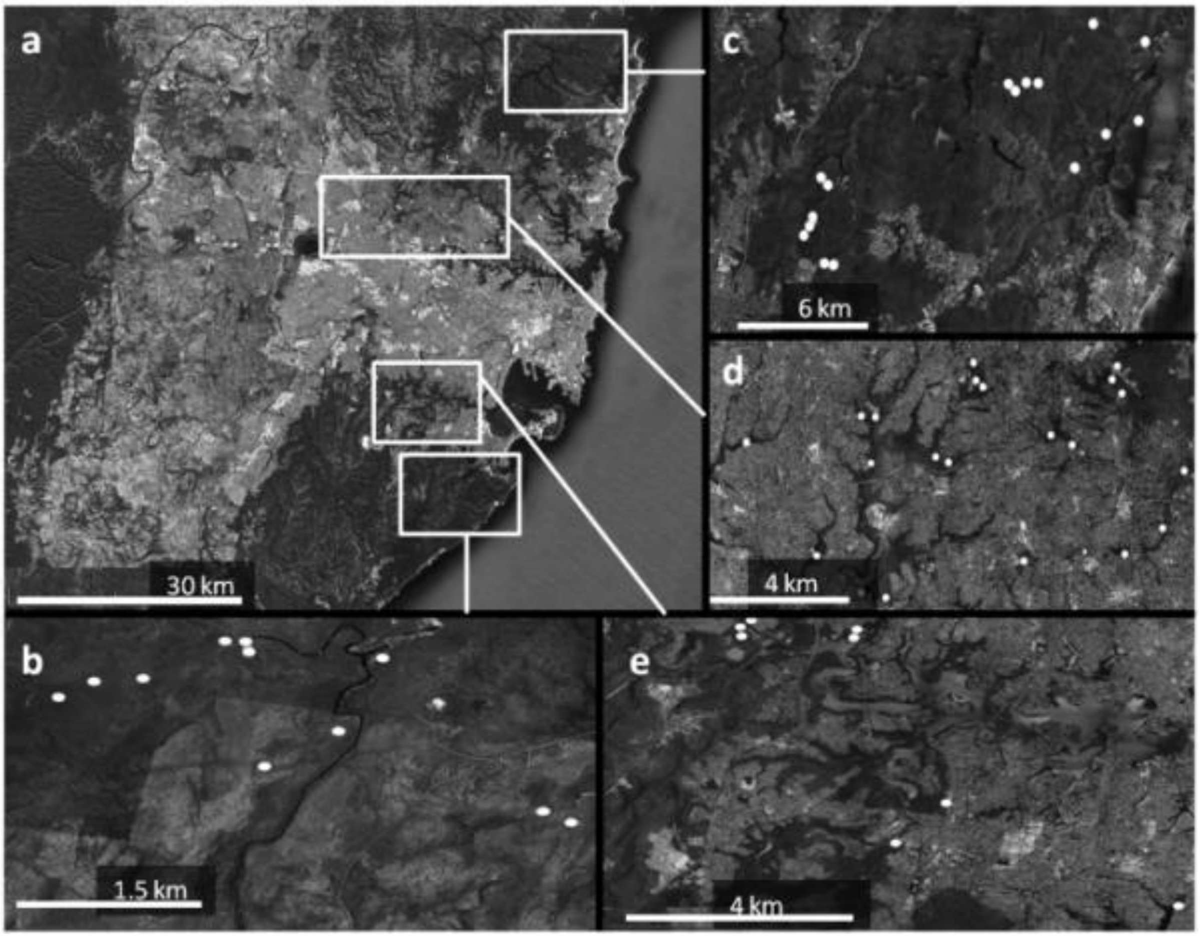

Fig. 6.1 a) Map of Sydney, Australia with the surrounding continuous forest National Parks to the north (Kur-ring-gai Chase National Park), south (Royal National Park) and west (Blue Mountains National Park). b) Camera locations within southern continuous forest. c) Camera locations in northern continuous forest. d) Camera locations in the northern half of Sydney. e) Camera locations in the southern half of Sydney. All images modified from Google Earth.

the same months in 2010. This period included the breeding season of all local parrots (excluding the yellow-tailed black-cockatoo) during 2009 and 2010 (Higgins, 1999). Data from the two years were pooled for analysis.

Once a tree-hollow had been selected, a single surveillance camera (Faunatech Scout Guard SG550V) was installed nearby. The camera was strapped to a branch or trunk that was either in front of, above, or to the side of the hollow, with the constraint that the camera could not impede access to the hollow. Cameras were positioned between 1 and 5 m from the entrance to the hollow and positioning of the camera depended upon tree and hollow morphology. Cameras were motion-triggered using passive infrared sensors with a 1 second shutter response time and a trigger range of up to 10 m. Twenty seconds of video footage were recorded each time the camera was triggered, during either day or night. An infrared LED flash was used at night so that no visible flash was produced. Two-gigabyte SD memory cards were used and cameras were inspected every three weeks to download data and replace batteries.

Each video was viewed and the species that triggered the camera, along with the time and date, were recorded. Footage arising from false triggers by wind-blown leaves was discarded. The cameras had a built-in delay of 2 seconds between subsequent video records, with the consequence that if an animal paused in front of a hollow for an extended period before entering, the moment of entry was not always recorded. Accordingly, all species that were recorded on camera in front of a hollow, in addition to species that were recorded actually entering or exiting the hollow, were included in subsequent analyses as hollow users. A control study, with cameras trained on hollows in hollow-bearing trees, as well as the branch/trunk of the nearest non-hollow-bearing tree of the same species and similar size, confirmed that negligible records of visits were made away from hollows (5.00 ± 2.20 SE independent visits at hollow-bearing trees and 0.85 ± 0.41 SE independent visits at non-hollow-bearing trees, $t_{(12)} = 2.75, p < 0.05$).

6.3.3 Hollow measurements.

Hollow type, opening diameter, opening height and depth of each hollow to be monitored were measured by climbing the tree. Types of hollows were classified as 'trunk', 'pipe' (a short section of hollowed residual branch that connects to the main trunk (Gibbons and Lindenmayer, 2002) or 'branch' (Gibbons et al., 2002) (Table 6.1). DBH, tree height and hollow height (height from the ground to the cavity entrance) were also recorded (Table 6.1). DBH was measured with a diameter tape and tree height and hollow height were measured with a vertex laser. Differences in hollow characteristics between remnants and continuous forest were determined by using independent t-tests. All variables met the assumption of normality as determined by Kolmogorov-Smirnov tests ($p > 0.05$).

6.4.4 Community structure of the hollow-using assemblage.

Species utilising each tree hollow were identified and differences in the structure of the hollow-using assemblage between remnants and forest were analysed with multidimensional scaling using the PRIMER (version 5.2) statistical package (Clarke, 1993). For community structure analyses, presence/absence data were used in order to eliminate the influence of multiple visits by the same individual. If a species was recorded once throughout the entire recording period for a particular hollow, it was recorded as present. The percentage contribution of each species to the differences in community structure of visitors, between hollows in remnants and forest, were then determined using the SIMPER routine in PRIMER and species evenness was displayed

Table 6.1 Characteristics of monitored hollows and trees that contained the hollow.

Hollow Characteristic	**Remnant (n = 32)**	**Forest (n = 29)**
Hollow entrance length (cm)	19.75 ± 2.24	19.07 ± 2.45
Hollow entrance width (cm)	15.58 ± 1.76	15.57 ± 1.85
Hollow depth (cm)	87.09 ± 12.67	56.77 ± 8.69
Tree height (m)	21.57 ± 1.47	17.04 ± 1.39
Hollow height from ground (m)	10.80 ± 0.75	9.37 ± 0.81
Hollow type (number present)		
pipe	11	14
trunk	17	10
branch	4	5

with a rank abundance graph. The multivariate dispersion (variation among assemblages within each habitat, measured by the deviations from centroid) between remnants and forest was compared using the PERMDISP function in PRIMER (version 6.1.6).

6.4.5 Species visitation, diversity and nest occupancy.

The automatically-triggered cameras frequently recorded several segments of footage from the same visit or multiple visits on a single day from the same species. To remove this source of bias we analysed "independent visits", which we defined as a single visit per species per day that did not include the 'owner' of the hollow. Ownership of a hollow was assigned to a species if that species was responsible for in excess of 50% of the total number of visitations made by all species to the hollow. The total number of independent visits by each species was then divided by the total number of days that the camera was recording, to generate an index of visitation, which corrected for differences in recording time between cameras. Most species were recorded infrequently, and so for the purpose of statistical analysis the records of some species were pooled into groups. Thus the crimson rosella, Australian king parrot, eastern rosella, musk lorikeet, scaly-breasted lorikeet and yellow-tailed black-cockatoo were combined into a single 'Other Parrot' variable. (Scientific names of all species throughout the manuscript are given in Table 6.2) The common brushtail possum, lace monitor, common ringtail possum, eastern pygmy possum, sugar glider, squirrel glider, feathertail glider, white-throated treecreeper, laughing kookaburra, grey shrike-thrush, Australian wood duck, southern boobook and powerful owl were also pooled into a single 'Other Fauna' variable for statistical analysis. The rainbow lorikeet and sulphur-crested cockatoo were recorded frequently enough to be analysed as separate variables. The rainbow lorikeet, sulphur-crested cockatoo, 'Other Parrots' and 'Other Fauna' variables were transformed with either a log or square root transformation. Assumptions

Table 6.2 The number of independent visitations of taxa recorded at hollows in both remnants and continuous forest and whether or not they are known to use hollows.

SPECIES	CLASS	HOLLOW USAGE	INDEPENDENT VISITATIONS REMNANTS	INDEPENDENT VISITATIONS FOREST	AVERAGE BODY LENGTH (CM)
Pied butcherbird (*Cracticus nigrogularis)*	Aves	No	13	5	35
Sulphur-crested cockatoo (*Cacatua galerita)*	Aves	Yes (Barnard, 1914)	145	200	48
Rainbow lorikeet (*Trichoglossus haematodus)*	Aves	Yes (Lamont, 1997)	522	49	30
Crimson rosella (*Platycercus elegans*)	Aves	Yes (Hyem, 1936)	31	7	34
Australian raven (*Corvus coronoides*)	Aves	No	1	0	52
White-throated treecreeper (*Cormobates leucophaeus*)	Aves	Yes (Higgins et al., 2001)	2	2	15
White-browed wood swallow (*Artamus superciliosus*)	Aves	Yes (Lasouef, 1903)	1	0	20
Australian king parrot (*Alisterus scapularis*)	Aves	Yes (Favaloro, 1931)	14	3	42
Galah (*Eolophus roseicapilla*)	Aves	Yes (Higgins, 1999)	40	0	36
Laughing kookaburra (*Dacelo novaeguineae*)	Aves	Yes (Hindwood, 1959)	25	0	42
Noisy miner (*Manorina melanocephala*)	Aves	No	32	0	26
Eastern rosella (*Platycercus eximius*)	Aves	Yes (Higgins, 1999)	17	0	30
Powerful owl (*Ninox strenua*)	Aves	Yes (Gibbons, 1989)	4	2	55
Southern boobook (*Ninox novaeseelandiae*)	Aves	Yes (Bryant, 1941)	0	1	29
Grey shrike-thrush (*Colluricincla harmonica*)	Aves	Yes (Higgins and Peter, 2002)	0	7	24
Musk lorikeet (*Glossopsitta concinna*)	Aves	Yes (Higgins, 1999)	4	0	22
Australian wood duck (*Chenonetta jubata*)	Aves	Yes (Frith, 1982)	16	9	47
Yellow-tufted honeyeater (*Lichenostomus melanops*)	Aves	No	0	2	11
Scaly-breasted lorikeet (*Trichoglossus chlorolepidotus*)	Aves	Yes (Higgins, 1999)	1	0	23

Yellow-tailed black-cockatoo (*Calyptorhynchus funereus*)	Aves	Yes (Higgins, 1999)	0	1	60
European honey bee (*Apis mellifera*)	Insecta	Yes (Oldroyd et al., 1994)	N/A	N/A	1.6
Eastern pygmy possum (*Cercartetus nanus*)	Mammalia	Yes (Jones and Parish, 2006)	0	29	90
Common brushtail possum (*Trichosurus vulpecula)*	Mammalia	Yes (Jones and Parish, 2006)	195	11	450
Common ringtail possum (*Pseudocheirus peregrinus*)	Mammalia	Yes (Jones and Parish, 2006)	11	13	325
Sugar glider (*Petaurus breviceps*)	Mammalia	Yes (Jones and Parish, 2006)	5	12	185
Squirrel glider (*Petaurus norfolcensis*)	Mammalia	Yes (Jones and Parish, 2006)	0	6	205
Feathertail glider (*Acrobates pygmaeus*)	Mammalia	Yes (Jones and Parish, 2006)	0	27	73
Lace monitor (*Varanus varius)*	Reptilia	Yes (Russell et al., 2003)	0	21	55
Skink (*Scincidae*)	Reptilia	Yes (Munks et al., 2007)	8	8	VARIES WITH SPECIES

of normality were checked by assessing skewness and kurtosis values (Tabachnick and Fidell, 2007).

Differences in visitation rate between hollows in remnants and forests, and between the four taxon variables, were analysed using a two-factor ANOVA. As significant interactions existed, post-hoc Scheffé controlled contrasts were then used to further explore differences between habitat and fauna.

Species diversity at each hollow was calculated with the Shannon Wiener Diversity Index using the number of independent visits. The difference in mean species diversity between remnant and forest hollows was then tested using a t-test.

During climbed inspections, hollows within both remnants and forest that had either eggs or chicks present were deemed to be occupied nests and the identity of the parents was inferred both from the species of chick and video footage at the nest entrance. It was not possible to determine if all nests contained eggs or chicks, as some hollows were too deep to observe the cavity floor.

6.4.6 Species interactions at hollows

At some hollows interactions both between species, and within species, were recorded in the video footage. Both interspecific and intraspecific interactions were divided by the number of recording days for each hollow and were compared between remnants and forests using a t-test. These data did not meet the assumption of normality as determined by the Kolmogorov-Smirnov test ($p > 0.05$), however skewness values (1.54) and kurtosis values (1.14) were deemed acceptable and the t-test was run with alpha adjusted to 0.01 (Tabachnick and Fidell, 2007).The number of intraspecific interactions compared to interspecific interactions was compared for both the rainbow lorikeet and the sulphur-crested cockatoo using a Chi-square test. Interspecific interactions were compared for both the sulphur-crested cockatoo and the rainbow lorikeet. Species interactions were classified as either an attack or a defence. Successful attacks occurred when an individual executing the attack successfully displaced the individual who was present at the hollow at the time of attack. Attack behaviours usually consisted of swooping, lunging, charging or fighting. Attacks were considered unsuccessful if the attacker failed to displace the individual present at the hollow at the time of attack. A successful defence occurred when the individual at the hollow was able to remain at the hollow when under attack, whereas an unsuccessful defence resulted in the individual being displaced from the hollow. The number of attacks and defences was compared using Chi-Square tests for both the rainbow lorikeet and the sulphur-crested cockatoo respectively. Chi-Square tests were then used to compare the successful and unsuccessful execution of the most frequent behaviour (either attack or defence) for the sulphur-crested cockatoo and the rainbow lorikeet respectively.

6.5 Results

A total of 11 879 episodes of visitation was recorded from the 61 hollows during 5401 camera-days of recording. Thirty-one species were detected, of which 23 are known to use hollows for nesting (Table 6.2). Occupying and visiting species comprised mammals (6 species), birds (14 species) reptiles (2 species) and insects (one species), and of the birds, 9 species were parrots. Whilst insects were not included in analyses, it should be noted that European honey bees were present at 6 out of 61 hollows. Using the definition of an independent visit as a daily visit of a particular species that was not an 'owner' of a hollow, 1502 independent visits were recorded.

6.5.1 Hollow measurements

Hollow depth in remnants was significantly greater compared to hollows in continuous forest ($t_{59} = 2.11$, $p < 0.05$) (Table 6.1). Hollow-bearing trees within remnants were also significantly taller than hollow-bearing trees within continuous forest ($t_{59} = 2.53$, $p < 0.05$) (Table 6.1). There was no significant difference in either the height of cavities from the ground or hollow entrance dimensions in remnants compared to forest (Table 6.1).

6.5.2 Community structure and species diversity

Hollows within remnants had a significantly different assemblage of occupying and visiting species compared to hollows in forest (*Global* R = 0.457, $p <0.05$) (Fig. 6.2). Both the rainbow lorikeet and the sulphur-crested cockatoo were the most characteristic species associated with hollows in remnants, accounting for 56% and 19% of the within-habitat similarity, but they contributed only 3% and 12% of the within-habitat similarity in the hollow-using assemblage in forest (Fig. 6.2). The high abundance of the rainbow lorikeet at hollows in remnants is primarily responsible for the steep decline in relative abundance, indicating an uneven species diversity of the hollow-utilising community within remnants (Fig. 6.2). The pygmy possum, lace monitor and sulphur-crested cockatoo characterised visitors to hollows in forest, collectively contributing 54% of the within-habitat similarity and greater species evenness. The composition of the assemblage of hollow users within forest was significantly more variable than the assemblage-using hollows within remnants ($F_{1,50} = 22.66$, $p < 0.01$) as is indicated by the wider spread of points in Fig. 6.3.

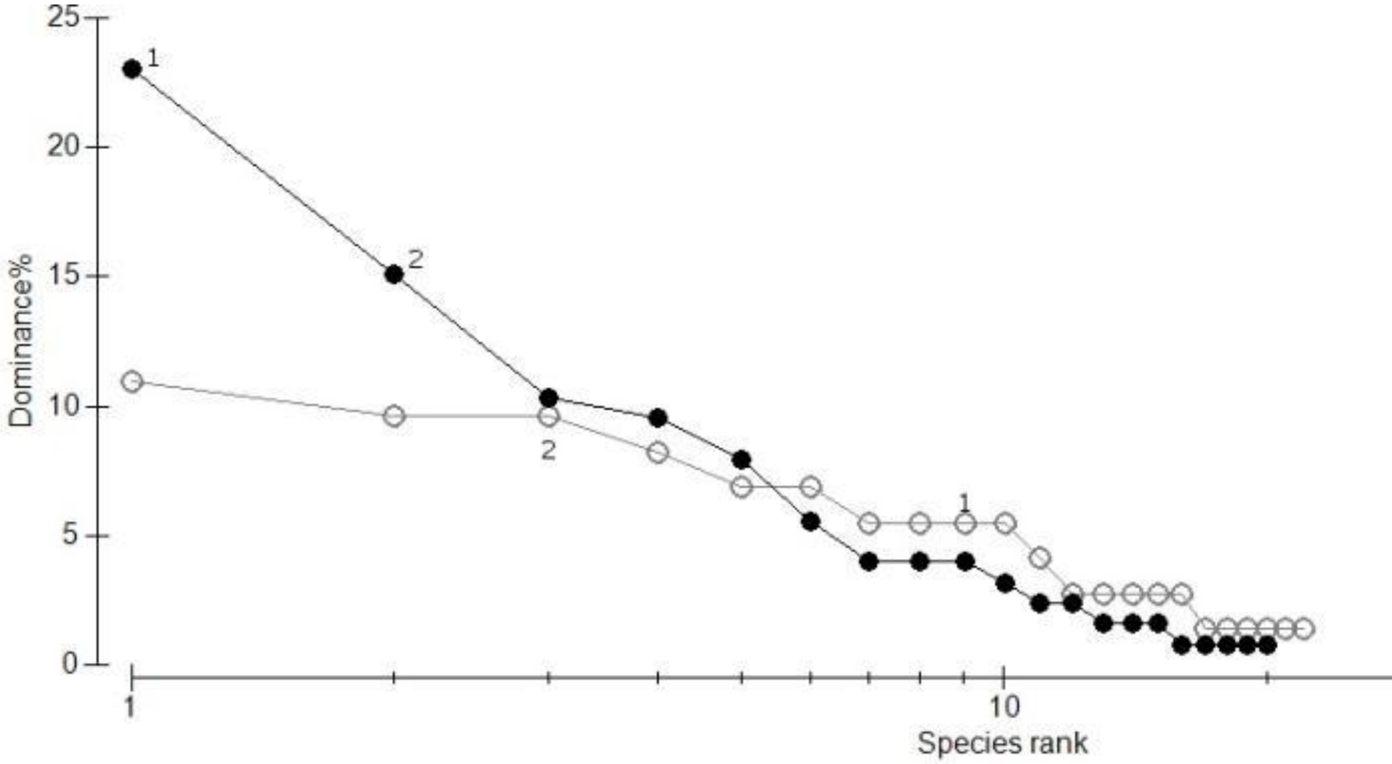

Fig. 6.2 Rank abundance curve of independent visits to hollows showing within-habitat similarity of the species assemblage at hollows in remnants (black line with closed circles) and continuous forest (grey line with open circles). '1' denotes the rainbow lorikeet. '2' denotes the sulphur-crested cockatoo.

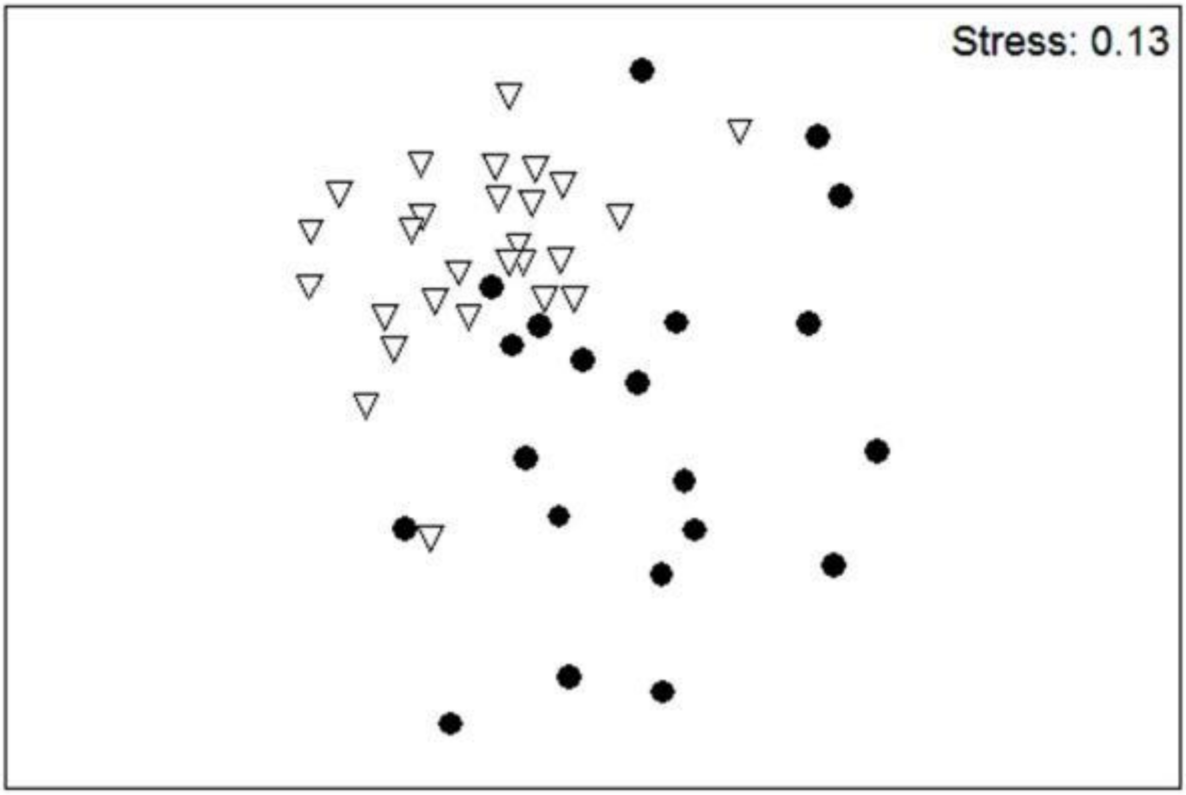

Fig. 6.3 Multi-dimensional scaling plot showing the differences in the fauna assemblage between hollows in remnants (open triangle) hollows in continuous forest (filled circle).

6.5.3 Visitation

Hollows in remnants had significantly more faunal visitations than did hollows in forest, with a visitation rate of 0.074 ± 0.035 (se) independent visits (exclusive of owners) per day at hollows in remnants compared with a visitation rate of 0.027 ± 0.017 (se) at hollows in forest ($F_{1,\,59} = 21.35, p < 0.05$). As expected, the visitation rate differed significantly between the arbitrary taxon groupings ($F_{3,\,59} = 4.03, p < 0.01$), however the more important interaction between habitat and fauna was also significant ($F_{3,\,59} = 4.46, p < 0.01$). Using Scheffé controlled comparisons, hollows within remnants had significantly more visitations from both rainbow lorikeets ($F_{1,\,59} = 78.05, p < 0.01$) and Other Parrots ($F_{1,\,59} = 11.13, p < 0.01$) than did hollows in forest (Fig. 6.4). There was no difference in visitation rate between hollows in remnants and hollows in forest for either the sulphur-crested cockatoo or Other Fauna. Furthermore, hollows within remnants had significantly more visitations by rainbow lorikeets than by sulphur-crested cockatoos, Other Parrots and Other Fauna combined ($F_{3,\,59} = 88.54, p < 0.01$) (Fig. 6.4). Other Fauna made significantly more visitations to hollows in both remnant and forest than did Other Parrots ($F_{1,\,59} = 13.86, p < 0.01$) (Fig. 6.4).

There was no significant difference in species diversity, as expressed in terms of the Shannon Wiener diversity index ($t_{59} = 1.32, p > 0.05$), between hollows within remnants (2.39 ± 0.17 se) and forest (2.01 ± 0.24 se).

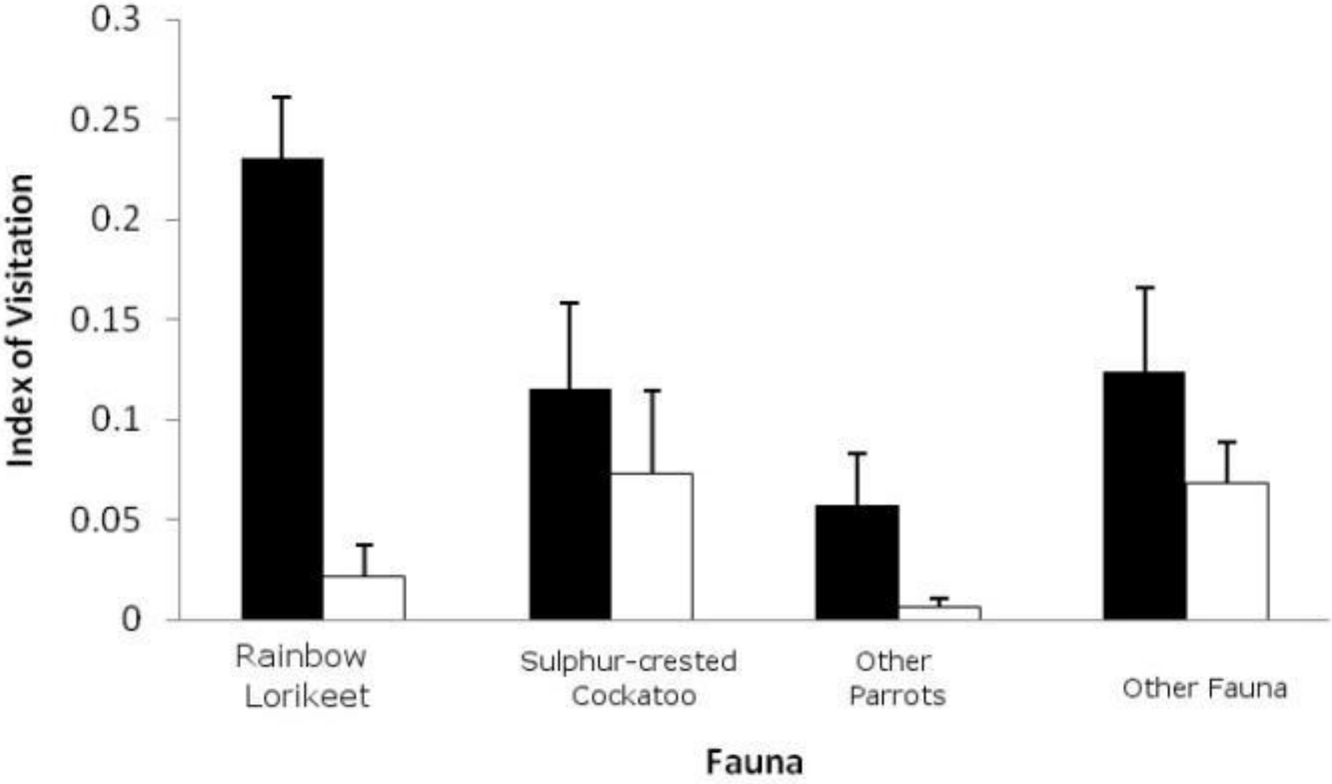

Fig. 6.4 Index of visitation for the rainbow lorikeet, sulphur-crested cockatoo, Other Parrots and Other Fauna at hollows in urban remnants (closed bars) and hollows in continuous forest (open bars). Index of visitation was calculated by dividing the number of independent visits (one visit per species per day) by the number of days the camera was recording.

In hollows within remnant vegetation where the hollow floor was visible, eggs were observed in two hollows and sulphur-crested cockatoo chicks were observed in one hollow. One of the clutches of eggs belonged to a pair of galahs. The identity of the parents of the second clutch was unable to be determined and the eggs appeared to have been abandoned. Neither the galah eggs nor sulphur-crested cockatoo chicks were present at the next inspection three weeks later. In hollows within forest where the hollow floor was visible, eggs were present within one hollow, but they were not present at the next inspection. Lace monitors were observed visiting the hollow and most likely preyed on the eggs. One other hollow within continuous forest was observed with a nestling, and a juvenile cockatoo eventually fledged from this hollow.

6.5.4 Species interactions

One hundred and thirty-seven aggressive interactions were recorded across all hollows in both remnants and forest, involving eight species of birds and one species of mammal, and comprising both interspecific and intraspecific interactions. There were significantly more interactions per hollow per day at remnant hollows (mean = 0.081 ± 0.025 (se)) than at hollows in forest (mean = 0.053, ± 0.021 (se)) (t_{59} = 2.39, $p < 0.05$).

Significantly more intraspecific interactions (n = 70) than interspecific interactions (n = 37) were recorded for the rainbow lorikeet ($\chi^2_{(1)} = 10.18$, $p < 0.01$). Interspecific interactions (Table 6.3) involving the rainbow lorikeet were comprised of significantly more defences than attacks ($\chi^2_{(1)} = 9.0$, $p < 0.01$), of which significantly more defences were unsuccessful ($\chi^2_{(1)} = 8.33$, $p < 0\ .01$) (Fig. 6.5), with the rainbow lorikeet failing to defend against the sulphur-crested cockatoo, the galah and the Australian wood duck. The rainbow lorikeet successfully defended against the laughing kookaburra and the noisy miner, as well as one successful defence against the sulphur-crested cockatoo. The rainbow lorikeet successfully attacked the pied butcherbird, Australian king

Table 6.3 The number of aggressive interactions recorded within and between species pooled for urban remnants and continuous forest.

Species	*Sulphur-crested cockatoo*	*Rainbow lorikeet*	*Eastern rosella*
Sulphur-crested cockatoo	27	14	0
Rainbow lorikeet	17	70	3
Galah	0	9	0
Australian king parrot	0	1	1
Laughing kookaburra	0	1	0
Crimson rosella	1	0	0
Pied butcherbird	0	1	0
Noisy miner	0	3	0
Common brushtail possum	1	0	0
Australian wood duck	0	1	0
Unidentified	1	0	0

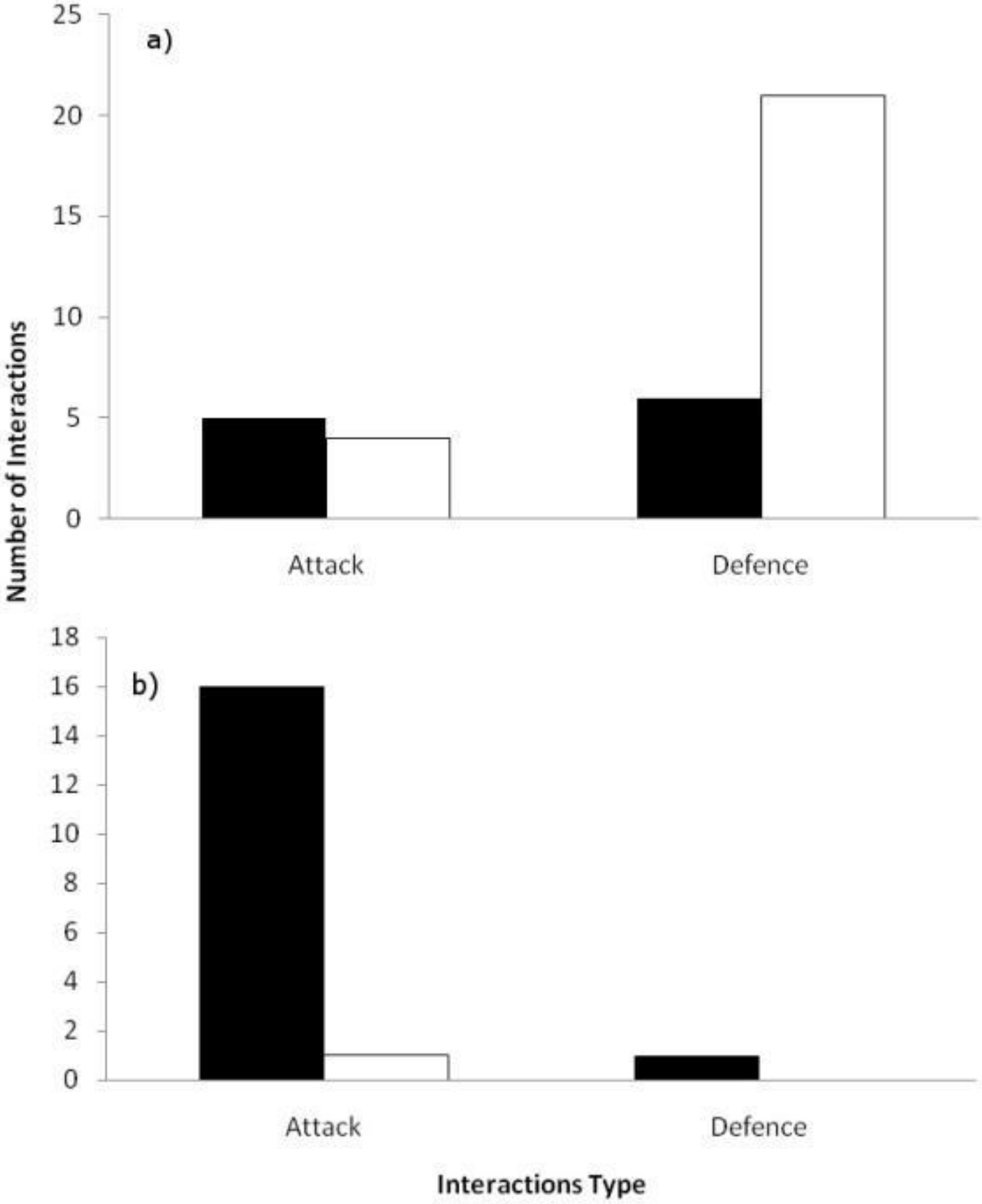

Fig. 6.5 Number of aggressive interactions observed at hollows in both urban remnants and continuous forest for the a) rainbow lorikeet and the b) sulphur-crested cockatoo separated into attacks and defences. Closed bars denote successful interactions. Open bars denote unsuccessful interactions.

parrot, eastern rosella, and the galah, but was unsuccessful when attempting to attack the sulphur-crested cockatoo, as well as once against the galah and the eastern rosella.

The sulphur-crested cockatoo made significantly more attacks than defences ($\chi^2_{(1)} = 14.22$, $p < 0.01$), of which significantly more attacks were successful than unsuccessful ($\chi^2_{(1)} = 13.24$, $p < 0.01$) (Fig. 6.5). Successful attacks were made against the rainbow lorikeet, crimson rosella and the common brushtail possum. One unsuccessful attack was made against the rainbow lorikeet. There was no significant difference in the number of intraspecific attacks.

6.6 Discussion

Tree hollows within urban remnants had a significantly different assemblage of visiting taxa than hollows within continuous forest, with parrots, in particular the rainbow lorikeet, making significantly more visitations than other taxa to hollows within remnants. The high rate of visitation to urban hollows compared to hollows within forest may be associated with high densities of rainbow lorikeets and other parrots within the urban landscape (Davis et al., 2012; Strubbe and Matthysen, 2007; Wenner and Hirth, 1984). Alternatively, it may be indicative of a shortage of suitable nesting cavities within urban remnants.

The number of interactions at hollows within remnants was significantly higher than at hollows within forest and the number of intraspecific interactions between rainbow lorikeets was significantly higher than interspecific interactions between rainbow lorikeets and other taxa. High rates of intraspecific interactions at hollows have previously been observed in habitat with limited cavity availability (Beissinger et al., 1998; Heinsohn et al., 2003; Murphy et al., 2003; Waltman and Beissinger, 1992) and significantly fewer hollow-bearing trees have been observed within Sydney remnant vegetation (2.8 ha^{-1}) than in continuous forest (6.5 ha^{-1}). Additionally within the urban region, hollow-bearing trees tend to be 'clumped' within remnants, which has been previously associated with a higher number of intraspecific interactions, as species attempt to maintain nesting trees or territories (Cockle et al., 2011).

A high number of intraspecific interactions has also been associated with competition for high quality nesting sites (Gustafsson, 1988) and may not necessarily indicate a lack of available hollows. When a diverse supply of suitable nesting hollows is present, species may choose hollows with characteristics specific to their body size or breeding requirements (Gibbons et al., 2002; Lohmus and Remm, 2005; Remm et al., 2008). Remnants contained significantly more hollows that were deeper and present in the main trunk of the tree, and in trees that were taller than those in continuous forest. As they are large birds, cockatoos need hollows large enough to provide shelter and to rear nestlings, and have often been recorded using hollows that occur within the main trunk of the tree (Goldingay, 2009; Higgins, 1999; Saunders et al., 1982). The higher number of main trunk cavities in remnants may therefore be sufficient to support the population of sulphur-crested cockatoos within the urban region. The lack of a significant difference between the number of intraspecific and interspecific interactions for the cockatoo may further support this. The high number of intraspecific interactions for the rainbow lorikeet may suggest that optimal hollows for this species are in lower abundance than those suited to sulphur-crested cockatoos.

As previously noted, the higher abundance of the rainbow lorikeet and other parrot species in the urban region compared to continuous forest (Davis et al., 2012a), coupled with the high number of intraspecific interactions between rainbow lorikeets, the high number of interactions in remnants may be due to an inadequate supply of suitable hollows.

A shortage of suitable nesting hollows is capable of influencing faunal assemblage composition through competition. Interference competition may limit availability of and access to nesting hollows for breeding pairs, particularly in habitat with clumped nesting hollows, as nesting pairs of some species defend territory around the nest or attempt to maintain multiple cavities suitable for nesting (Renton, 2004; Salinas-Melgoza et al., 2009). High levels of interference competition may explain the low number of nesting attempts in this study, as nest establishment or breeding attempts are known to fail due to a greater investment in nest defence (Brown, 1969; Heinsohn et al., 2003; Saunders, 1979; Walker et al., 2005). Alternatively, low numbers of nesting attempts may either be due to hollows selected for the study having sub-optimal characteristics or due to some parrots maintaining several potential nesting hollows within their territory (Renton, 2004; Salinas-Melgoza et al., 2009)

Whilst there is currently no evidence of a decline in urban parrot diversity, the urban avian community may still be reaching equilibrium (Sattler et al., 2010). Rainbow lorikeets have only recently established in southern Sydney and, should they continue to further increase in both density and abundance, there is the possibility that this may lead to the exclusion of less competitive parrots (Waterhouse, 1997).

There is a need for wildlife managers to understand the complex relationship between human activities, subsequent habitat modification and biodiversity decline. Potential shortages in either hollow availability or suitable nesting sites and a subsequently higher number of competitive interactions at hollows may represent an increasing threat to biodiversity. In addition, increasing densities of certain native species may pose a threat that is greater than that of exotic species such as the common myna, which is commonly perceived to have a detrimental impact on native cavity-nesting wildlife (Grarock et al., 2012), and consequently being the focus of costly eradication programs. Interestingly, common mynas, were not recorded at any tree hollows in this study, and the species is not likely to be a structuring force in this urban assemblage. While a common species in Sydney, and the subject of much anecdotal discussion in terms of its possible impact, its effect may well be completely confined to urban parks and suburban gardens (Lowe et al., 2011; Parsons et al., 2006).

Further research is needed into urban hollow usage, particularly to determine the availability of hollows as well as if, and the extent to which, hollows may be limiting within urban environments. More data are required to determine species-specific preferences for hollows with particular characteristics as well as information on the reproductive success of parrots in urban remnants. Finally, the conservation of urban wildlife is integral to ensuring that people living within cities maintain both an appreciation of wildlife and recognise the value of wildlife conservation

Chapter 7: Distribution of Tree Hollows and Hollow Preferences by Parrots in an Urban Landscape.

Photo: A Davis

Davis, A., Major, R.E. and Taylor, C.E. Distribution of tree hollows and hollow preferences by parrots in an urban landscape. *Emu*. In review.

7.1 Abstract

The number of hollow-bearing trees, and the associated density of hollows contained within urban habitats, continues to decline as cities expand. Many faunal species rely on hollows at some stage in their life cycle, and whilst there is an emerging campaign to retain trees within the urban landscape, there is a general lack of knowledge about the distribution and density of tree hollows contained with urban habitats. Additionally, remaining hollows may be unsuitable for individual species which may have specific preferences or requirement for certain characteristics of tree hollows. To determine the distribution of hollow-bearing trees and tree hollows in the urban region of Sydney, Australia, we surveyed 264 sites within parks, streets, golf courses, remnant vegetation and continuous forest. To determine whether particular species of hollow-utilising fauna were associated with specific hollow characteristics, motion-activated video cameras were installed to monitor usage of hollows in 61 randomly selected hollow-bearing trees in a subset of sites in remnant vegetation and continuous forest. Measurements of 12 characteristics, taken from both the hollow and the hollow-bearing tree, were analysed using GLM to determine whether they were associated with the fauna recorded utilising the hollow. The number of both hollows and of hollow-bearing trees varied significantly amongst habitats, with all urban habitats having significantly fewer hollow-bearing trees than did continuous forest. There was no significant difference in the number of hollows contained within remnant vegetation and continuous forest. Hollow visitation by the rainbow lorikeet, sulphur-crested cockatoo and the Australian king parrot was significantly associated with particular hollow characteristics, most importantly hollow type, hollow orientation and tree species. Knowledge of the distribution of hollow-bearing trees throughout landscapes, as well as the characteristics of hollows that are present within hollow-bearing trees, is crucial in decision making to ensure that a diversity of hollows is maintained within the urban landscape.

7.2 Introduction

Over 360 species of birds and mammals worldwide utilise tree hollows for nesting, denning, shelter, protection or breeding (Goldingay, 2009; Lindenmayer et al., 2003; Martin, 1996; Saunders et al., 1982). Australia contains more obligate cavity nesters than either Europe, South America, South Africa and New Zealand (Blakely et al., 2008; Newton, 1994; Saunders et al., 1982) with 11 % of all Australian birds relying on hollows to breed. Psittaciformes comprise 21 % of Australian hollow-nesting species with 17 of these species currently appearing on the IUCN red list of threatened species (Garnett et al., 2010; Saunders et al., 1982).

At the same time however, some species of Australian parrots have increased in abundance to the point where they are now present in higher densities within cities than in their natural habitat (Davis et al., 2012a) and some species have colonised areas from which they were historically absent (Higgins, 1999; Major and Parsons, 2010). This increasing density of both endemic and non-endemic parrots, combined with several "increaser" species of native hollow-utilising mammals (e.g. common brushtail possum (*Trichosurus vulpecula*) (Harper et al., 2005b; Marsden and Jones, 1997) and exotic hollow-nesting birds (e.g. common myna (Grarock et al., 2012)) may result in high rates of competition, and ultimately limit the abundance of hollow-utilising fauna if there is a shortage of adequate tree-hollows (Ardia et al., 2006; Harper et al., 2005a; Shukuroglou and McCarthy, 2006; Strubbe and Matthysen, 2007; Veerman, 1991).

The number of hollows in many landscapes is declining as hollow-bearing trees are removed by processes such as grazing, firewood collection, dieback, altered fire regimes and, in particular, urbanisation (Bennett et al., 1991; Davis et al., 2011; Emison, 1996; Lindenmayer et al., 1997; Martin, 1996). Urbanisation, however, does not result in uniform land clearing, but rather creates a mosaic of habitats with varying tree cover, ranging from natural remnant bushland, through sparsely vegetated parks, streets and golf courses to industrial regions devoid of trees (Crooks et al., 2004; Major and Parsons, 2010; White et al., 2005; Young et al., 2007). As remaining trees within these habitats senesce, they may be removed by land managers, for reasons of public safety, before adequate hollows have time to develop (Carpaneto et al., 2010; Terho and Hallaksela, 2008). It has been estimated that the number of hollows in urban landscapes may be as low as 1 % of that of continuous forest (Shukuroglou and McCarthy, 2006).

The number of tree hollows present within a given habitat does not in itself determine the carrying capacity for the number of hollow-reliant species that may be present (Bennett et al., 1994). Some species are known to choose tree hollows with particular characteristics, including the type of hollow (e.g. spout, trunk), the depth of the hollow, width of the hollow entrance or the species of tree in which the hollow occurs (Blakely et al., 2008; Cameron, 2006; Courtney and Debus, 2006; Inions et al., 1989; Martin, 1996; Mawson and Long, 1994; Nelson and Morris, 1994; Salinas-Melgoza et al., 2009; Saunders et al., 1982). With Australian parrots ranging in size from 14 cm (double-eyed fig parrot (*Cyclopsitta diophthalma*)) to 60 cm (palm cockatoo (*Probosciger aterrimus*)) in length, a diverse range of hollows is necessary to accommodate the specific requirements of individual species. Additionally, arboreal mammalian fauna also require a similar diversity of hollows (Lindenmayer et al., 2008; Lindenmayer et al., 2003) and competition for suitable hollows can be high with some taxa even sharing hollows between their respective breeding seasons (Courtney and Debus, 2006).

The loss of hollow-bearing trees, however, is a threat that is directly amenable to good management and planning. In order for land managers to properly manage the retention of hollow-bearing trees, and the hollows they contain, information on what taxa may be associated with which, if any, hollow characteristics must be available. Such information, however, is poorly known and, of the few studies that have been carried out, the majority have been either ground-based surveys or have utilised felled trees (Harper et al., 2004; Koch et al., 2008a; Lindenmayer et al., 1993; Lindenmayer et al., 2000). Whilst the ground-based detection of hollow-bearing trees is largely reliable, the number of hollows may be either overestimated or underestimated as many hollows are not visible from the ground, or what appears to be a hollow from the ground may only be a knot or depression (Blakely et al., 2008; Harper et al., 2004; Lindenmayer et al., 2000). Moreover, ground-based assessment cannot directly measure hollow dimensions and is therefore unable to evaluate the utility of particular hollows for all potential taxa.

By combining ground-based and canopy-based assessment of hollows in four urban habitats and in continuous forest, we aimed to determine the relative abundance of hollows in urban habitats compared to natural forest, and if characteristics of measured hollows were associated with particular hollow-utilising fauna. We expected streets and parks to contain the least number of hollows, compared to both remnants and natural forest, with remnants being equivalent to natural forest. We expected hollow characteristics to vary with species, with larger fauna such as the sulphur-crested cockatoo, being associated with larger and deeper hollows.

7.3 Methods

7.3.1 Study sites

The study area encompassed the Sydney urbanised landscape on the east coast of New South Wales, Australia bounded by the Pacific Ocean to the east and three major national parks to the north, south and west (see Fig. 6.1 for map of study area).

We selected four distinct types of urban habitat known to be important to parrots: parks (n= 56), streets (n= 62), remnants (n= 42) and golf courses (n = 40) (Davis et al., 2012a). Sites for the fifth habitat, continuous forest (hereafter referred to as ‘forest) (n= 64) were selected from within Ku-ring-gai Chase National Park (13 500 ha) and Royal National Park (15 068 ha) to the north and south of Sydney respectively and comprised of Sydney Coastal or Sydney Hinterland Dry Sclerophyll or Sydney Forest (Keith 2006).

7.3.2 Hollow Assessment

A total of 264 ground-based surveys of trees within a two-hectare area were undertaken in all five habitats. Trees with a diameter at breast height (DBH) of 50 cm or greater were scanned with binoculars. Any trees containing hollows were counted as hollow-bearing trees and in each such tree, we counted hollows visible within the crown, main branches or trunk that were higher than 3 m above the ground and which had a hollow entrance greater than 3 cm. Longitudinal fissures or cracks less than 3 cm wide were not counted.

Canopy-based counts of hollow abundance were undertaken in a subset of surveyed sites (one tree in each of 20 sites), selected only from 'remnants' and 'continuous forests' using "Single Rope Technique", by which a slingshot was used to launch a temporary climbing rope into the tree that could then be ascended using climbing equipment. During the climbed inspections, all suspected hollows within the tree were inspected to ensure that they had a depth greater than 15 cm (Davis et al., 2013). This 'double sampling method' (Harper et al., 2004), which involves ground-based surveys interspersed with periodic climbing surveys, ensures accuracy of ground-based hollow estimation. The same criteria used for ground-based surveys were applied to climbing surveys.

7.3.3 Identifying hollow users

To determine associations between particular parrot species and hollow characteristics, a sample of tree hollows within remnants and continuous forest was monitored with motion-activated video cameras. These two habitats were selected because they contained the highest number of hollow-bearing trees and thus a greater diversity of hollow options for parrots to select from. Trees were selected from the genera *Angophora*, *Eucalyptus* and *Corymbia*, which comprise both the dominant canopy vegetation, and the main species of hollow-forming trees in the Sydney region. Criteria used in hollow selection are described in section 6.3.2 with 32 hollow-bearing trees from 22 remnants, and 29 hollow-bearing trees from surrounding forest included in the study. All 61 hollows were monitored with video cameras for six months throughout June to November during 2009 and 2010 (Davis et al., 2013).

7.3.4 Hollow Measurements

The substrate, entry angle, orientation, opening diameter and depth of each hollow monitored by a camera were measured. Hollow substrates were classified as one of ‘main trunk’, ‘branch’ or ‘spout’ (Gibbons et al., 2002). A hollow that was at the top of a trunk or flush against a vertical trunk was given an angle of 0 degrees (facing up), 90 degrees (facing out) and below 90 degrees was facing down (Blakely et al., 2008). The orientation of the hollow in reference to magnetic north was also recorded. Additional characteristics of species of tree, DBH, tree height, hollow height and the presence of other hollows were also recorded. The DBH was measured with a diameter tape and the height of the tree and height of the hollow in the tree were measured with a Vertex Laser. A summary of the hollow measurements from the five most common species of tree is given in Table 7.1.

Table 7.1 Characteristics (mean ± SE) of the five main hollow-bearing species of tree (n = 56), and their component hollows, obtained from canopy inspection, included in the models. Characteristics of hollow-bearing trees in the 'other' category are not included.

	A. costata	*E. pilularis*	*C. gummifera*	*E. piperita*	*E. haemastoma*
Abundance (n)	22	11	11	6	6
Hollow height (m)	10 ± 2	14 ± 1	9 ± 1	7 ± 1	7 ± 2
Number of hollows per tree	2.5 ± 0.53	3.8 ± 1.2	2.1 ± 0.63	2 ± 0.82	4.7 ± 1.9
Entrance width (cm)	22.9 ± 4.7	12.5 ± 3.8	10.6 ± 3.2	9.9 ± 4.0	11.5 ± 4.7
Type of hollow (n)					
main	10	2	3	5	2
spout	8	7	6	0	2
branch	4	2	2	1	0
Direction (n)					
north	7	1	6	1	2
south	2	3	0	0	1
east	5	3	2	2	0
west	8	4	3	3	3
Hollow angle (º)	41 ± 8.74	45 ± 13.6	38 ± 10.2	17 ± 6.9	61 ± 24.9
Depth (cm)	91.8± 19.6	98.5 ± 29.7	33.7 ± 10.2	56.7 ± 22.7	66.0 ± 26.9

7.3.5 Analysis

To determine the accuracy of ground assessment of hollow density, we used regression analysis to determine the extent to which hollows counted from the ground predicted those counted by canopy inspection of the same 20 trees.

To identify differences in the number of hollow-bearing trees and the number of hollows per tree between habitats we used single factor ANOVA with planned Bonferroni adjusted contrasts. Due to the uneven sample size, to ensure contrasts were orthogonal, each planned contrast between habitats was tested as a set of orthogonal contrasts using multiple regression analysis (SPSS version 17.0), which tests relevant contrasts based on cell means (Pedhazur, 1997; Quinn and Keough, 2002).

Video footage from the hollow cameras was viewed and the species of bird that triggered the camera, along with the time and date, was recorded. Where possible, we confirmed nesting in a hollow by the presence of eggs, young or adults spending sufficient time in the cavity to be incubating eggs (Cockle et al., 2010). Birds were considered to be prospecting hollows if they were filmed landing on or next to the hollow, entering/exiting the hollow, disappearing within the hollow for extended periods or poking their head into the hollow (Cockle et al., 2011). We do not assume that all visitations were attempts at nesting, as some parrots may maintain multiple hollows within their territory (Salinas-Melgoza et al., 2009), may be prospecting hollows for future breeding attempts or may find the hollow unsuitable (Renton and Brightsmith, 2009). Some parrots made multiple visits within the one-day and to correct for this, we calculated an index of independent visitations for each species per hollow per day (see section 6.4.5) to control for multiple visits within the same day.

Hollow visitation data were transformed into presence/absence data at each hollow and associations between hollow characteristics and visitation by parrots were tested using Generalised Linear Modelling in R (version 2.15), with the Akaike Information Criterion (AIC) used to select the best models (Manning et al., 2007; Pearce and Ferrier, 2000). ΔAIC values were calculated as the difference between a candidate model's AIC and the lowest AIC value, and AIC weightings (w_i) were calculated for each model to determine the likelihood that each candidate model was the best model (Mazerolle, 2006). ΔAIC values less than 2 indicate substantial support for the model (Burnham and Anderson, 2002) and thus only models with ΔAIC values less than 2 are presented. We used the ROC (receiver operating characteristic) curves to test the capacity of each model to successfully discriminate between presence and absence. Values of c that are greater than 0.70, 0.80 and 0.90, respectively, suggest acceptable, excellent or outstanding model discrimination (Lemeshow and Legall, 1994).

The models included the following variables: visiting species, hollow entrance width, hollow depth, hollow height, direction, DBH, hollow angle and the presence of other hollows. Hollow entrance height and tree height were excluded from analysis as they were strongly correlated with other variables ($r > 0.7$) (Tabachnick and Fidell, 2007; While and McArthur, 2005). All other variables were included in the analysis. Only the sulphur-crested cockatoo, rainbow lorikeet, crimson rosella, Australian king parrot, galah and eastern rosella were included in the analysis. Due to the infrequency of visitations at hollows, the musk lorikeet (n = 2 hollows), scaly-breasted lorikeet (n = 1 hollow) and yellow-tailed black-cockatoo (*Calyptorhynchus funereus*) (n = 1 hollow) were excluded.

Where evidence of nesting was present at a hollow or the percentage of visitations from a single species was more than 50% visitations from all other species, we designated this species as the 'owner' of the hollow (see section 6.4.5). The sulphur-crested cockatoo and the rainbow lorikeet made up the majority of hollow owners and we compared characteristics of these hollows to characteristics predicted by the model.

7.4 Results

7.4.1 Distribution of hollows across the urban environment

The number of hollow-bearing trees per two hectares varied significantly between habitats, with continuous forest containing the highest number of hollow-bearing trees (Fig. 7.1). More hollow-bearing trees were present in two hectares of forest than in two hectares of street ($F_{1,263} = 164.61, p < 0.01$), park ($F_{1,263} = 108.58, p < 0.01$), golf course ($F_{1,263} = 70.06, p < 0.01$) and remnant ($F_{1,263} = 28.62, p < 0.01$) (Fig. 7.1).

Remnants also contained a significantly higher number of hollow-bearing trees than parks ($F_{1,263} = 14.52, p <0.01$) and streets ($F_{1,263} = 37.45, p < 0.01$) but there was no significant difference in the number of hollow-bearing trees between remnants and golf courses (Fig. 7.1). There was no difference in the number of hollow-bearing trees between golf courses and parks, however, golf courses contained significantly more hollow-bearing trees than streets ($F_{1,263} = 8.70, p < 0.05$). The number of hollow-bearing trees did not vary significantly between remnants and golf courses.

There was a strong correlation between the number of hollows per tree observed from the ground and counted via canopy inspection ($R^2 = 0.75$, $F_{1,19} = 54.4, p < 0.01$) (Fig. 7.2). The slope of the relationship was positive ($\beta = 0.89$), indicating that if anything, ground surveys slightly overestimated (or underestimated the abundance of hollows suitable for parrots based on *a priori* criteria.

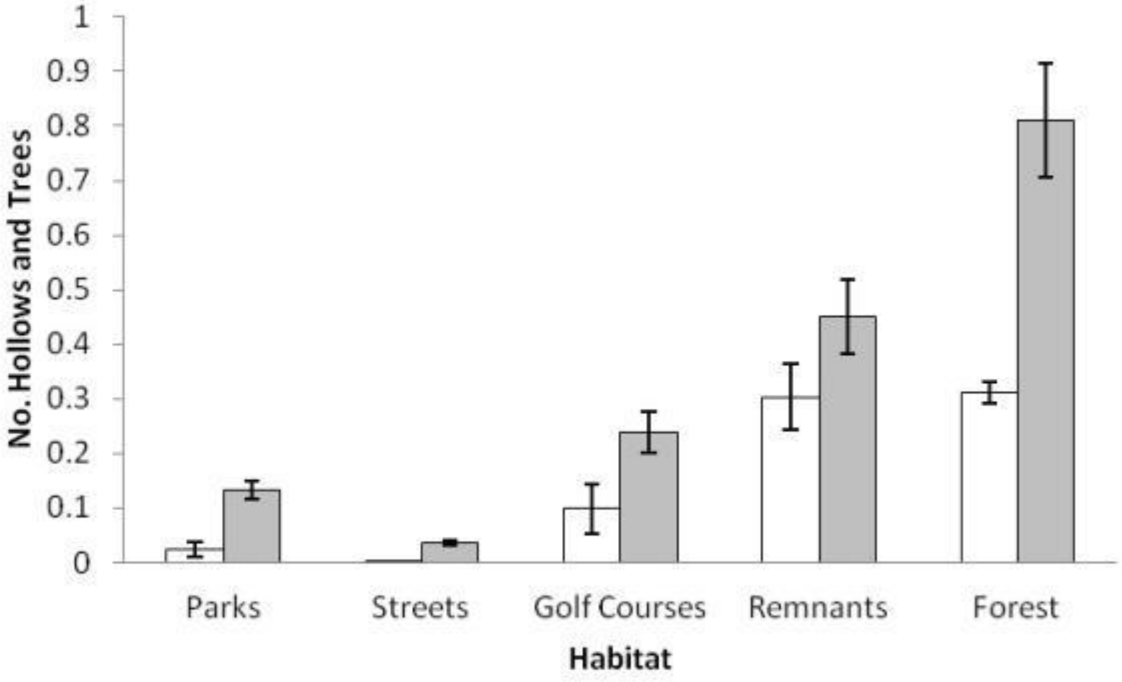

Fig. 7.1 Mean (±SE) number of hollows per tree (open bars) and hollow-bearing trees per hectare (shaded bars) found in parks, streets, golf courses, small urban remnants and continuous forest. Data are $\log_{10}$ transformed.

Forest sites contained significantly more hollows per tree than streets ($F_{1,263} = 68.11, p < 0.01$), parks ($F_{1,263} = 55.46, p < 0.01$) and golf courses ($F_{1,263} = 25.16, p < 0.0$), but did not contain significantly more hollows per tree than remnants (Fig. 7.1). Remnant vegetation also contained a significantly higher number of hollows per tree than parks ($F_{1,263} = 41.65, p < 0.01$), streets ($F_{1,263} = 50.88, p < 0.01$) and golf courses ($F_{1,263} = 19.11, p < 0.01$) (Fig. 7.1). There was no significant difference in the number of hollows per tree between parks, streets and golf courses (Fig. 7.1).

7.4.2 Parrot associations with particular hollow characteristics

Visitation by four out of six species of parrot were explained by the particular characteristics of hollows. Models for these species are shown in Table 7.2 along with ΔAIC and w_i values.

The best fitting model explaining hollow visitation by the sulphur-crested cockatoo included the terms 'hollow angle', 'habitat', 'hollow height' and 'tree species' (Table 7.2). Sulphur-crested cockatoos were more likely to visit hollows in *Angophora costata* that were closer to vertical and located higher up in the tree, and visitations were less likely in continuous forest compared to remnant vegetation.

The best fitting model explaining hollow visitation by the rainbow lorikeet included the variables 'depth', 'direction', 'other hollows' and 'species'. Visitations by rainbow lorikeets were explained by deeper hollows that faced either east or west in *Angophora costata*, *Eucalyptus pilularis* and 'other species' that had multiple hollows within the same tree (Table 7.2).

No models significantly predicted visitations at hollows by either the eastern rosella or the galah.

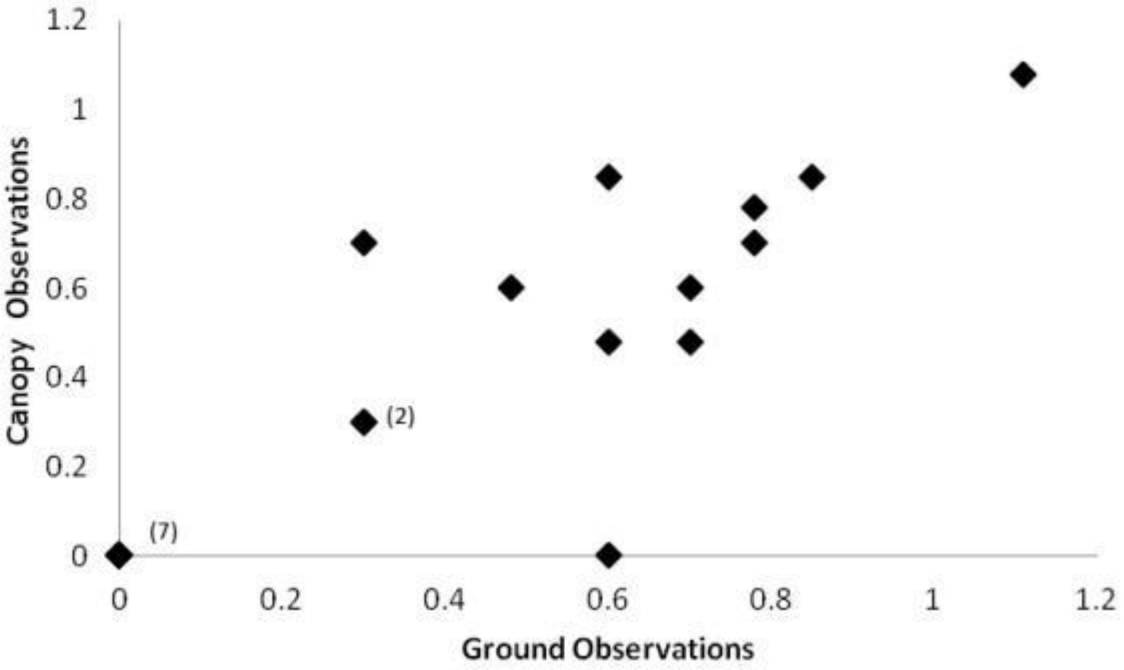

Fig. 7.2 Relationship between the number of hollows observed from the ground and the number of hollows in the same tree from the canopy. Data are $\log_{10}$ transformed. Number in brackets indicates the number of data points of the same value superimposed on top of each other.

Table 7.2 Model results for the association between the sulphur-crested cockatoo, rainbow lorikeet, Australian king parrot and the crimson rosella and characteristics of hollow-bearing trees and tree hollows.

Sulphur-crested cockatoo				
Model 1	***AIC*****=60.48**	**Δ = 1.91**	***w* = 0.21**	***c* = 0.80**
		Factor	*Beta Weight*	*P value*
		Angle	0.071	0.018
		Habitat (forest)	-4.33	0.02
		Hollow height	0.36	0.037
Model 2	***AIC=58.57***	**Δ = 0**	***w* = 0.56**	***c* = 0.91**
		Factor	*Beta Weight*	*P value*
		Angle	0.071	0.016
		Habitat (forest)	-4.23	0.02
		Hollow height	0.35	0.034
		Species (*Angophora costata*)	6.3	0.047
Rainbow lorikeet				
Model 1	***AIC=64.9***	**Δ = 1.54**	***w* = 0.26**	***c* = 0.81**
		Factor	*Beta Weight*	*P value*
		Depth	0.03	0.0083
		Direction (east)	6.8	0.01
		Direction (west)	4.19	0.01
		Species (*Angophora costata*)	5.12	0.03
		Species (other)	6.6	0.02
Model 2	***AIC=63.36***	**Δ = 0**	***w* = 0.57**	***c* = 0.82**
		Factor	*Beta Weight*	*P value*
		Depth	0.029	0.01
		Direction (east)	6.85	0.05
		Direction (west)	4.25	0.01
		Other hollows	0.72	0.04
		Species (*Angophora costata*)	4.95	0.03
		Species (*Eucalyptus pilularis*)	4.25	0.048
		Species (other)	6.4	0.02
Australian king parrot				
Model 1	***AIC=41.52***	**Δ = 0**	***w* = 0.52**	***c* =0.78**
		Factor	*Beta Weight*	*P value*
		Hollow type (spout)	4.05	0.024
Crimson rosella				
Model 1	***AIC=41.52***	**Δ = 0**	***w* = 0.47**	***c* =0.64**
		Factor	*Beta Weight*	*P value*
		Habitat (remnants)	-2.49	0.041

‘Type of hollow’ was the only significant term in the model that best explained visitation by the Australian king parrot. Hollow visitations by the Australian king parrot were more likely at ‘spout’ hollows rather than either ‘main trunk’ or ‘branch’ hollows (Table 7.2). The model that best explained hollow visitation by the crimson rosella contained only ‘habitat’ and suggested that visitations by this species were less likely to occur in continuous forest compared to remnants (Table 7.2).

Using the definition of a hollow ‘owner’, we considered 10 hollows to be ‘owned’ by rainbow lorikeets. Hollows facing east and west within *A. costata* and *E. pilularis* were strongly associated with the rainbow lorikeet (Table 7.3). Eight hollows ‘owned’ by rainbow lorikeets were either in *A. costata* or *E. pilularis* with 6 facing either east or west.

Table 7.3 Characteristics of trees and their component hollows that contained nesting sulphur-crested cockatoos and rainbow lorikeets considered to have claimed ownership of a hollow. These characteristics were significant predictors in the models for hollow visits for the two species respectively.

Sulphur-crested cockatoo

Hollow height (m)	*Tree species*	*Hollow angle (degrees from vertical)*
15 ± 1.58 (SE)	*A. costata* (n = 3)	31.83 ± 12.69 (SE)

Rainbow lorikeet

Hollow depth	*Hollow direction*	*species*
74 ± 12.33 (SE)	west (n = 4) east (n = 2)	*A. costasta* (n = 4) *E. pilularis* (n = 4)

7.5 Discussion

This study revealed significant differences in both the number of hollow-bearing trees and the number of hollows per tree between urban habitats and continuous forest as well as within urban habitats. It also revealed that there were particular characteristics of tree hollows within these habitats that significantly explained visitation by three of the six species of parrot that were sufficiently common for analysis.

7.5.1 Hollow Distribution

Continuous forest contained both significantly more hollow-bearing trees and significantly more hollows per tree than all urban environments. Of all the urban habitats, remnants contained the highest density of hollow-bearing trees, but contained only 45 % of the density of hollow-bearing trees found in continuous forest. Streets contained only 1 % the density of hollow-bearing trees found in continuous forest, which is consistent with previous estimates of the percentage of hollow-bearing trees in urban landscapes (Shukuroglou and McCarthy, 2006). The significantly higher density of hollow-bearing trees on golf courses than streets is potentially due to remnant trees that are often retained when the golf course is constructed (Hodgkison et al., 2007). Such remnant trees are often mature, containing multiple hollows, and their presence is indicative of the potential role that golf courses may play in urban conservation if they are managed appropriately (Terman, 1997).

Streets contained the lowest density of hollow-bearing trees, followed by parks. Both habitats often comprise a mix of mature natural vegetation, exotic vegetation and newly planted vegetation (Parsons et al., 2006; White, et al., 2005) that may not have the propensity to develop hollows or may not be mature enough for hollows to have formed. Additionally, in public streets and parks, large mature trees are typically maintained by councils for their aesthetic value (French et al., 2005; Strubbe and Matthysen, 2007). Decaying branches on mature trees, however, may be removed for reasons of public safety and liability, which prevents hollow development (Harper et al., 2005a; Ranius et al., 2009; Terho and Hallaksela, 2008). Decaying branches present on trees within golf course ‘roughs’ may be more likely to be left on the tree and thus have a greater opportunity for hollow development.

Habitats within the urban environment not only contained fewer than half the hollows of natural forest, but many of these hollows may be unsuitable for occupation by parrots. Within primary forest, in Argentina, over half the hollows that were identified by ground-based assessment turned out to be unsuitable for nesting birds (Cockle et al., 2010), with realistic estimates of suitable hollows within logged forest placed at 0.5/ha (Cockle et al., 2008). Specific hollow characteristics have been found to be an important factor in determining the presence of parrot and other secondary cavity-nesting species (Cockle et al., 2011; Marsden and Jones, 1997; Politi et al., 2010; Stojanovic et al., 2012) and when the number of cavities within the four urban environments in this study is considered, the number of available hollows with appropriate species specific characteristics may be considerably less.

7.5.2 Bird Species Associations with Hollow Characteristics

Of the seven hollow variables measured, specific categories within each variable were each significant in explaining visitation by at least one species of parrot. Hollows that were higher up in the tree and more vertically oriented explained visitations from sulphur-crested cockatoos, while visitations from rainbow lorikeets were associated with hollows that faced either east or west and were situated in a tree that had other hollows present. Deeper hollows, hollow direction and the presence of other hollows also explained visitations by rainbow lorikeets. Species of tree significantly explained visitations by both the sulphur-crested cockatoo and the rainbow lorikeet and the 'type' of hollow was significant for the Australian king parrot. Sulphur-crested cockatoos were also significantly associated with habitat, with visitations from sulphur-crested cockatoos less likely in continuous forest.

A more vertically angled hollow may be more attractive to sulphur-crested cockatoos due to its potential for increased run off after rain (Symes and Perrin, 2004) or, if situated within a main trunk, may result in a reduced amount of precipitation entering the hollow. A similar preference for vertically oriented hollows has been observed in grey-headed parrots (*Poicephalus fuscicollis suahelicus*) in South Africa as well as other secondary cavity nesters in South America, but this is not a universal choice as parrots within Indonesia did not appear to preferentially select hollows based on angle (Marsden and Jones, 1997; Symes and Perrin, 2004). This may be due to differences in climate, particularly rainfall, with South Africa and South East Australia positioned on similar latitudes. Poaching pressure may also determine nest selection in Indonesian parrots, with evidence of some species selecting high hollows that are inaccessible to poachers (Marsden and Jones, 1997). High hollows have also been associated with increased nesting success due to increased protection from ground-based predators (Castillo and Eberhard, 2006), which may explain the increased visitations of the sulphur-crested cockatoo at hollows situated higher in the tree. Hollow height was also significantly associated with swift parrots (Stojanovic et al., 2012) and other secondary cavity nesters, with nests more likely to be found in trees that had hollows situated higher above the ground (Cockle et al., 2011; Martin et al., 2004).

Species of tree was an important explanatory variable for hollow choice by both sulphur-crested cockatoos and rainbow lorikeets. *A. costata* was the only species that significantly explained visitation by the sulphur-crested cockatoo. In the study region, *A. costata* had the highest number of main stem hollows that typically have an angle closer to vertical and may therefore be more attractive to sulphur-crested cockatoos. Given the significant association of *A. costata* with the sulphur-crested cockatoo, this species of tree may have higher conservation value in urban regions for the sulphur-crested cockatoo than other species of tree. Additionally, the presence of rainbow lorikeets was significantly explained by the presence of multiple hollows in the same tree, which is concordant with previous observations of several pairs nesting within the same tree (Higgins, 1999).

Visitations by rainbow lorikeets were significantly explained by increased hollow depth but interestingly the large sulphur-crested cockatoo was not significantly associated with hollow depth. Similarly, hollow depth was not recorded as an important characteristic for the red-tailed black-cockatoo (*Calyptorhynchus banksii*) and Carnaby's cockatoo nor for the grey-headed parrot but was important for swift parrots (Saunders et al., 1982; Stojanovic, et al., 2012; Symes and Perrin, 2004). Hollow depth may be less important, providing the hollow floor is sufficiently far below the hollow entrance to provide shelter and stop young from falling out of the nest (Saunders et al., 1982). Internal volume may be a more important characteristic than hollow depth and floor diameter was an important characteristic for the location of swift parrot nests (Cockle et al., 2011; Stojanovic et al., 2012; Symes and Perrin, 2004). As long as a hollow has enough space to raise young and sleep (Cockle et al., 2011; Martin et al., 2004) depth may not be important once the critical depth between the floor and the entrance has been reached.

Type of hollow is thought to be one of the most important hollow characteristics influencing choice by hollow-nesting animals (Goldingay, 2009) and a hollow spout was the only significant characteristic that explained visitations by the Australian king parrot. Vertical spouts have been associated with larger parrots (Goldingay, 2009) and comprised 53 % of urban hollows in the current study. Ensuring that a diversity of different types of hollows is retained is important for the maintenance of diversity of hollow-utilising fauna.

Direction of the hollow entrance was important for the rainbow lorikeet with east and west being significant predictors. Direction may be a surrogate for internal hollow temperature and when optimal hollows are not limiting, secondary cavity nesters may preferentially select hollows with specific aspects in order to moderate temperature (Ardia et al., 2006; Goldingay, 2009). Preferences for hollow entrance direction have also been recorded for both the yellow-crowned parrot (*Amazona ochrocephala*) as well as grey-headed parrot (Castillo and Eberhard, 2006; Symes and Perrin, 2004).

This study showed that, whilst remnant vegetation contained both the highest density of hollow-bearing trees and the highest number of hollows per tree of all the urban habitats, the urban landscape overall provides few hollow-bearing trees, and those trees that do have hollows contain significantly fewer than trees in natural landscapes. Moreover, different species of parrot appeared to choose hollows with specific characteristics. This may be because of differences in their biology or it may be because there is a shortage of hollows and a superior competitor occupies the universally preferred hollows. Given the decline of hollow-bearing trees in urban landscapes and the lack of recruitment, there may be a potential paucity of hollows in the future before planted species mature (Goldingay and Stevens, 2009; Saunders et al., 1982).

To address this potential shortage in suitable hollows, people living in urban areas are being encouraged to use nest boxes, however this assumes that target species will utilise nest boxes in place of natural hollows (Durant et al., 2009). Information on associations between species of hollow users and nest box characteristics should be available to the public and strategic deployment of nest boxes (e.g. by local councils) should be undertaken. It is therefore important for land managers to document and understand the distribution of hollow-bearing trees throughout landscapes as well as the type of hollows that are present within hollow-bearing trees. For example parks, streets and golf courses all have significantly fewer hollow-bearing trees and hollows per tree than continuous forest. These habitats and, in particular streets, may benefit from supplementation with specifically designed nest boxes to substitute hollow substrates that may be lacking. Spouts, for example, have been associated with parrots, particularly the Australian king parrot, and were most commonly found in *A. costata* and *E. pilularis*. Streets and parks commonly comprise exotic and non-endemic native trees (E.g. *E. sideroxylon*) that may not produce as many spouts. Planting endemic *A. costata* and *E. pilularis* could therefore help to ensure persistence of urban parrots. Further research should focus on determining the association between different types of nestboxes and particular parrot species. Other urban open spaces such as golf courses also have potential conservation value and supplementation with appropriate nest boxes and plantings may benefit hollow-utilising fauna. Once such knowledge is available, specifically designed or positioned nest boxes can be deployed to target particular species whose preferred hollow characteristics may be limited in the landscape.

Chapter 8: General Discussion

Photo: A Davis

This study arose from the observation that, despite a general decline in avian diversity within cities worldwide, parrots have become a conspicuous component of the avifauna, in Australian cities, including Brisbane (Catterall et al., 2010; Sewell and Catterall, 1998), Sydney (Burgin and Saunders, 2007; Major and Parsons, 2010; Parsons et al., 2006), Canberra (Veerman, 1991) and Melbourne (Lowry and Lill, 2007; Shukuroglou and McCarthy, 2006; Smith and Lill, 2008). The aim of this study was to investigate the composition and distribution of the parrot assemblage within a large urban centre, with respect to the relative importance of key abiotic and biotic factors that influence the parrot assemblage.

The Sydney urban parrot assemblage comprised 13 species, of which 10 species had a significantly higher abundance in the urban landscape compared to that in surrounding forest. Parrot abundance was highest in the suburban and outer suburban regions of the urban landscape, except for the rainbow lorikeet, which was ubiquitous. The abundance of the rainbow lorikeet, along with five other species, responded to changes in rainfall and the crimson rosella increased in abundance in the urban landscape following wild fire. The urban landscape was characterised by a significantly greater amount of nectar energy as compared to that available in forest. Streets provided a higher amount of nectar throughout the year and street trees produced more flowers, and flowered for longer, than trees within forest. This increased availability of nectar appears to contribute to the high abundance of urban nectarivorous parrots. The high abundance of all parrots within the urban landscape, combined with the fact that urban landscapes have significantly fewer hollows compared to forest, explains the relatively high number of both visitations and aggressive interactions at urban tree hollows.

8.1 The urban parrot community

Droughts and wild fires have previously purported to explain influxes of parrots into the urban landscape (Hindwood, 1939; Recher, 1997). This study provided some support for this, with the abundance of the sulphur-crested cockatoo and the galah increasing in the urban landscape during periods of decreased rainfall in rural regions. Wild fire also significantly influenced the abundance of the crimson rosella, with more crimson rosellas present in the urban landscape following fire. During times of environmental stress, when resources outside the urban landscape may be in short supply, the urban region may provide stable resources through artificial substitutes, such as water fountains (Oprea et al., 2009) and watered and fertilised lawns. In this study, lawns of golf courses and parks were observed to regularly have large numbers of corellas foraging on them during summer. Corellas may move into the urban landscape during summer to exploit softer foraging ground and more readily available water supplies. Such resource-driven movements have previously been observed in Western Australia, where corellas and cockatoos made resource-related movements to the coast during summer (Saunders, 1980; Smith and Moore, 1992). Corellas do, however, have strong site fidelity (Higgins, 1999) and may return to previous breeding sites outside the urban landscape for the breeding season, which would explain their decrease in abundance during the breeding season and subsequent absence at any urban tree hollows during the breeding season.

This study showed that there is undoubtedly a higher abundance of parrots in the urban landscape, compared to surrounding forest. Whilst drought and wild fire may result in periodic boosts to the abundance of parrots within the urban region, it is more likely that the majority of individuals are resident. Rainbow lorikeets, in particular, appear to be resident, being ubiquitous in all components of the urban landscape. The ubiquity of the rainbow lorikeet throughout many Australian cities is similar to that of the ringneck parrot and the monk parakeet throughout many northern hemispheric cities (Butler, 2005; Minor et al., 2012; Pruett-Jones et al., 2012; Strubbe and Matthysen, 2009). The rainbow lorikeet however, differs, in being a nectarivore, which feeds upon both mid-storey shrubbery and in the canopy of trees, and is capable of tracking nectar at the level of the individual tree (Franklin and Noske, 1999; Higgins, 1999). This allows the rainbow lorikeet to exploit a variety of resources across all urban habitats, including small gardens and sporadically flowering street trees within the inner suburbs, as well as resources on larger green spaces, such as golf courses and remnants.

The suburban and outer suburban regions contained the highest abundance of all other parrots, which is typical of many urban regions due to the diversity of habitat and resources present in the suburbs (Meffert and Dziock, 2013; Tratalos et al., 2007). The musk lorikeet, another highly mobile nectarivore that is capable of tracking nectar, was common throughout the suburban and outer suburban regions, however, unlike the rainbow lorikeet, its abundance varied between breeding and non-breeding seasons. This change in abundance may be due to females leaving nesting hollows and fledged juveniles being recruited into the population (Wenner and Hirth, 1984), which would increase flock size. However, given that the non-breeding season coincided with the flowering of locally-occurring trees within the urban landscape, it is also possible that the higher abundance of musk lorikeets may be due to some individuals entering the urban landscape to take advantage of resources that may be more reliable compared to resources in natural forest. Similar exploitation of urban resources and resource-driven movements has also been observed by the musk lorikeet in Sydney (Hindwood, 1939) and Melbourne (Stanford and Lill, 2008).

8.2 Increased Availability of Nectar Resources

Nectar is not only the primary food source of the rainbow lorikeet, the most abundant urban parrot, but is also a resource that may be profoundly affected by urbanisation. Gardens are a dominant component of the urban landscape, particularly within the suburbs (Goddard et al., 2010), and previously-existing vegetation may be replaced with either flowering exotics or native hybrid 'wildlife-friendly' or 'bird-attracting' plants that produce large amounts of nectar (French et al., 2005; Sewell and Catterall, 1998). Nectar availability is also likely to be positively altered due to the landscaping of public green spaces, which further alters the composition of vegetation and consequent availability of nectar within the urban landscape. This was the first study to quantify the nectar-yielded energy at the habitat scale within the urban landscape.

This study conclusively demonstrated that suburban habitat has a rich nectar resource that is sufficient to explain the high abundance of several species of nectar-feeding parrots in Australian cities. Streets, as compared to other habitats, yielded a high amount of nectar energy that was consistent throughout the year, with only heath yielding comparable energy when the large *Banksia* species flowered. *Eucalyptus* trees provided the majority of nectar energy within streets, as well as in forest remnants. In addition to the greater number of endemic street trees that flowered in the urban landscape compared to forest, the asynchronously flowering non-endemic Eucalypt street trees added additional nectar to the system, which may explain the significant association between lorikeets and flowering *Eucalyptus* spp. Non-endemic street trees that flowered asynchronously to endemic trees in Melbourne comprised a significant component of the diet of rainbow lorikeets and musk lorikeets, particularly through the winter when local trees were not in flower (Stanford and Lill, 2008). *Callistemon* and *Grevillea* species contributed the majority of the remaining nectar to the system. Hybrid *Grevillea* spp. are a popular 'native' garden choice and are also marketed as 'bird attracting', due to the large amounts of nectar they yield

(Burgin and Saunders, 2007; French et al., 2005; Sewell and Catterall, 1998), with *Callistemon* spp. frequently planted as street vegetation throughout Sydney. Planting a diverse range of high nectar-yielding plants has allowed larger mobile nectarivores to exploit a supply of nectar that is greater than in both forests and remnants. Additionally the diversity of nectar-bearing plants, particularly *Eucalyptus* spp, along with hybrid garden plants, may sustain populations of lorikeets through the winter when other sources of nectar are reduced. Whilst remnants appear not to have the abundant supply of nectar, they do contain tree hollows, a necessary breeding resource for parrots.

8.3 Hollow Abundance and Competition

The urban landscape is generally assumed to contain fewer hollows compared to natural forest (Durant et al., 2009; Harper et al., 2005a; Harper et al., 2005b), however the hollow resource availability in different habitats within the same city had never previously been quantified. Parrots, as obligate cavity-nesters, rely on tree hollows, and with the increasing density of parrots within the urban landscape, there may not be enough hollows to support the current diversity of hollow-utilising urban taxa. Knowledge of hollow distribution and hollow usage is crucial to prevent future declines in biodiversity.

This study demonstrated that there is less than half the density of hollows in a major city compared to that of surrounding forest, and provided compelling evidence for there being a shortage of tree hollows in the urban landscape. Whilst remnant vegetation contained a comparable number of hollow-bearing trees compared to forest, it contained only half the number of hollow cavities. Other habitats within the urban landscape contained even fewer hollows than remnants. Perhaps as a result, the visitation rate at urban hollows was much higher compared to hollows in forest, and two parrot species, the rainbow lorikeet and the sulphur-crested cockatoo, dominated the urban hollow community. The rainbow lorikeet also made more visits than other taxa to hollows, and had the highest number of intraspecific interactions compared to other taxa. High intraspecific aggression is often seen in habitats where resources are limiting or when resources are clumped (Cockle et al., 2011), such as in remnants, where a high number of hollows occur within a relatively small sized patch of isolated vegetation. Whilst the total number of hollows may not be limiting, the number of suitable hollows for nesting (e.g. hollows that don't flood during rain) or hollows with requirements for specific species (type of hollow) can be limiting (Bennett et al., 1994; Cockle et al., 2010; Goldingay, 2009; Symes and Perrin, 2004; Wesolowski et al., 2002). Availability of hollows within the Sydney urban landscape may not yet have reached carrying capacity, since the increase in the abundance of many species of parrot is still a relatively recent phenomenon. Given that nearly all the parrot species sighted within Sydney during this project have increased in abundance over the last 30 years, there is clearly the potential for a future shortage of hollows. The rainbow lorikeet appears to be particularly adaptable with its nesting requirements, having been observed nesting in a variety of tree hollows as well as chimneys, power poles and under tree roots (Higgins, 1999). Additionally, it preferred to nest in trees with multiple hollows, indicating that it may guard several hollows. If the rainbow lorikeet continues to increase in both density and abundance, there is the potential that it may outcompete less competitive species if the number of suitable nesting hollows decreases. If hollows are not currently limiting and the number of suitable and available hollows remains constant, the rainbow lorikeet may still pose a threat to other cavity-nesting taxa as it continues to increase in abundance and occupy more hollows.

8.4 Conclusions

The urban landscape has benefited many species of parrot, providing them with good foraging and nesting resources, as compared to natural forest. Streets, golf courses, ovals and gardens provide constant and abundant food resources for nectarivorous and granivorous parrots, which are typically within a short flight to nesting sites within remnant vegetation. This close proximity means that nesting parrots do not need to forage far from nesting sites and have a consistent supply of food resources during both the breeding season as well as the harsher summer months. This reliability and consistency of food resources means we may see a greater number of species using cities and urban landscapes as a stable resource, compared to the natural environment, which is characterised by dynamic and unpredictable natural events. Streets, in particular, supply a high amount of nectar with relatively low seasonal variation in availability. Stable supplies of food resources appear to sustain densities of parrots above that which would normally exist in natural habitat.

Despite a higher abundance of parrots and a lower density of tree hollows compared to natural forest, the urban landscape currently appears to contain enough available nesting resources to sustain the present assemblage and density of parrots. The rainbow lorikeet and the sulphur-crested cockatoo are the two most prominent parrots in the urban assemblage, with not only the highest abundance, but also the most visitations at tree hollows. In addition they are responsible for more aggressive interactions at tree hollows compared to other parrot species. If populations of the rainbow lorikeet and the sulphur-crested cockatoo continue to increase throughout the urban landscape and/or the number of hollows decline, we may see an eventual reduction in avifaunal diversity as the density of parrots surpasses the carrying capacity of available hollows, and less competitive parrots are excluded (Bennett et al., 1994; Goldingay and Stevens, 2009; Waterhouse, 1997). A greater understanding of the fine scale processes and patterns associated with urbanisation and the biological consequences of how changes within the urban landscape affect the ecology of wildlife, at the species, population and community level is needed (Clergeau et al., 2006; de Toledo et al., 2012).

Further research into how planted vegetation affects the ecology of the avifaunal community is necessary. If the total amount of green space continues to decrease, the remaining green spaces will be become critical in providing wildlife habitat (Ikin et al., 2013). Knowledge of how to landscape green spaces, such as small parks, streets and gardens, in order to conserve ecological functions and maintain biodiversity is crucial. Gardens potentially contribute the collective majority of green space within cities (Smith et al., 2006), and, in some countries, are now incorporated into conservation initiatives (Smith et al., 2006). Eucalypts provide an important foraging source for rainbow lorikeets and musk lorikeets, as well as noisy miners (Sewell and Catterall, 1998). The current diversity of native Eucalypts that are endemic to the region and those that aren't endemic, provides an abundant and constant supply of nectar, especially given that the Eucalypts within the urban region flower more profusely and more frequently than the forest, which helps sustain the a high abundance of large-bodied native nectarivores. Indigenous native eucalypts are also characterised by a greater arthropod biomass (Bhullar and Majer, 2000), which attracts insectivorous birds (Recher et al., 1996), and the combination of increased nectar from non-indigenous native eucalypts and a smaller invertebrate biomass appears to favour nectarivores over insectivores. Small insectivores are further disadvantaged due to the lack of dense cover-providing mid-storey vegetation that is typically absent in many landscaped urban green spaces (Sewell and Catterall, 1998; White et al., 2005). This open and sparse vegetation that characterises the urban landscape has replaced what was once a continuous forest mosaic, with patches of rainforest, as well as open woodland and grassland (Benson and Howell, 1995; Sewell and Catterall, 1998). The simplified urban vegetation contains a variety of different plant types, which offer a variety of resources that elicit different responses from different bird species (Catterall et al., 1998; Sewell and Catterall, 1998; White et al., 2005). Rather than advocating for the 're-creation' of 'native' vegetation within urban green spaces, green spaces should be landscaped with respect to previously existing indigenous vegetation and understanding of the responses of different taxonomic guilds, as well as individual bird species, to changes in urban plantings.

A thorough understanding of the hollow resources within the urban region is also necessary to manage and conserve urban wildlife. In addition to the relative density of hollows in urban habitats, it is important to know what types of hollows are available within the urban landscape. Consequently, the types of hollows (or even species of tree) that are present within the urban landscape may select for certain taxa, due to the existence (or lack thereof) of species-specific hollow requirements (Aitken and Martin, 2004; Cockle et al., 2011; Gibbons et al., 2002; Newton, 1994). Further work is required to determine the proportions of different hollow types within the urban region as well as the number of available hollows that are suitable for particular species. Further research is also needed to determine the proportion of hollows that are currently available for nesting and the extent that a shortage of hollows may be limiting reproduction, if at all. Given the lack of hollows in the urban region, compared to forested regions, and the amount of time required for existing and newly planted trees to form hollows, it may be decades before more suitable hollows become available. To compensate for such lack of natural hollows, nest boxes are frequently utilised (Harper et al., 2005b). To aid in effective nest box design and placement however, a thorough understanding of the distribution and types of hollows throughout the urban landscape, as well as specific hollow characteristics that may be required for target species, by land-management agencies such as councils is necessary (Durant et al., 2009; Goldingay and Stevens, 2009; Harper et al., 2005b; Menkhorst, 1984).

Understanding how to sustainably design and manage urban environments to conserve biodiversity can help to alleviate some of the negative effects typically associated with urbanisation, to both wildlife and humans (Shwartz et al., 2008). Urbanisation typically isolates and disconnects people from nature, which can result in an apathy towards conservation objectives, however it does also provide an opportunity to educate large numbers of people about conservation, particularly those who are unable to travel outside of the city (Dearborn and Kark, 2010; Dunn et al., 2006; Miller, 2005). For many city dwellers, urban green spaces may provide the only exposure to nature, which is becoming increasingly important for quality of life within urban society (Chiesura, 2004; Fuller et al., 2007). Exposure to nature within cities is associated with a range of social and psychological benefits, and these benefits become more pronounced as species richness increases within urban green spaces (Chiesura, 2004; Dearborn and Kark, 2010; Fuller et al., 2007).

Australian cities are currently characterised by not only a diverse avifauna, but also a colourful and charismatic avifauna including many species of parrots. Understanding how these parrots utilise the urban landscape and how they respond to anthropogenically induced biotic and abiotic changes to the landscape has the potential to allow both humans and wildlife to live together and to prevent the loss of diversity that has been typically seen in cities with longer histories of human habitation.

References

Aitken, K. E. H., Martin, K., 2004. Nest cavity availability and selection in aspen-conifer groves in a grassland landscape. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 34*, 2099-2109.

Aitken, K. E. H., Martin, K., 2007. The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forests of western Canada. *Journal of Ornithology 148*, S425-S434.

Altermatt, F., 2012. Temperature-related shifts in butterfly phenology depend on the habitat. *Global Change Biology 18*, 2429-2438.

Anderies, J. M., Katti, M., Shochat, E., 2007. Living in the city: Resource availability, predation, and bird population dynamics in urban areas. *Journal of Theoretical Biology 247*, 36-49.

Anderson, T. R., 2006. *Biology of the Ubiquitous House Sparrow: From Genes to Populations*. Oxford University Press, Oxford.

Ardia, D. R., Perez, J. H., Clotfelter, E. D., 2006. Nest box orientation affects internal temperature and nest site selection by Tree Swallows. *Journal of Field Ornithology 77*, 339-344.

Arizmendi, M. D., Constanza, M. S., Lourdes, J., Ivonne, F. M., Edgar, L. S., 2007. Effect of the presence of nectar feeders on the breeding success of Salvia mexicana and Salvia fulgens in a suburban park near Mexico City. *Biological Conservation 136*, 155-158.

Armstrong, D. P., 1991. Nectar Depletion And Its Implications For Honeyeaters In Heathland Near Sydney. *Australian Journal of Ecology 16*, 99-109.

Armstrong, D. P., Paton, D. C., 1990. Methods For Measuring Amounts Of Energy Available From Banksia Inflorescences. *Australian Journal of Ecology 15*, 291-297.

Ashley, L. C., Major, R. E., Taylor, C. E., 2009. Does the presence of grevilleas and eucalypts in urban gardens influence the distribution and foraging ecology of Noisy Miners? *Emu 109*, 135-142.

Australian Bureau of Statistics, 2008, Australian Social Trends, Australian Bureau of Statistics. July 28th 2013, http://www.abs.gov.au/AUSSTATS/abs@.nsf/Lookup/4102.0Chapter3002008

Baker, A. J., Moeed, A., 1987. Rapid Genetic Differentiation And Founder Effect In Colonizing Populations Of Common Mynas (*Acridotheres tristis*). *Evolution 41*, 525-538.

Bang, C., Faeth, S. H., Sabo, J. L., 2012. Control of arthropod abundance, richness, and composition in a heterogeneous desert city. *Ecological Monographs 82*, 85-100.

Barrett, G., Silcocks, A., Barry, S. C., Cunningham, R. B., Poulter, R.. 2003. *The New Atlas of Australian Birds*. Birds Australia, Victoria.

Beadle, N. C. W., 1962. Soil Phosphate And Delimitation Of Plant-Communities In Eastern Australia. *Ecology 43*, 281-288.

Beissinger, S. R., Osborne, D. R., 1982. Effects Of Urbanization On Avian Community Organization. *Condor 84*, 75-83.

Bekessy, S. A., White, M., Gordon, A., Moilanen, A., McCarthy, M. A., Wintle, B. A., 2012. Transparent planning for biodiversity and development in the urban fringe. *Landscape and Urban Planning 108*, 140-149.

Benedict, M. A., Mcmahon, E. T., 2006. *Green infrastructure: linking landscapes and communities*. Island Press, Washington DC.

Bennett, A., Lumsden, L., Alexander, J., Duncan, P., Johnson, P., Robertson, P., Silveira, C., 1991. Habitat Use by Arboreal Mammals along an Environment Gradient in North-eastern Victoria. *Wildlife Research 18*, 125-146.

Bennett, A. F., Lumsden, L. F., Nicholls, A. O., 1994, Tree hollows as a resource for wildlife in remnant woodlands: spatial and temporal patterns across the northern plains of Victoria, Australia., *Pacific Conservation Biology* **1:**222-235.

Benson, D., Howell, J., 1995. *Taken for granted: the bushland of Sydney and it's suburbs*. Kangaroo Press, Kenthurst.

Bertoncini, A. P., Machon, N., Pavoine, S., Muratet, A., 2012. Local gardening practices shape urban lawn floristic communities. *Landscape and Urban Planning 105*, 53-61.

Bhullar, S., Majer, J., 2000. Arthropods on Street Trees: A Food Resource for Wildlife, *Pacific Conservation Biology 6*, 171-173.

Biamonte, E., Sandoval, L., Chacon, E., Barrantes, G., 2011. Effect of urbanization on the avifauna in a tropical metropolitan area. *Landscape Ecology 26*, 183-194.

Blair, R., 2001, Creating a homogeneous., in: *Avian ecology and conservation in an urbanizing world.* (J. M. Marzluff, R. Bowman, R. Donelly, eds.), Kluwer Academic, Boston MA pp. 459-486.

Blair, R., 2004. The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society 9*, 2.

Blair, R., Johnson, E., 2008. Suburban habitats and their role for birds in the urban–rural habitat network: points of local invasion and extinction? *Landscape Ecology 23,* 1157-1169.

Blair, R. B., 1996. Land Use and Avian Species Diversity Along an Urban Gradient. *Ecological Applications 6*, 506-519.

Blakely, T. J., Jellyman, P. G., Holdaway, R. J., Young, L., Burrows, B., Duncan, P., Thirkettle, D., Simpson, J., Ewers, R., Didham, R. K., 2008. The abundance, distribution and structural characteristics of tree-holes in *Nothofagus* forest, New Zealand. *Austral Ecology 33*, 963-974.

Bolger, D. T., Alberts, A. C., Sauvajot, R. M., Potenza, P., McCalvin, C., Tran, D., Mazzoni, S., Soule, M. E., 1997. Response Of Rodents To Habitat Fragmentation In Coastal Southern California. *Ecological Applications 7*, 552-563.

Bolton, A. B., Bolten, A. B., Feinsinger, P., Baker, H. G., Baker, I., Freisinger, P., 1979. On the Calculation of Sugar Concentration in Flower Nectar. *Oecologia 41*, 301-304.

Bonan, G. B., 2002. *Ecological climatology: concepts and applications*. Cambridge University Press, New York.

Bonnington, C., Gaston, K. J., Evans, K. L., 2013. Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. *Journal of Applied Ecology 50*, 15-24.

Bradstock, R. A., 2008. Effects of large fires on biodiversity in south-eastern Australia: disaster or template for diversity? *International Journal of Wildland Fire 17***,** 809-822.

Brearley, G., McAlpine, C., Bell, S., Bradley, A., 2012. Influence of urban edges on stress in an arboreal mammal: a case study of squirrel gliders in southeast Queensland, Australia. *Landscape Ecology* **27**, 1407-1419.

Breuste, J., Niemelä, J., Snep, R., 2008. Applying landscape ecological principles in urban environments. *Landscape Ecology 23*, 1139-1142.

Brittingham, M. C., 1991. Effect of winter feeding on wild birds., in: *Wildlife conservation in metropolitan environments.* (L. W. Adams, D. L. Leedy, eds.), National Institute for urban wildlife. Columbia.

Brooker, M. G., 1998. Fire and birds in a Western Australian heathland. *Emu 98,* 276-287.

Brown, J. L., 1969. Territorial Behavior And Population Regulation In Birds. *Wilson Bulletin 81*, 293-329.

Bryant, M. M., 2006. Urban landscape conservation and the role of ecological greenways at local and metropolitan scales. *Landscape and Urban Planning 76*, 23-44.

Burgin, S., Saunders, T., 2007. Parrots of the Sydney region: population changes over 100 years., in: *Pest or guest: the zoology of overabundance.* (D. Lunney, P. Eby, P. Hatchings, S. Burgin, eds.). The Royal Zoological Society of New South Wales, Mosman, NSW.

Burnham, K. P., Anderson, D. R., 2002. Model Selection and Multimodel Inference: a practical information-theoretic approach, 2nd edition. , in: *Wilelife*, Springer-Verlag, New York.

Butler, C. J., 2005. Feral parrots in the continental United States and United Kingdom: Past, present, and future. *Journal of Avian Medicine and Surgery 19*, 142-149.

Cameron, M., 2006. Nesting habitat of the glossy black-cockatoo in central New South Wales. *Biological Conservation 127*, 402-410.

Cannon, C. E., 1979. Observations on the food and energy-requirements of rainbow lorikeets, *Trichoglossus haematodus* (Aves, Psittacidae). *Australian Wildlife Research 6*, 337-346.

Carbo-Ramirez, P., Zuria, I., 2011. The value of small urban green spaces for birds in a Mexican city. *Landscape and Urban Planning 100*, 213-222.

Cardilini, A. P. A., Weston, M. A., Nimmo, D. G., Dann, P., Sherman, C. D. H., 2013. Surviving in sprawling suburbs: Suburban environments represent high quality breeding habitat for a widespread shorebird. *Landscape and Urban Planning 115*, 72-80.

Carpaneto, G., Mazziotta, A., Coletti, G., Luiselli, L., Audisio, P., 2010. Conflict between insect conservation and public safety: the case study of a saproxylic beetle (*Osmoderma eremita*) in urban parks. *Journal of Insect Conservation 14*, 555-565.

Carreiro, M. M., Tripler, C. E., 2005. Forest remnants along urban-rural gradients: Examining their potential for global change research. *Ecosystems 8*, 568-582.

Case, T. J., 1996. Global patterns in the establishment and distribution of exotic birds. *Biological Conservation 78*, 69-96.

Castillo, A. M. R., Eberhard, J. R., 2006. Reproductive behavior of the Yellow-crowned Parrot (Amazona ochrocephala) in western Panama. *Wilson Journal of Ornithology 118*, 225-236.

Catterall, C. P., 2004. Birds, garden plants and suburban bushlots: where good intentions meet unexpected outcomes, in: *Urban wildilfe: more than meets the eye* (D. Lunney, S. Burgin, eds.), Royal Zoological Society of New South Wales, Mosman, NSW.

Catterall, C. P., 2009. Responses of faunal assemblages to urbanisation: global research paradigms and an avian case study, in: *Ecology of Cities and Towns: A Comparative Approach* (M. J. McDonnell, A. K. Hahs, J. H. Breuste, eds.), pp. 129-155.

Catterall, C. P., Cousin, J. A., Piper, S., Johnson, G., 2010. Long-term dynamics of bird diversity in forest and suburb: decay, turnover or homogenization? *Diversity and Distributions 16*, 559-570.

Catterall, C. P., Kingston, M. B., Park, K., Sewell, S., 1998. Deforestation, urbanisation and seasonality: Interacting effects on a regional bird assemblage. *Biological Conservation 84*, 65-81.

Chace, J. F., Walsh, J. J., 2006. Urban effects on native avifauna: a review. *Landscape and Urban Planning 74*, 46-69.

Chamberlain, D. E., Cannon, A. R., Toms, M. P., Leech, D. I., Hatchwell, B. J., Gaston, K. J., 2009. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis 151*, 1-18.

Chiesura, A., 2004. The role of urban parks for the sustainable city. *Landscape and Urban Planning 68*, 129-138.

Chiron, F., Shirley, S., Kark, S., 2009. Human-related processes drive the richness of exotic birds in Europe. *Proceedings of the Royal Society B-Biological Sciences 276*, 47-53.

Chudoba, E. A., Mallin, M. A., Cahoon, L. B., Skrabal, S. A., 2013. Stimulation of fecal bacteria in ambient waters by experimental inputs of organic and inorganic phosphorus. *Water Research 47*, 3455-3466.

Chung, U., Jung, J. E., Seo, H. C., Yun, J. I., 2009. Using urban effect corrected temperature data and a tree phenology model to project geographical shift of cherry flowering date in South Korea. *Climatic Change 93*, 447-463.

Clarke, K. R., 1993. Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology 18*, 117-143.

Clergeau, P., Croci, S., Jokimaki, J., Kaisanlahti-Jokimaki, M. L., Dinetti, M., 2006. Avifauna homogenisation by urbanisation: Analysis at different European latitudes. *Biological Conservation 127*, 336-344.

Clergeau, P., Savard, J. P. L., Mennechez, G., Falardeau, G., 1998. Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. *Condor 100*, 413-425.

Cockle, K., Capuzzi, G., Bodrati, A., Clay, R., del Castillo, H., Velazquez, M., Areta, J. I., Farina, N., Farina, R., 2007. Distribution, abundance, and conservation of vinaceous amazons (*Amazona vinacea*) in Argentina and Paraguay. *Journal of Field Ornithology 78*, 21-39.

Cockle, K., Martin, K., Wiebe, K., 2008. Availability of cavities for nesting birds in the Atlantic forest, Argentina. *Ornitologia Neotropical 19,* 269-278.

Cockle, K., Martin, K., Wiebe, K., 2011. Selection of Nest Trees by Cavity-nesting Birds in the Neotropical Atlantic Forest. *Biotropica 43*, 228-236.

Cockle, K. L., Martin, K., Drever, M. C., 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biological Conservation 143*, 2851-2857.

Collins, B. G., Newland, C., 1986. Honeyeater population-changes in relation to food availability in the jarrah forest of western australia. *Australian Journal of Ecology 11*, 63-76.

Collins, L., Bradstock, R. A., Tasker, E. M., Whelan, R. J., 2012. Impact of fire regimes, logging and topography on hollows in fallen logs in eucalypt forest of south eastern Australia. *Biological Conservation 149*, 23-31.

Commonwealth Bureau of Meteorology, 2011a. Average annual and monthly maximum, minimum and mean temperature., Australian Government, Canberra. November 7th 2012, http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index.jsp

Commonwealth Bureau of Meteorology, 2011b, Average annual, seasonal and monthly rainfall., Australian Government, Canberra. November 7th 2012, http://www.bom.gov.au/jsp/ncc/climate_averages/temperature/index.jsp

Conole, L. E., Kirkpatrick, J. B., 2011. Functional and spatial differentiation of urban bird assemblages at the landscape scale. *Landscape and Urban Planning 100*, 11-23.

Cotton, P. A., 2007. Seasonal resource tracking by Amazonian hummingbirds. *Ibis 149*, 135-142.

Courtney, J., Debus, S. J. S., 2006. Breeding habits and conservation status of the Musk Lorikeet (*Glossopsitta concinna*) and Little lorikeet (*G. pusilla*) in Northern New South Wales. *Australian Field Ornithology 23,* 109-124.

Crome, F., Shields, J., 1992. *Parrots and Pigeons of Australia.* Angus and Roberston, Sydney.

Crooks, K. R., Suarez, A. V., Bolger, D. T., 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biological Conservation 115*, 451-462.

Davis, A., Taylor, C. E., Major, R. E., 2011. Do fire and rainfall drive spatial and temporal population shifts in parrots? A case study using urban parrot populations. *Landscape and Urban Planning 100*, 295-301.

Davis, A., Taylor, C. E., Major, R. E., 2012a, Seasonal abundance and habitat use of Australian parrots in an urbanised landscape, *Landscape and Urban Planning* **106**(2)**:**191-198.

Davis, J. R., Boyle, S. A., Khan, A. A., Gay, A. L. J., Grisham, J. M., Luque, L. E., 2012b. Snake parasitism in an urban old-growth forest. *Urban Ecosystems 15*, 739-752.

Day, T. D., 1995. Bird species composition and abundance in relation to native plants in urban gardens, Hamilton, New Zealand. *Notornis 42,* 172-186.

de Toledo, M. C. B., Donatelli, R. J., Batista, G. T., 2012. Relation between green spaces and bird community structure in an urban area in Southeast Brazil. *Urban Ecosystems 15*, 111-131.

Dearborn, D. C., Kark, S., 2010. Motivations for Conserving Urban Biodiversity, *Conservation Biology 24*, 432-440.

Ding, H. Y., Shi, W. Z., 2013. Land-use/land-cover change and its influence on surface temperature: a case study in Beijing City. *International Journal of Remote Sensing 34*, 5503-5517.

Dixon, M. D., 2012. Relationship between land cover and insectivorous bat activity in an urban landscape. *Urban Ecosystems 15*, 683-695.

Dunn, R. R., Gavin, M. C., Sanchez, M. C., Solomon, J. N., 2006. The pigeon paradox: Dependence of global conservation on urban nature. *Conservation Biology 20*, 1814-1816.

Durant, R., Luck, G. W., Matthews, A., 2009. Nest-box use by arboreal mammals in a peri-urban landscape. *Wildlife Research 36*, 565-573.

Ellis, M. F., Sedgley, M., 1992. Floral morphology and breeding system of 3 species of *Eucalyptus*, section bisectaria (myrtaceae). *Australian Journal of Botany 40*, 249-262.

Emison, W. B., 1996. Use of supplementary nest hollows by an endangered subspecies of Red-tailed Black-cockatoo. *The Victorian Naturalist 113,* 262-263.

Emlen, J. M., 1966. Role of time and energy in food preference. *American Naturalist 100*, 611-617.

Emlen, J. T., 1974. Urban bird community in Tucson, Arizona - derivation, structure, regulation. *Condor* ***76***, 184-197.

Espeland, E. K., Carlsen, T. M., Macqueen, D., 2005. Fire and dynamics of granivory on a California grassland forb. *Biodiversity and Conservation 14*, 267-280.

Estoque, R. C., Murayama, Y., 2013. Landscape pattern and ecosystem service value changes: Implications for environmental sustainability planning for the rapidly urbanizing summer capital of the Philippines. *Landscape and Urban Planning 116,* 60-72.

Evans, K. L., Newson, S. E., Gaston, K. J., 2009. Habitat influences on urban avian assemblages. *Ibis 151*, 19-39.

Fensham, R. J., Fairfax, R. J., 2008. Water-remoteness for grazing relief in Australian arid-lands. *Biological Conservation 141*, 1447-1460.

FitzGibbon, S. I., Putland, D. A., Goldizen, A. W., 2007. The importance of functional connectivity in the conservation of a ground-dwelling mammal in an urban Australian landscape. *Landscape Ecology 22*, 1513-1525.

Fitzsimons, J. A., Palmer, G. C., Mark J, A., White, J. G., 2003. Refugees and Residents: densities and habitat preferences of lorikeets in urban Melbourne. *Australian Field Ornithology 20,* 2-7.

Franklin, D. C., Noske, R. A., 1999. Birds and Nectar in a Monsoonal Woodland: Correlations at Three Spatio-temporal Scales. *Emu* 99, 15-28.

Fraser, M., McMahon, L., 1992. Habitat change by Cape sugarbirds and orangebreasted sunbirds in an apparent response to fire in old mountain fynbos. *Safring News 21*, 51-54.

French, K., Major, R., Hely, K., 2005. Use of native and exotic garden plants by suburban nectarivorous birds. *Biological Conservation 121*, 545-559.

Fuller, R. A., Irvine, K. N., Devine-Wright, P., Warren, P. H., Gaston, K. J., 2007. Psychological benefits of green space increase with biodiversity. *Biology Letters 3*, 390-394.

Garden, J., Mcalpine, C., Peterson, A., Jones, D., Possingham, H., 2006. Review of the ecology of Australian urban fauna: A focus on spatially explicit processes. *Austral Ecology 31*, 126-148.

Garnett, S. T., Szabo, J. K., Duton, G., 2010. *The Action Plan for Australian Birds 2010.* CSIRO Publishing, Collingwood.

Garrett, K. L., 1997. Population status and distribution of naturalized parrots in southern California. *Western Birds 28,* 181-195.

Garrott, R. A., White, P. J., White, C. A. V., 1993. Overabundance - an issue for conservation biologists. *Conservation Biology 7*, 946-949.

Garson, G. D., 2007. Linear mixed models, from statnotes: topics in multivariate analysis. December 12th 2010. http://www2.chass.ncsu.edu/garson/pa765/statnote.htm.24/05/2007.

Gaston, K. J., Smith, R. M., Thompson, K., Warren, P. H., 2005. Urban domestic gardens (II): experimental tests of methods for increasing biodiversity, *Biodiversity and Conservation 14*, 395-413.

Gero, A. F., Pitman, A. J., Narisma, G. T., Jacobson, C., Pielke, R. A., 2006. The impact of land cover change on storms in the Sydney Basin, Australia. *Global and Planetary Change 54*, 57-78.

Gibbons, P., Lindenmayer, D. B., 1996. Issues associated with the retention of hollow-bearing trees within eucalypt forests managed for wood production. *Forest Ecology and Management 83*, 245-279.

Gibbons, P., Lindenmayer, D. B., Barry, S. C., Tanton, M. T., 2002. Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management. *Biological Conservation 103*, 1-12.

Gilbert, O. L., 1991. *The ecology of urban habitats*. Chapman and Hall, London.

Gill, A. M., Williams, J. E., 1996. Fire regimes and biodiversity: The effects of fragmentation of southeastern Australian eucalypt forests by urbanisation, agriculture and pine plantations. *Forest Ecology and Management 85*, 261-278.

Goddard, M. A., Dougill, A. J., Benton, T. G., 2010. Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology & Evolution 25,* 90-98.

Goldingay, R. L., 2009. Characteristics of tree hollows used by Australian birds and bats. *Wildlife Research 36*, 394-409.

Goldingay, R. L., Stevens, J. R., 2009. Use of artificial tree hollows by Australian birds and bats. *Wildlife Research 36*, 81-97.

Grarock, K., Tidemann, C. R., Wood, J., Lindenmayer, D. B., 2012. Is It Benign or Is It a Pariah? Empirical Evidence for the Impact of the Common Myna (*Acridotheres tristis*) on Australian Birds. *PLoS ONE* 7, e40622.

Green, R. J., 1984, Native and Exotic Birds in a Suburban Habitat. *Wildlife Research 11*, 181-190.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J. G., Bai, X. M., Briggs, J. M., 2008. Global change and the ecology of cities. *Science 319*, 756-760.

Guittar, J. L., Dear, F., Vaughan, C., 2009. Scarlet Macaw (Ara macao, Psittaciformes: Psittacidae) Nest Characteristics in the Osa Peninsula Conservation Area (ACOSA), Costa Rica. *Revista De Biologia Tropical 57*, 387-393.

Gustafsson, L., 1988. Interspecific and intraspecific competition for nest holes in a population of the collared flycatcher *Ficedula albicollis*. *Ibis 130*, 11-16.

Harper, M. J., McCarthy, M. A., van der Ree, R., 2005a. The abundance of hollow-bearing trees in urban dry sclerophyll forest and the effect of wind on hollow development. *Biological Conservation 122*, 181-192.

Harper, M. J., McCarthy, M. A., van der Ree, R., 2005b. The use of nest boxes in urban natural vegetation remnants by vertebrate fauna. *Wildlife Research 32*, 509-516.

Harper, M. J., McCarthy, M. A., van der Ree, R., Fox, J. C., 2004. Overcoming bias in ground-based surveys of hollow-bearing trees using double-sampling. *Forest Ecology and Management 190*, 291-300.

Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V., Brown, C. J., 1997. *The atlas of south African birds. Vol. 1: Non-passerines.* BirdLife South Africa, Johannesburg.

Hasebe, M., Franklin, D., 2004. Food sources of the rainbow lorikeet *Trichoglossus haematodus* during the early wet season on the urban fringe of Darwin, Northern Australia. *Corella 28*, 68-74.

Heinsohn, R., Murphy, S., Legge, S., 2003. Overlap and competition for nest holes among eclectus parrots, palm cockatoos and sulphur-crested cockatoos. *Australian Journal of Zoology 51*, 81-94.

Heterick, B. E., Lythe, M., Smithyman, C., 2013. Urbanisation factors impacting on ant (Hymenoptera: Formicidae) biodiversity in the Perth metropolitan area, Western Australia: Two case studies. *Urban Ecosystems 16*, 145-173.

Higgins, P. J., 1999. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 4: Parrots to Dollarbird.* Oxford University Press, Melbourne.

Higgins, P. J., Peter, J. M., Steele, W. K., 2001. *Handbook of Australian, New Zealand and Antarctic Birds, Volume 5 (Tyrant-flycatchers to Chats).* Oxford University Press, Melbourne.

Hindwood, K. A., 1939. Nectar-feeding Birds near Sydney. *Emu 39*, 40-44.

Hindwood, K. A., 1962a, The birds of Sydney, in: The Natural History of Sydney. Australian Museum, Sydney.

Hindwood, K. A., 1962b, The Birds of Sydney, in: *The Natural History of Sydney* (J. W. Evans, ed.), The Trustees of the Australian Museum, Sydney.

Hitchmough, J., Woudstra, J., 1999. The ecology of exotic herbaceous perennials grown in managed, native grassy vegetation in urban landscapes. *Landscape and Urban Planning 45*, 107-121.

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vila, M., Zamora, R., Zobel, M., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography 15*, 1-7.

Hodgkison, S., Hero, J. M., Warnken, J., 2007. The efficacy of small-scale conservation efforts, as assessed on Australian golf courses. *Biological Conservation 135*, 576-586.

Hoskin, E. S., 1991. *Birds of Sydney.* Surrey Beatty & Sons, Chipping Norton.

Huhtalo, H., Järvinen, O., 1977. Quantitative Composition of the Urban Bird Community in Tornio, Northern Finland. *Bird Study **24***, 179 - 185.

Hunt, B. G., 2009. Multi-annual dry episodes in Australian climatic variability, *International Journal of Climatology 29*, 1715-1730.

Ikin, K., Beaty, R. M., Lindenmayer, D. B., Knight, E., Fischer, J., Manning, A. D., 2013. Pocket parks in a compact city: how do birds respond to increasing residential density? *Landscape Ecology 28*, 45-56.

Inions, G. B., Tanton, M. T., Davey, S. M., 1989. Effect of Fire on the Availability of Hollows in Trees Used by the Common Brushtail Possum, Trichosurus Vulpecula Kerr, 1792, and the Ringtail Possum, Pseudocheirus Peregrinus Boddaerts, 1785. *Wildlife Research 16*, 449-458.

Isaac, B., Cooke, R., Simmons, D., Hogan, F., 2008. Predictive mapping of powerful owl (*Ninox strenua*) breeding sites using Geographical Information Systems (GIS) in urban Melbourne, Australia. *Landscape and Urban Planning 84*, 212-218.

Jochner, S. C., Sparks, T. H., Estrella, N., Menzel, A., 2012. The influence of altitude and urbanisation on trends and mean dates in phenology (1980-2009). *International Journal of Biometeorology 56*, 387-394.

Johnson, L. C., 2006. Style wars: revolution in the suburbs? *Australian Geographer 37*, 259-277.

Jokimäki, J., 1999. Occurrence of breeding bird species in urban parks: Effects of park structure and broad-scale variables. *Urban Ecosystems 3*, 21-34.

Jokimaki, J., Suhonen, J., 1998. Distribution and habitat selection of wintering birds in urban environments. *Landscape and Urban Planning 39*, 253-263.

Jones, D., 1981. Temporal Changes in the Suburban Avifauna of an Inland City. *Wildlife Research 8*, 109-119.

Kalnay, E., Cai, M., 2003. Impact of urbanization and land-use change on climate. *Nature 423*, 528-531.

Kark, S., Iwaniuk, A., Schalimtzek, A., Banker, E., 2007. Living in the city: can anyone become an 'urban exploiter'? *Journal of Biogeography 34*, 638-651.

Keane, R. E., Agee, J. K., Fule, P., Keeley, J. E., Key, C., Kitchen, S. G., Miller, R., Schulte, L. A., 2008. Ecological effects of large fires on US lanscapes: benefit or catastrophe? *International Journal of Wildland Fire 17,* 696-712.

Keast, A., 1995, Habitat loss and species loss: the birds of Sydney 50 years ago and now. *Australian Zoologist 30,* 3-25.

Keith, D., 2006. *Ocean Shores to Desert Dunes*. New South Wales Department of Environment and Conservation, Hurstville, NSW.

Khera, N., Mehta, V., Sabata, B. C., 2009. Interrelationship of birds and habitat features in urban green spaces in Delhi, India. *Urban Forestry & Urban Greening 8*, 187-196.

Koch, A., Munks, S., Driscoll, D., 2008a. The use of hollow-bearing trees by vertebrate fauna in wet and dry Eucalyptus obliqua forest, Tasmania. *Wildlife Research 35*, 727-746.

Koch, A. J., Munks, S. A., Woehler, E. J., 2008b. Hollow-using vertebrate fauna of Tasmania: distribution, hollow requirements and conservation status. *Australian Journal of Zoology 56*, 323-349.

Kowarik, I., 2011. Novel urban ecosystems, biodiversity, and conservation. *Environmental Pollution 159*, 1974-1983.

Krebs, E. A., 1998. Breeding biology of crimson rosellas (*Platycercus elegans*) on Black Mountain, Australian Capital Territory. *Australian Journal of Zoology 46*, 119-136.

Lake, J. C., Leishman, M. R., 2004. Invasion success of exotic in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation 117*, 215-226.

Lambert, M. S., Massei, G., Bell, J., Berry, L., Haigh, C., Cowan, D. P., 2009. Reproductive success of rose-ringed parakeets *Psittacula krameri* in a captive UK population. *Pest Management Science 65*, 1215-1218.

Lamont, D., Burbidge, A., 1996. Rainbow Lorikeets: Invaders of the Suburbs. *Landscope 12,* 17-21.

Landsberg, H., 1981. The Urban Climate, in: *International Geophysical Series*. Academic Press, New York.

Law, B., Mackowski, C., Schoer, L., Tweedie, T., 2000. Flowering phenology of myrtaceous trees and their relation to climatic, environmental and disturbance variables in northern New South Wales. *Austral Ecology 25*, 160-178.

Law, B. S., 1992. The maintenance nitrogen requirements of the queensland blossom bat (*Syconycteris-australis*) on a sugar pollen diet - is nitrogen a limiting resource. *Physiological Zoology 65*, 634-648.

Law, B. S., 1994. Banksia nectar and pollen - dietary items affecting the abundance of the common blossom bat, *Syconycteris australis*, in southeastern australia, *Australian Journal of Ecology 19*, 425-434.

Legault, A., Theuerkauf, J., Rouys, S., Chartendrault, V., Barre, N., 2012. Temporal variation in flock size and habitat use of parrots in New Caledonia. *Condor 114*, 552-563.

Leishman, M. R., Hughes, M. T., Gore, D. B., 2004. Soil phosphorus enhancement below stormwater outlets in urban bushland: spatial and temporal changes and the relationship with invasive plants. *Australian Journal of Soil Research 42*, 197-202.

Lemeshow, S., Legall, J. R., 1994. Modeling the severity of illness of ICU patients - a systems update. *Jama-Journal of the American Medical Association 272*, 1049-1055.

Lever, C., 2005. Naturalised birds of the world. T and AD Poyser. London.

Lim, H. C., Sodhi, N. S., 2004. Responses of avian guilds to urbanisation in a tropical city. *Landscape and Urban Planning 66*, 199-215.

Lindenmayer, D. B., Cunningham, R. B., Donnelly, C. F., Tanton, M. T., Nix, H. A., 1993. The abundance and development of cavities in Eucalyptus trees: a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecology and Management 60*, 77-104.

Lindenmayer, D. B., Cunningham, R. B., Pope, M. L., Gibbons, P., Donnelly, C. F., 2000. Cavity sizes and types in Australian eucalypts from wet and dry forest types-a simple of rule of thumb for estimating size and number of cavities. *Forest Ecology and Management 137,* 139-150.

Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C. F., Brown, D., 2008. The use of hollows and dreys by the common ringtail possum (*Pseudocheirus peregrinus*) in different vegetation types. *Australian Journal of Zoology 56*, 1-11.

Lindenmayer, D. B., MacGregor, C. I., Cunningham, R. B., Incoll, R. D., Crane, M., Rawlins, D., Michael, D. R., 2003. The use of nest boxes by arboreal marsupials in the forests of the Central Highlands of Victoria. *Wildlife Research 30*, 259-264.

Lindenmayer, D. B., Welsh, A., Donnelly, C. F., 1997. Use of nest trees by the mountain brushtail possum (*Trichosurus caninus*) (Phalangeridae : Marsupialia). III. Spatial configuration and co-occupancy of nest trees. *Wildlife Research 24*, 661-677.

Lohmus, A., Remm, J., 2005. Nest quality limits the number of hole-nesting passerines in their natural cavity-rich habitat. *Acta Oecologica-International Journal of Ecology 27*, 125-128.

Low, T., 2002. *The New Nature.* Penguin Books, Camberwell.

Lowry, H., Lill, A., 2007. Ecological factors facilitating city-dwelling in red-rumped parrots. *Wildlife Research 34*, 624-631.

Loyn, R. H., 1999. Effects of an extensive wildfire on birds in far eastern Victoria. *Pacific Conservation Biology 3,* 221-234.

Lu, P. L., Yu, Q., Liu, J. D., Lee, X. H., 2006. Advance of tree-flowering dates in response to urban climate change. *Agricultural and Forest Meteorology 138*, 120-131.

Luo, Z. K., Sun, O. J., Ge, Q. S., Xu, W. T., Zheng, J. Y., 2007. Phenological responses of plants to climate change in an urban environment. *Ecological Research 22*, 507-514.

MacGregor-Fors, I., Morales-Perez, L., Quesada, J., Schondube, J. E., 2010. Relationship between the presence of House Sparrows (*Passer domesticus*) and Neotropical bird community structure and diversity. *Biological Invasions 12,* 87-96.

Magle, S. B., Hunt, V. M., Vernon, M., Crooks, K. R., 2012. Urban wildlife research: Past, present, and future. *Biological Conservation 155,* 23-32.

Major, R. E., Gowing, G., Kendal, C., 1996. Nest predation in Australian urban environments and the role of the pied currawong, *Strepera graculina*, *Austral Ecology 21*, 399-409.

Major, R. E., Parsons, H., 2010. What do museum specimens tell us about the impact of urbanisation? A comparison of the recent and historical bird communities of Sydney. *Emu 110,* 92-103.

Manning, A. D., Lindenmayer, D. B., 2009. Paddock trees, parrots and agricultural production: An urgent need for large-scale, long-term restoration in south-eastern Australia. *Ecological Management & Restoration 10*, 126-135.

Manning, A. D., Lindenmayer, D. B., Barry, S. C., Nix, H. A., 2007. Large-scale spatial and temporal dynamics of the vulnerable and highly mobile superb parrot. *Journal of Biogeography 34*, 289-304.

Maron, M., Grey, M. J., Catterall, C. P., Major, R. E., Oliver, D. L., Clarke, M. F., Loyn, R. H., Mac Nally, R., Davidson, I., Thomson, J. R., 2013. Avifaunal disarray due to a single despotic species., *Diversity and Distributions.* DOI: 10.1111/ddi.12128 http://wileyonlinelibrary.com/journal/ddi

.

Marsden, S. J., Jones, M. J., 1997. The nesting requirements of the parrots and hornbill of Sumba, Indonesia. *Biological Conservation 82*, 279-287.

Martin, J. M., French, K., Major, R. E., 2007. The pest status of Australian white ibis (*Threskiornis molucca*) in urban situations and the effectiveness of egg-oil in reproductive control. *Wildlife Research 34*, 319-324.

Martin, K., Aitken, K. E. H., Wiebe, K. L., 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning. *Condor 106*, 5-19.

Martin, W. K., 1996. The current and potential distribution of the common myna Acridotheres tristis in Australia. *Emu 96,* 166-173.

Marzluff, J. M., 2001. Worldwide urbanization and its effects on birds., in: *Avian ecology and conservation in an urbanizing world.* (J. M. Marzluff, R. Bowman, R. Donelly, eds.), Kluwer Academic Publishers, Boston.

Mathieu, R., Freeman, C., Aryal, J., 2007. Mapping private gardens in urban areas using object-oriented techniques and very high-resolution satellite imagery. *Landscape and Urban Planning 81*, 179-192.

Mawson, P. R., Long, J. L., 1994. Size and age parameters of nest trees used by 4 species of parrot and one species of cockatoo in south-west australia. *Emu 94*, 149-155.

Mazerolle, M. J., 2006. Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia 27*, 169-180.

McCaffrey, R. E., Mannan, R. W., 2012. How scale influences birds' responses to habitat features in urban residential areas. *Landscape and Urban Planning 105*, 274-280.

McDonnell, M. J., Pickett, S. T. A., 1990. Ecosystem Structure and Function along Urban-Rural Gradients: An Unexploited Opportunity for Ecology. *Ecology 71*, 1232-1237.

McGoldrick, J. M., Mac Nally, R., 1998. Impact of flowering on bird community dynamics in some central Victorian eucalypt forests. *Ecological Research 13*, 125-139.

McIntyre, N. E., 2000. Ecology of urban arthropods: A review and a call to action. *Annals of the Entomological Society of America 93*, 825-835.

McKinney, M., 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems 11*, 161-176.

McKinney, M. L., 2002. Urbanization, Biodiversity, and Conservation. *Bioscience 52*, 883-891.

McKinney, M. L., 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation 127*, 247-260.

McKinney, M. L., Lockwood, J. L., 1999. Biotic homogenization: a few winners replacing losers in the next mass extinction. *Trends in Ecology & Evolution*, 450-453.

Meffert, P. J., Dziock, F., 2013. The influence of urbanisation on diversity and trait composition of birds. *Landscape Ecology 28*, 943-957.

Menke, S. B., Guenard, B., Sexton, J. O., Weiser, M. D., Dunn, R. R., Silverman, J., 2011. Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants. *Urban Ecosystems 14*, 135-163.

Menkhorst, P. W., 1984. Use of nest boxes by forest vertebrates in Gippsland - acceptance, preference and demand. *Australian Wildlife Research 11*, 255-264.

Meyer-Gleaves, S., Jones, D. N., 2007. Relative abundance of Australian White Ibis *Threskiornis molluca* across the Greater Brisbane region, in: *Pest of Guest: the zoology of overabundance* (D. Lunney, Eby, P., Hutchings, P. Burgin, S., ed.), Royal Zoological Society of NSW, Mosman, NSW.

Miller, J. R., 2005. Biodiversity conservation and the extinction of experience,.*Trends in Ecology & Evolution 20*, 430-434.

Mimet, A., Pellissier, V., Quenol, H., Aguejdad, R., Dubreuil, V., Roze, F., 2009. Urbanisation induces early flowering: evidence from *Platanus acerifolia* and *Prunus cerasus*. *International Journal of Biometeorology 53*, 287-298.

Minor, E. S., Appelt, C. W., Grabiner, S., Ward, L., Moreno, A., Pruett-Jones, S., 2012. Distribution of exotic monk parakeets across an urban landscape. *Urban Ecosystems 15*, 979-991.

Møller, A. P., 2012. Urban areas as refuges from predators and flight distance of prey. *Behavioral Ecology 23*,1030-1035.

Møller, , A. P., Diaz, M., Flensted-Jensen, E., Grim, T., Ibanez-Alamo, J. D., Jokimaki, J., Mand, R., Marko, G., Tryjanowski, P., 2012. High urban population density of birds reflects their timing of urbanization. *Oecologia 170*, 867-875.

Møller, , A. P., Ibanez-Alamo, J. D., 2012. Escape behaviour of birds provides evidence of predation being involved in urbanization. *Animal Behaviour 84*, 341-348.

Moseley, D., Marzano, M., Chetcuti, J., Watts, K., 2013. Green networks for people: Application of a functional approach to support the planning and management of green space. *Landscape and Urban Planning 116*, 1-12.

Murphy, S., Legge, S., Heinsohn, R., 2003. The breeding biology of palm cockatoos (*Probosciger aterrimus*): a case of a slow life history. *Journal of Zoology 261,* 327-339.

Nagendra, H., Gopal, D., 2010. Street trees in Bangalore: Density, diversity, composition and distribution. *Urban Forestry & Urban Greening 9*, 129-137.

Neil, K., Wu, J., 2006. Effects of urbanization on plant flowering phenology: A review. *Urban Ecosystems 9*, 243-257.

Neil, K. L., Landrum, L., Wu, J. G., 2010. Effects of urbanization on flowering phenology in the metropolitan Phoenix region of USA: Findings from herbarium records. *Journal of Arid Environments 74*, 440-444.

Nelson, J. L., Morris, B. J., 1994. Nesting requirements of the yellow-tailed black-cockatoo, *Calyptorhynchus funereus*, in *Eucalyptus regnans* forest, and implications for forest management. *Wildlife Research 21*, 267-278.

Newson, S. E., Johnston, A., Parrott, D., Leech, D. I., 2011. Evaluating the population-level impact of an invasive species, Ring-necked Parakeet *Psittacula krameri*, on native avifauna. *Ibis 153*, 509-516.

Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation 70*, 265-276.

North, A. J., 1914. *Nests and Eggs of Birds Found Breeding in Australia and Tasmania*. Australian Museum, Sydney.

Ohashi, Y., Kawakami, H., Shigeta, Y., Ikeda, H., Yamamoto, N., 2012. The phenology of cherry blossom (*Prunus yedoensis* "Somei-yoshino") and the geographic features contributing to its flowering. *International Journal of Biometeorology 56*, 903-914.

Oprea, M., Mendes, P., Vieira, T. B., Ditchfield, A. D., 2009. Do wooded streets provide connectivity for bats in an urban landscape? *Biodiversity and Conservation 18*, 2361-2371.

Orians, G. H., Milewski, A. V., 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews 82*, 393-423.

Ortega-Alvarez, R., MacGregor-Fors, I., 2009. Living in the big city: Effects of urban land-use on bird community structure, diversity, and composition. *Landscape and Urban Planning 90*, 189-195.

Parris, K. M., Hazell, D. L., 2005. Biotic effects of climate change in urban environments: The case of the grey-headed flying-fox (*Pteropus poliocephalus*) in Melbourne, Australia. *Biological Conservation 124*, 267-276.

Parsons, H., French, K., Major, R. E., 2003. The influence of remnant bushland on the composition of suburban bird assemblages in Australia. *Landscape and Urban Planning 66*, 43-56.

Parsons, H., Major, R. E., French, K., 2006. Species interactions and habitat associations of birds inhabiting urban areas of Sydney, Australia. *Austral Ecology 31*, 217-227.

Pauw, A., Louw, K., 2012. Urbanization Drives a Reduction in Functional Diversity in a Guild of Nectar-feeding Birds. *Ecology and Society 17*, 27-35.

Pearce, J., Ferrier, S., 2000. An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological Modelling 128*, 127-147.

Pećarević, M., Danoff-Burg, J., Dunn, R. R., 2010. Biodiversity on Broadway - Enigmatic Diversity of the Societies of Ants (Formicidae) on the Streets of New York City. *PLoS ONE 5*, e13222.

Pedhazur, E. J., 1997. *Multiple Regression in Behavioural Research: Explanation and Prediction.* Wadsworth, Crawfordsville.

Pinto, U., Maheshwari, B. L., Ollerton, R. L., 2013. Analysis of long-term water quality for effective river health monitoring in peri-urban landscapes-a case study of the Hawkesbury-Nepean river system in NSW, Australia. *Environmental Monitoring and Assessment 185*, 4551-4569.

Politi, N., Hunter, M., Rivera, L., 2009. Nest Selection by Cavity-nesting Birds in Subtropical Montane Forests of the Andes: Implications for Sustainable Forest Management. *Biotropica 41*, 354-360.

Politi, N., Hunter, M., Rivera, L., 2010. Availability of cavities for avian cavity nesters in selectively logged subtropical montane forests of the Andes. *Forest Ecology and Management 260*, 893-906.

Pouyat, R. V., McDonnell, M. J., Pickett, S. T. A., 1995. Soil characteristics of oak stands along an urban-rural land-use gradient. *Journal of Environmental Quality 24*, 516-526.

Pruett-Jones, S., Appelt, C. W., Sarfaty, A., Van Vossen, B., Leibold, M. A., Minor, E. S., 2012. Urban parakeets in Northern Illinois: A 40-year perspective. *Urban Ecosystems 15*, 709-719.

Pyke, G. H., O'Connor, P. J., Recher, H. F., 1993. Relationship between nectar production and yearly and spatial variation in density and nesting of resident honeyeaters in heathland near Sydney. *Australian Journal of Ecology 18,* 221-229.

Quinn, G. P., Keough, M. J., 2002. *Experimental Design and Data Analysis for Biologists.* Cambridge University Press, Cambridge.

Ramsay, M. W., 1989. The seasonal abundance and foraging behaviour of honeyeaters and their potential role in the pollination of *Banksia menziesii. Australian Journal of Ecology 14*, 33-40.

Ranius, T., Niklasson, M., Berg, N., 2009. Development of tree hollows in pedunculate oak (*Quercus robur*). *Forest Ecology and Management 257*, 303-310.

Rebele, F., 1994. Urban Ecology and Special Features of Urban Ecosystems. *Global Ecology and Biogeography Letters 4*, 173-187.

Recher, H. F., 1997. Impact of wildlife on the avifauna of Kings Park, Perth, Western Australia. *Wildlife Research 24,* 745-761.

Recher, H. F., Majer, J. D., Ganesh, S., 1996. Eucalypts, arthropods and birds: on the relation between foliar nutrients and species richness. *Forest Ecology and Management 85*, 177-195.

Reilly, P., 1991. The efect of wildfire on bush bird populations in six Victorian coastal habitats. *Corella 15*, 134-142.

Reis, E., Lopez-Iborra, G. M., Pinheiro, R. T., 2012. Changes in bird species richness through different levels of urbanization: Implications for biodiversity conservation and garden design in Central Brazil. *Landscape and Urban Planning 107*, 31-42.

Remm, J., Lohmus, A., Rosenvald, R., 2008. Density and diversity of hole-nesting passerines: dependence on the characteristics of cavities. *Acta Ornithologica 43*, 83-91.

Renton, K., 2004. Agonistic interactions of nesting and nonbreeding Macaws. *Condor 106*, 354-362.

Renton, K., Brightsmith, D. J., 2009. Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru. *Journal of Field Ornithology 80*, 1-8.

Rodriguez, D., Cure, J. R., Cotes, J. M., Gutierrez, A. P., Cantor, F., 2011. A coffee agroecosystem model: I. Growth and development of the coffee plant. *Ecological Modelling 222*, 3626-3639.

Rose, E., Nagel, P., 2006. Spatio-temporal use of the urban habitat by feral pigeons (*Columba livia*). *Behavioral Ecology and Sociobiology 60*, 242-254.

Rose, S., 1997. Influence of suburban edges on invasion of Pittosporum undulatum into the bushland of northern Sydney, Australia. *Australian Journal of Ecology 22*, 89-99.

Rottenborn, S. C., 1999. Predicting the impacts of urbanization on riparian bird communities. *Biological Conservation 88*, 289-299.

Saetre, G. P., Riyahi, S., Aliabadian, M., Hermansen, J. S., Hogner, S., Olsson, U., Rojas, M. F. G., Saether, S. A., Trier, C. N., Elgvin, T. O., 2012. Single origin of human commensalism in the house sparrow. *Journal of Evolutionary Biology 25*, 788-796.

Salinas-Melgoza, A., Salinas-Melgoza, V., Renton, K., 2009. Factors influencing nest spacing of a secondary cavity-nesting parrot: habitat heterogeneity and proximity of conspecifics. *Condor 111*, 305-313.

Sandström, U. G., Angelstam, P., Mikusinski, G., 2006. Ecological diversity of birds in relation to the structure of urban green space. *Landscape and Urban Planning* 77, 39-53.

Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M. K., Moretti, M., 2010. Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology 91*, 3343-3353.

Saunders, D. A., 1979. The Availability of Tree Hollows for Use as Nest Sites by White-tailed Black Cockatoos. *Wildlife Research 6*, 205-216.

Saunders, D. A., 1980. Food and Movements of the Short-Billed Form of the White-Tailed Black Cockatoo. *Wildlife Research 7*, 257-269.

Saunders, D. A., Smith, G. T., Rowley, I., 1982. The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. *Wildlife Research 9*, 541-556.

Savard, J.-P. L., Clergeau, P., Mennechez, G., 2000. Biodiversity concepts and urban ecosystems. *Landscape and Urban Planning 48*, 131-142.

Savignac, C., Desrochers, A., Huot, J., 2000. Habitat use by Pileated Woodpeckers at two spatial scales in eastern Canada. *Canadian Journal of Zoology-Revue Canadienne De Zoologie 78*, 219-225.

Schodde, R., Tidemann, S., 1986. *Readers Digest Complete Book of Australian Birds.* Readers Digest Services Pty Ltd, Sydney.

Sewell, S. R., Catterall, C. P., 1998. Bushland modification and styles of urban development: their effects on birds in south-east Queensland. *Wildlife Research 25*, 41-63.

Shannon, C. E., 1948. A mathematical theory of communication. *Bell System Technical Journal 27*, 379-423.

Shochat, E., 2004. Credit or debit? Resource input changes population dynamics of city-slicker birds. *Oikos 106*, 622-626.

Shochat, E., Stefanov, W. L., Whitehouse, M. E. A., Faeth, S. H., 2004. Urbanization and spider diversity: Influences of human modification of habitat structure and productivity. *Ecological Applications 14*, 268-280.

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., Hope, D., 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution 21*, 186-191.

Shukuroglou, P., McCarthy, M. A., 2006, Modelling the occurrence of rainbow lorikeets (*Trichoglossus haematodus*) in Melbourne. *Austral Ecology 31*, 240-253.

Shwartz, A., Shirley, S., Kark, S., 2008. How do habitat variability and management regime shape the spatial heterogeneity of birds within a large Mediterranean urban park? *Landscape and Urban Planning 84*, 219-229.

Slater, P. J., 1995. The interaction of bird communities with vegetation and season in brisbane-forest-park. *Emu 95,* 194-207.

Smith, G. T., Moore, L. A., 1992. Patterns of Movement in the Western Long-billed Corella *Cacatua pastinator* in the South-west of Western Australia. *Emu 92,* 19-27.

Smith, J., Lill, A., 2008. Importance of eucalypts in exploitation of urban parks by Rainbow and Musk Lorikeets. *Emu 108,* 187-195.

Smith, K. W., 2006. The implications of nest site competition from starlings *Sturnus vulgaris* and the effect of spring temperatures on the timing and breeding performance of great spotted woodpeckers *Dendrocopos major* in southern England. *Annales Zoologici Fennici 43,* 177-185.

Smith, R. M., Thompson, K., Hodgson, J. G., Warren, P. H., Gaston, K. J., 2006. Urban domestic gardens (IX): Composition and richness of the vascular plant flora, and implications for native biodiversity. *Biological Conservation 129*, 312-322.

Smucker, N. J., Becker, M., Detenbeck, N. E., Morrison, A. C., 2013. Using algal metrics and biomass to evaluate multiple ways of defining concentration-based nutrient criteria in streams and their ecological relevance. *Ecological Indicators 32,* 51-61.

Specht, R., 1963. Dark Island heath (Ninety-mile plain, South Australia). VII. The effect of fertilizers on composition and growth, 1950-60. *Australian Journal of Botany 11*, 67-94.

Stanford, I., Lill, A., 2008. Out on the town: winter feeding ecology of lorikeets in urban parkland. *Corella 32,* 49-57.

Stojanovic, D., Webb, M., Roshier, D., Saunders, D., Heinsohn, R., 2012. Ground-based survey methods both overestimate and underestimate the abundance of suitable tree-cavities for the endangered Swift Parrot. *Emu 112*, 350-356.

Strubbe, D., Matthysen, E., 2007. Invasive ring-necked parakeets *Psittacula krameri* in Belgium: habitat selection and impact on native birds. *Ecography 30*, 578-588.

Strubbe, D., Matthysen, E., 2009. Establishment success of invasive ring-necked and monk parakeets in Europe. *Journal of Biogeography 36*, 2264-2278.

Symes, C. T., Nicolson, S. W., McKechnie, A. E., 2008. Response of avian nectarivores to the flowering of *Aloe marlothii*: a nectar oasis during dry South African winters. *Journal of Ornithology 149*, 13-22.

Symes, C. T., Perrin, M. R., 2004. Breeding biology of the Greyheaded Parrot (*Poicephalus fuscicollis suahelicus*) in the wild. *Emu 104*, 45-57.

Tabachnick, B. G., Fidell, L. S., 2007. *Using Multivariate Statistics*. Allyn and Bacon, Boston.

Terho, M., Hallaksela, A. M., 2008. Decay characteristics of hazardous Tilia, Betula, and Acer trees felled by municipal urban tree managers in the Helsinki City Area. *Forestry 81*, 151-159.

Terman, M. R., 1997. Natural links: naturalistic golf courses as wildlife habitat. *Landscape and Urban Planning 38*, 183-197.

Threlfall, C., Law, B., Penman, T., Banks, P. B., 2011. Ecological processes in urban landscapes: mechanisms influencing the distribution and activity of insectivorous bats. *Ecography 34*, 814-826.

Todarello, P., Chalmers, A., 2007. The characteristics of five species of hollow-bearing trees on the New South Wales central coast. *Proceedings of the Linnean Society of New South Wales 128*, 1-14.

Tratalos, J., Fuller, R. A., Evans, K. L., Davies, R. G., Newson, S. E., Greenwood, J. J. D., Gaston, K. J., 2007. Bird densities are associated with household densities, *Global Change Biology 13*, 1685-1695.

Tzilkowski, W. M., Wakeley, J. S., Morris, L. J., 1986. Relative use of municipal street trees by birds during summer in state college, pennsylvania. *Urban Ecology* ***9***, 387-398.

Ummenhofer, C. C., England, M. H., McIntosh, P. C., Meyers, G. A., Pook, M. J., Risbey, J. S., Gupta, A. S., Taschetto, A. S., 2009. What causes southeast Australia's worst droughts?, *Geophysical Research Letters, 36*, L04706.

United Nations, 2004. *World urbanization prospects: the 2003 revision*. United Nations, New York.

van der Ree, R., McCarthy, M. A., 2005. Inferring persistence of indigenous mammals in response to urbanisation. *Animal Conservation 8,* 309-319.

van Heezik, Y., Smyth, A., Mathieu, R., 2008. Diversity of native and exotic birds across an urban gradient in a New Zealand city. *Landscape and Urban Planning 87*, 223-232.

VanBael, S., PruettJones, S., 1996. Exponential population growth of Monk Parakeets in the United States. *Wilson Bulletin 108*, 584-588.

Veerman, P. A., 1991. The changing status of the Rainbow Lorikeet *Trichoglossus haematodus* in South-east Australia: the role of wild and escaped birds. *Australian Bird Watcher 14*, 3-9.

Walker, J. S., Cahill, A. J., Marsden, S. J., 2005. Factors influencing nest-site occupancy and low reproductive output in the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea* on Sumba, Indonesia. *Bird Conservation International 15*, 347-359.

Waltman, J. R., Beissinger, S. R., 1992. Breeding behaviour of the Green-rumped Parrotlet. *Wilson Bulletin 104,* 65-84.

Waterhouse, R. D., 1997. Some observations on the ecology of the Rainbow Lorikeet *Trichoglossus heamatodus* in Oatley, South Sydney. *Corella 21*, 17-24.

Wenner, A. S., Hirth, D. H., 1984. Status of the feral budgerigar in Florida. *Journal of Field Ornithology 55*, 214-219.

Wesolowski, T., Czeszczewik, D., Rowinski, P., Walankiewicz, W., 2002. Nest soaking in natural holes - a serious cause of breeding failure? *Ornis Fennica 79*, 132-138.

Whelan, R. J., 1995. *The Ecology of Fire.* Cambridge University Press, Cambridge.

While, G. M., McArthur, C., *2005*. Foraging in a risky environment: a comparison of Bennett's wallabies *Macropus rufogriseus rufogriseus* (Marsupialia: Macropodidae) and red-bellied pademelons *Thylogale billiardierii* (Marsupialia: Macropodidae) in open habitats. *Austral Ecology 30*, 756-764.

White, J. G., Antos, M. J., Fitzsimons, J. A., Palmer, G. C., 2005. Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. *Landscape and Urban Planning 71*, 123-135.

Williams, N. S. G., Mcdonnell, M. J., M., Phelan, G. K., Keim, L. D., Rodney van der, R. E. E., 2006. Range expansion due to urbanization: Increased food resources attract Grey-headed Flying-foxes (*Pteropus poliocephalus*) to Melbourne, *Austral Ecology 31*, 190-198.

Wilson, J., Bennett, A. F., 1999. Patchiness of a floral resource: flowering of Red Ironbark *Eucalyptus tricarpa* in a box and ironbark forest. *Victorian Naturalist 116,* 48-53.

Woinarski, J., 2005. Fire and birds: fire management for biodiversity. *Wingspan 15,* S1-32.

Wolf, P., Häbich, A. C., Bürkle, M., Kamphues, J., 2007. Basic data on food intake, nutrient digestibility and energy requirements of lorikeets. *Journal of Animal Physiology and Animal Nutrition 91*, 282-288.

Woodall, P. R., 1995, Results of the QOS garden survey, 1979-1980, with particular reference to South-east Queensland., *Sunbird 25*, 1-17.

Woodall, P. R., 2002. *The Birds Queensland garden bird survey, 1999. Sunbird 32,* 37-51.

Xia, X. H., Zhao, X. L., Lai, Y. J., Dong, H. Y., 2013. Levels and distribution of total nitrogen and total phosphorous in urban soils of Beijing, China, *Environmental Earth Sciences 69*, 1571-1577.

Young, K. M., Daniels, C. B., Johnston, G., 2007. Species of street tree is important for southern hemisphere bird trophic guilds. *Austral Ecology 32*, 541-550.

Ziska, L. H., Gebhard, D. E., Frenz, D. A., Faulkner, S., Singer, B. D., Straka, J. G., 2003. Cities as harbingers of climate change: Common ragweed, urbanization, and public health. *Journal of Allergy and Clinical Immunology 111*, 290-295.