Deconstructing urban tolerance: a bird's–eye view

Landscape–scale perspectives on the behavioural and community ecology of urban birds in Melbourne, Australia

A thesis submitted in fulfilment of the requirements for the Degree of Doctor of Philosophy in the School of Land & Food (Geography & Environmental Studies), University of Tasmania, Australia.

BY:

Lawrence Edwin Conole

Graduate Certificate in Ornithology, Charles Sturt University

September 2015

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The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, and rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

Signed

Lawrence Edwin Conole

July 2014

Statement of Co-Authorship
(for inclusion in the thesis)

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Lawrence Edwin CONOLE, School of Land & Food = **Candidate**
Professor Jamie Kirkpatrick, University of Tasmania = **Author 1**

Author details and their roles:

Paper 1: Functional and spatial differentiation of urban bird assemblages at the landscape scale
Located in chapter 3
Candidate conducted the literature review, formulated the research questions, undertook the analyses, and wrote the paper. Author 1 contributed to the processes of refining the research direction, and interpretation of results.

Paper 2: Diverse responses of exotic birds to urbanisation
Located in chapter 4
Candidate was the sole author on this paper.

Paper 3: Habitat-of-origin predicts degree of adaptation in urban birds
Located in chapter 5
Candidate was the sole author on this paper.

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Signed:

(Name) J.B. Kirkpatrick   *(Name) Holger Meinke*
Supervisor   *Head of School*
School Of Land and Food   *School of Land and Food*
University of Tasmania   University of Tasmania

Date: 11 July 2014

Abstract

Cities, while being the most anthropogenic of landscapes, often incorporate modified remnants of original habitats and also represent novel habitats for plants and animals. Urbanisation affects birds directly and indirectly, leading to changes in ecological processes, habitat, food supply, predator and competitor ecology, and disease epidemiology.

The following questions were asked in relation to the birds of Melbourne, Victoria, Australia. Are there are distinct urban tolerator and urban avoider assemblages, and are these urban tolerant assemblages simplified when compared to the urban avoider assemblages? Does bird mass significantly differ between urban tolerant and avoider species? Do exotic and native urban tolerant species exhibit similar functional responses to urbanisation? Do the urban exploiter and suburban adapter assemblages within the broad urban tolerant grouping in Melbourne vary in their responses to predictor variables, and does habitat-of-origin have predictive utility in determining which urban tolerant birds become exploiters or adapters? Does the variability in birds' natural states of fearfulness of humans predict their likelihood of becoming successful urban species?

For this study a sample of 141 species (including 13 non-indigenous species) and *circa* 220,000 individual data points within a 50km radius of the Melbourne General Post Office were drawn from BirdLife Australia's 'Atlas II' project. The data set was objectively classified into five assemblages. Two urban tolerant assemblages contain the more commonly encountered bird species of Melbourne; exploiters occurred widely across the whole city but adapters mostly in the eastern suburbs. Three avoider assemblages occurred within particular spatial and habitat nodes of the city; such as riparian and bush remnants of eastern Melbourne, wetland margins and in coastal vegetation, or on the margins of the urban matrix or in larger remnant native vegetation patches within it. Urban tolerant species were consistently larger in body size than most urban avoiders. Some combinations of foraging and nest substrate guild membership were exclusively urban avoiders. They tended to either nest on the ground, were gleaning species or frugivores, or were specialists such as brood-parasitic cuckoos. Urban tolerant species included many omnivorous or granivorous ground feeders that utilised cavities for nesting (including those in buildings). Nectarivores were often urban tolerant, whereas most raptors were not. All spring migrants were avoiders (except for the partial spring migrant Black-faced Cuckoo-shrike *Coracina novaehollandiae*, which was an adapter), as were most winter migrants, sedentary species, and nomadic species (more than expected by chance). The exotic species sort into three of Melbournes four urban bird assemblages, and exhibit similar functional and spatial responses to urbanisation as natives. The size differential between urban exploiter and urban avoider exotic birds also matches that in native urban birds, as do the nest substrate and foraging profiles. Two environmental or demographic factors that best explained the spatial and community structure of urban bird assemblages were *Frequency Greenspace* and $Index_{Combined}$. The former reflected structural habitat characteristics of the urban habitat matrix, while the latter represented its human demographic attributes. The spatial arrangement of most assemblages also showed a strong longitudinal gradient,

with bird species and assemblage diversity increasing from west to east. The diversity of urban adapters along the gradient of urban intensity (measured by $Index_{Combined}$) follows a humped distribution, and the trend is more pronounced when viewed as landscape-scale preference for points on the gradient; resembling the trend seen for urban tolerant birds in other studies, and for bird species richness in response to environmental factors at a landscape scale. The inverted, humped curve for exploiters is atypical of urban tolerant bird species richness seen in other studies, and marks a strong divergence in response by exploiters and adapters to urbanisation intensity. The response of urban tolerant birds to increasing *Frequency Greenspace* resembles much more the broad trends observed in other cities, and closely mirrors the relationship observed between bird species richness and foliage height diversity observed in non-urban landscapes. The divergent responses of each group to urbanisation intensity are largely explained by their ecological histories. The clear partitioning of adapters and exploiters within the urban tolerant grouping in this study reveals the degree to which spatial and habitat origins of members of bird assemblages influence the degree to which they become urban tolerant. As in other world cities, bird species that showed greater variability in their fear of humans (cv_{FID}) were more likely to be urban tolerant, though the best model had limited explanatory power.

Urban bird assemblages of Melbourne are broadly analogous in their organisation to those in other world cities, but they differ in ways that caution against broad generalisations of (i) what constitutes an urban bird, or (ii) where and how abundantly they occur within cities. Whilst others have examined a panoply of physiological and behavioural traits that may predispose birds to urban adaptation, this study has examined the higher order habitat filtering mechanism that may be explanatory at a more fundamental mechanistic level, and point to some broadly generalisable concepts at the scale of the landscape and the assemblage. Species-poor subsets of urban tolerant bird assemblages prosper at sites that are at the extremes of urban habitat gradients. Such highly urbanised sites are species poor for both native and exotic bird species, and therefore exotic bird dominance may simply be a marker of particular urban habitat types where overall bird species richness and individual native species abundance is low, rather than being sites where exotics displace natives from their niches.

Dedication

This thesis is dedicated to Abbe Villis who supported me through every step of this long process, from its inception to completion, and along with Marta Conole tolerated my frequent and occasionally intemperate calls for peace and quiet, and long hours of research and writing in the front, centre and various corners of the house. The realisation of this project after the forgoing of so many other possibilities, small and large, is a testament to their love and support.

Acknowledgements

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"... It would be my duty ...
as a penitent geographer,
as a swindled naturalist,
to open the travellers eyes ..."

'Morning with air'
Pablo Neruda 'The Yellow Heart' (1971–1972)

CHAPTER 1:

INTRODUCTION

1.1 Preamble

In recent years the global human population has been growing exponentially, and is not expected to level off for another few decades. The population of the world is becoming increasingly urbanised, with more than 50% of the global population now living in urban environments (United Nations 2012, 2014). The phenomenon of 'urban sprawl' and the development of new urban centres are symptoms of this growth, and these symptoms have resulted in loss, fragmentation and degradation of wildlife habitat on a large scale (Marzluff et al. 2001).

Cities, while being the most anthropogenic of landscapes, usually incorporate modified remnants of original habitats (Suhonen and Jokimäki 1988) and also represent novel habitats for biota (Pautasso 2007). Urbanisation affects birds directly and indirectly, leading to changes in ecological processes, habitat, food supply, predator and competitor ecology, and disease epidemiology (Martin and Boruta 2014; Shanahan et al. 2014). Urban areas often support denser but less diverse bird faunas than the natural systems they replace; and are often dominated by a small number of ubiquitous, adaptable and commensal species (Clergeau et al. 1998; Evans et al. 2007; Fontana 2004; Jokimäki and Suhonen 1998; Morneau et al. 1999; Palomino and Carrascal 2005; Park and Lee 2000). With increasing time since development, the trend is for increased differentiation of the urbanised bird assemblage from the original natural condition (Wood 1996; Edgar and Kershaw 1994). There is also a trend towards greater convergence, or biotic homogenization, with other urban bird communities (Blair 2001; McKinney 2006).

Birds can serve as useful surrogates for fauna in general, are easily surveyed and studied compared to other more cryptic animals, are suited to the relatively simple collection of large observational datasets, and are sensitive indicators of many of the effects of urbanisation on biodiversity (Chace and Walsh 2006; Fontana et al. 2011; Palomino and Carrascal 2006). Nevertheless, investigations of urban birds are still less common compared with investigations of natural systems where few or no humans live (Fontana 2004; Pautasso 2007). The significance of urban areas for conservation of some bird species or populations is becoming apparent (Ikin et al. 2013), but despite the potential importance of understanding bird ecology in urban habitats, studies in non-natural ecosystems were slow to receive legitimacy in the wider research community (Jokimäki and Huhta 2000). This trend has shifted in recent years, and there is a rapidly growing body of literature concerning biota in urban areas, and in particular of urban birds.

Much of the recent research on urban bird ecology has explored the effects on birds at a local scale along a linear gradient of urbanisation from urban (greatest intensity of urbanisation) to rural or wildland (least intensity of urbanisation), but there is a growing realisation that many of the processes that birds respond to are at larger landscape and regional scales. Attempts to study these larger scale interactions have largely been attempted by extrapolation from the local to the general. The focus has also to a large extent been on natural vegetation remnants in an urban matrix, and the extent to which natural habitat elements are missing (Donnelly and Marzluff 2006; Garden et al. 2006).

1.2 What is urban?

The concept of what defines urban as an environment or habitat type for birds has been treated somewhat superficially until comparatively recently. Marzluff et al. (2001) and Alberti et al.

(2001) provided a method and typology for defining points along the urban to wildland gradient, but not a definitive description of the urban habitat matrix *per se*.

The dictionary meaning of urban is given as:

> "... *of, pertaining to, or comprising a city or town* ..." (Delbridge et al. 1990).

In Australia urban areas are defined as those containing aggregations of greater than 1,000 people at a density of greater than 200/km² (Australian Bureau of Statistics 2006). Whilst these ordinary and demographic meanings of urban are instructive, in urban ecology the definition differs and is an expanded one to take account of the fluxes and interactions of high density human populations with and between areas outside the strict limits of the city (Pickett et al. 2001). Human demographic or socio-economic factors are also known to affect physical aspects of the urban environment for birds (Melles 2005), where 'leafiness' of neighbourhoods is positively correlated with affluence (Davis et al. 2012; Kinzig et al. 2005; Strohbach et al. 2009).

Hahs and McDonnell (2006) deal specifically with an environmental definition of landscapes along an urban-rural gradient. From their analysis of 17 commonly used measures of urbanisation that included demographic and physical variables and landscape metrics, four measures were identified as representing most of the variability:

- A combined index which measured the spectral mixture of the 2000 Landsat Enhanced Thematic Mapper Plus (ETM+) satellite image, and the proportion of people employed in non-agricultural (i.e. urban) work,

- The ratio of people per unit land cover,

- Landscape shape index, and

- Dominant land-cover.

This combination of measures more accurately captures what is urban than landscape metrics alone. Whilst landscape metrics typically only represent configuration of landscape elements within a cell of interest, the demographic and physical variables represent aspects of demography and land-use.

Beyond the definition of what an urban habitat is, the definition of an urban bird is not yet as settled. Blair's (1996) typology of urban exploiters, adapters and avoiders has been widely adopted as a *de facto* standard, but the methods by which bird species are assigned to these categories in individual studies is variable and relatively subjective. Typically bird species are assigned to categories of urban tolerance or intolerance in one of three ways:

- the extent to which bird species are regarded as urban tolerant is based on whether they are known to utilise urban habitats, including for breeding, and is taken from secondary and tertiary sources such as field guides and handbooks (e.g. Cardoso 2014) and assigned *a priori*,

- for studies undertaken in geographical areas where previous studies have been conducted, urban status is adopted from the earlier source (e.g. Croci et al. 2008) and assigned *a priori*,

- urban tolerant status is determined by objective classification based on primary data analysis (e.g. González-Oreja et al. 2007) and applied *a posteriori*.

Whilst the first two methods are entirely subjective, the third (and least often observed) amongst these current methods offers a truly objective classification. Despite the possibility that the subjective methods may introduce a substantially different and unrepresentative classification of urban avifaunas, the literature to date has reported broadly consistent trends in bird urban tolerance, regardless of initial classificatory scheme.

While the matter of which birds are urbanised is converging on a consensus which is global in nature, and therefore probably generalisable, the question of *why* or *how* birds are urban is still very much an open field of enquiry.

1.3   Synanthropy, commensalism and exotic species

The term synanthropy literally means 'with humans', and it refers to the subset of living creatures that can cohabit with humans (Johnston 2001). Commensalism takes the relationship with (in this case) humans further, and is defined as:

> "... *living with, on, or in another, but neither one at the expense of the other ...*"
> (Delbridge et al. 1990).

The list of birds than can cohabit with humans, and therefore at least potentially become urban birds, is legion. The number of true commensals with humans amongst birds is much smaller, and are typified by species such as the House Sparrow (*Passer domesticus*) and Common Myna (*Sturnus tristis*), the modern distributions of which are inextricably linked with human settlements and activities (Johnston 2001).

There have been assumptions made more widely that as many exotic bird species are at least in part synanthropic (Johnston 2001), that this conveys a competitive advantage in urban environments. An unstated assumption of this generalization is that exotic bird species introduced into urban habitats will be free of the environmental constraints operating on the range of formerly occurring and colonizing native bird species. The distributions of native and exotic birds in many cities are intermixed, suggesting that any presumed freedom from urban environmental constraints for exotics may be in error, and therefore worthy of exploration.

Exotic bird species are prominent members of urban avifaunas in many areas of the world (Blair 2001). An exotic species is defined as one that has established a reproductive population in an area not part of its natural range (Long 1981); the 'passive colonists' of Catterall (2009). Exotic bird species do not always establish self-sustaining populations in the locations to which they are introduced, despite sometimes considerable support and repeated attempts; they also suffer extinctions as well as going on to establish in new locations (Long 1981). Most exotic species also have extensive non-urban distributions in countries of introduction (Long 1981), and are not exclusively synanthropic.

Much has been generalized about the distribution, abundance and undesirability of exotic birds in general, including in urban habitats, particularly in the popular literature (Low 2002; Rolls 1969). For instance, it has been asserted that they reduce food production, compete with native species for resources and disperse invasive plants (Hart and Bomford 2006; Long 1981). Despite a bad press, little empirical research has been published which specifically targets the effects of exotic birds in urban systems (Chace and Walsh 2006; White et al. 2005), or their responses to environmental or habitat factors. In one of the few relevant studies, direct negative impacts of

the Common Myna on native birds through competition for nest sites have been demonstrated in Australia (Pell and Tidemann 1997), though the same species foraging strategy was found not to overlap with native species (Crisp and Lill 2006). Recher (2006) suggested that most exotic birds in urban habitats are essentially benign, and are cherished by many city dwellers for "… *colour, movement and song* …" in otherwise bland urban landscapes.

By their very presence, exotic species homogenize global urban avifaunas (McKinney 2008), but their distributions may not be homogeneous within cities (Natuhara and Hashimoto 2009). Exotic species are often present in urban native vegetation remnants, but at lower levels of abundance than in surrounding built-up areas (Antos *et al.* 2006; Catterall 2009). Global ubiquitists were found only to dominate bare suburbs in subtropical Brisbane (Catterall 2009), and the same is true for many other cities (Chace and Walsh 2006; Croci et al. 2008; Hugo and Rensburg 2009; Kark et al. 2007; ; Van Heezik et al. 2008). In studies of the distributions of plants it has been common to find that exotic species are as closely related to environmental variation as native plants (Fensham and Kirkpatrick 1989; McKinney 2004].

At the time of writing, Melbourne had 13 established non-native bird species present within its terrestrial bird assemblages (see Chapter 4). Most species are long established in Melbourne, having been introduced since the mid to late nineteenth century. This well-established and diverse exotic avifauna has parallels elsewhere in the temperate zones of the world, particularly in New Zealand, Western Europe and North America (Long 1981).

In Chapter 4 the hypothesis is advanced that as exotic and native urban tolerant species are similar in their range of spatial and functional responses to urbanization, environmental filters operating on the natives will also act on exotics. As subsets of the main hypothesis it is theorized that (i) most exotic species will be urban tolerant, but some more specialized species will be urban avoiders; (ii) exotic species diversity will vary proportionally with overall bird species diversity; and, (iii) most exotic species will be least abundant in areas of low urbanization intensity and higher native species richness.

1.4   The urbanisation gradient

The concept of an urbanisation gradient was introduced by McDonnell and Pickett (1990) as a way of conceptualising the various states of urbanisation intensity which occur between urban, suburban, rural/exurban and wildland sites (Marzluff et al. 2001). The urbanisation gradient has sometimes been conceived of as continuous with a monocentric distribution from greatest intensity in the urban core of a city through to least intensity on the exurban/rural fringe (also known as the 'peri-urban' fringe) (Alberti et al. 2001; Reale and Blair 2005). This simplified model fails to appreciate the complex reality that many cities are polycentric, and though the existence of a gradient is well demonstrated, it is typically non-linear in its distribution (Alberti et al. 2001; Hahs and McDonnell 2006), and usually in a constant and volatile state of flux (Garden et al. 2006; Ramalho and Hobbs 2012a). Nonetheless, the concept of an urban gradient offers a useful model for stratifying urban landscapes for study, based on the distribution of intensity of urbanisation (Chapman and Reich 2007; Luck and Wu 2002).

Gradient analysis (Ruszczyk et al. 1987) has been broadly applied in urban ecological studies over the past two decades (McDonnell and Hahs 2008), and much longer in ecology more generally (Whittaker 1967). It is intuitively compatible with a landscape ecology perspective (Breuste et al. 2008), and despite criticisms of the limitations of gradient analysis as an approach

for studying urban ecology (Catterall 2009; Ramalho and Hobbs 2012a,b), the potential remains for this approach to be the 'scaffolding' upon which deeper investigations are built (McDonnell et al. 2012).

1.5 Landscape ecology

The challenges for landscape ecologists are many, but in part relate to the choice of appropriate scales of study (Briggs 2001), selection of landscape metrics that have a meaningful relationship with ecological processes at different spatial and temporal scales (Lindenmayer et al. 2000), and the use of quantitative methods which can detect and measure effects that are ecologically meaningful (Ferson and Burgman 2000). Hence, the discipline of landscape ecology must draw on cutting edge ecological theoretical and applied research, GIS technology development, and debates such as those about competing statistical philosophies and re-examination of the traditional hypothesis-testing scientific method itself.

Several authors have recognised the need for a landscape ecology approach to studying urban birds, which can complement the fine-grained studies of local factors affecting urban birds (Miller et al. 2001). Such studies use remote sensing technologies to measure a range of landscape metrics that are likely to be significant for birds. The landscape metrics that have been used, or suggested for use, typically attempt to measure percentage land-use and land-cover, and various indices of fragmentation, connectivity, complexity, heterogeneity and disturbance (Alberti et al. 2001; Radford et al. 2005).

The rapid development in recent years of large databases of geographic, demographic and other data amenable to manipulation and interpretation by sophisticated geographic information systems (GIS) has led to a concomitant growth in the array of landscape metrics readily available to ecologists and other researchers. Indeed, it seems likely that the array of metrics has developed at a much greater rate than has our ability to meaningfully relate them to ecological processes. Are the patterns that these metrics represent important for birds or other organisms, and how can this best be tested?

Many of the studies of urban birds that have considered landscape elements have done so by studying species richness or diversity of birds at the patch scale, typically on an urbanisation gradient, and then relating local features to the landscape (Beissinger and Osborne 1982; Blair 1996; Drinnan 2005; Fernández-Juricic 2000; Jokimäki 1999; Jokimäki and Suhonen 1993; Melles et al. 2003; Suhonen and Jokimäki 1988). Few studies have analysed the structure of avian urban assemblages in relation to factors causing the urbanisation gradient (Daniels and Kirkpatrick 2006; Hahs and McDonnell 2006; Ruszczyk et al. 1987). Relationships between urban birds and landscape metrics appear strong when considering individual species, but habitat pattern can be less strongly linked to bird assemblage diversity (Donnelly and Marzluff 2006).

1.6 Community ecology

The concept of a guild was first formalised by Root (1967), and applied to foraging guilds of birds in oak woodland in the United States. The definition provided by Root (1967) remains a useful summation of the concept, as follows:

"... A guild is defined as a group of species that exploit the same class of environmental resources in a similar way. This term groups together species without regard to taxonomic position, that overlap significantly in their niche requirements. The guild has a position comparable in the classification of exploitation patterns to the genus in phylogenetic schemes ..." (Root 1967)

Though Root (1967) initially coined the term and concept to deal with foraging guilds of birds, it has since then been considerably expanded to include other categories of resource (as allowed for in the original description), and along the way it has assumed a central and important position in community ecology (Simberloff 1991).

Guild membership is not an immutable characteristic of bird species (Lopez de Casenave et al. 2008), but nonetheless, guilds have been widely used in interpreting varying aspects of the ecology and biology of assemblages of species, and particularly of birds (Simberloff 1991). For example, the avifauna of southern and central Victoria has been classified into guilds by a number of schemes. A typical and widely cited guild structure (Mac Nally 1994) includes 10 broad foraging guilds. The feeding guild has become one of the most useful tools for analysing community structure (Mac Nally 1994; Simberloff 1991). Classifying members of assemblages of birds according to guilds of resource use (e.g. foraging guilds, nest substrate guilds, dispersal ability guilds) potentially allows an understanding of structural ecological processes operating in the environment (Simberloff 1991). Whilst variations in simple measures of bird diversity can point to important structural or process changes in the urban environment, departures from typical assemblage structure (proportional representation of guild members as a percentage of the total assemblage) aid in understanding what the nature of the changes might be. For example, birds that nest on the ground typically disappear from urbanised areas due to high levels of disturbance and predation (White et al. 2005). Birds that forage by gleaning invertebrates from tree leaves, branches and may increase in urban areas as trees are planted (White et al. 2005).

1.7   Behavioural ecology

Behavioural ecologists study the fitness consequences of behaviour. Research in this field is predominantly concerned with questions of what an animal gains, in fitness terms, by choosing one behaviour over another. Behavioural ecology in its broadest sense combines the study of animal behavior with evolutionary biology and population ecology, physiology and molecular biology — unified by the central concept of adaptation, and the notion that natural selection operating on behaviour has the potential to produce evolutionary change.

Human disturbance of animals is a broad concern in a world with a rapidly increasing human population (Frid and Dill 2002). Effects of disturbance include direct and indirect, lethal and sublethal aspects. They may include pertubations to metabolic processes (Belanger and Bédard 1990; Wingfield and Ramenofsky 1999), reduction in foraging effectiveness (Madsen 1998a, 1998b), displacement from preferred habitat, and changes in activity cycles (Madsen and Fox 1995).

As the field has begun to deal with urbanised species, the research has centred largely around disturbance and predation risk, and the extent to which animals perceive humans as potential predators or that humans mediate or mitigate the actions of natural predators. The 'ecology of fearfulness' characterises disturbance responses to humans as a behavioural syndrome.

Responses an animal makes to threatening stimuli are frequently simple behavioral responses (Beale 2007), and it is therefore not surprising that measuring behavioral responses such the distance at which an animal flees (flight initiation distance, FID) have been widely used to address a number of related questions about the impacts of disturbance (Cooper and Blumstein 2015). Behavioral measures have also been used when human disturbance effects are assumed and the question is more to identify which populations or species are most susceptible to disturbance (Blumstein, Fernández-Juricicet al. 2005; Weston et al. 2012). Cooke (1980) first documented the shorter flight distances of urban birds than their rural conspecifics, and that this related to body size, the difference being larger in small species with high metabolism. This change in behavior between urban and rural habitats allowed birds to coexist with humans even at high human population densities, which are a cause of frequent disturbance. Parallel latitudinal trends in FID and raptor abundance in paired urban and rural sites suggest that birds, besides responding to human presence, also adjust their behavior in response to natural levels of disturbance by predators (see Díaz et al. 2013 and references therein).

It is also the case that behavioural responses involve the animal making a number of different decisions, so a simple interpretation of a simple behavioural response may be misleading. Predation could be an important determinant of the structure of urban bird communities, but some recent research indicates otherwise. A 'predation paradox' has been suggested — although vertebrate predator numbers increase with urbanisation, predation rates decline (Fischer et al. 2012). Hypotheses to explain the predation paradox suggest that urbanisation has changed trophic dynamics in reducing top–down control through multiple mechanisms, and by increasing bottom–up forces via the increased availability of human–provided food and other nutrients. On the other hand, Møller (2014) has argued that the ubiquitous presence of humans in urban areas selects for animals with short FIDs, and adaptation to urban environments results in further reductions in FID; and in addition that that birds experience decreased raptor predation by associating with humans.

Birds are frequently used as model organisms (e.g. Blumstein 2006) in ecology of fearfulness studies. The relevance of the concept in predicting urbanisation success of fauna has been broadly investigated in Northern Hemisphere Old World cities (Díaz et al. 2013; Møller 2008, 2009, 2010), and at least once in a Southern Hemisphere New World city (Carrete and Tella 2011). Fearfulness of humans as potential predators of birds — more specifically variation in fearfulness — may filter the bird species in urban environments (Møller 2014). FID as a measurable indicator of fearfulness is generally presented as species mean FID (m_{FID}). Recent research has pointed to the stronger predictive ability of variation in m_{FID} (the Coefficient of Variation in FID, or cv_{FID}) in modelling urban invasiveness of bird species (Møller 2010), along with relative brain size (Carrete and Teller 2011).

Several authors have shown that m_{FID} was consistently lower in urban species cohorts than in their rural conspecifics, but that the m_{FID} of urban individuals was generally within the lower-range distribution of their rural conspecifics (Carrete and Tella 2011; Cooke 1980; Møller 2008, 2010). Although body size explained significant variation in birds' FID, and diet and sociality were also important, many other potential correlates of FID still remain to be closely investigated (Blumstein 2006; Carrete and Tella 2011). Candidates include age, sex, morphology, study site features such as distance from cover and the physical barriers such as fences, weather, and clothing colour (see Fernández-Juricic et al. 2006). Environmental and behavioural factors acting in concert explain the urban tolerance of bird species and assemblages.

1.8 Spatial autocorrelation

Spatial autocorrelation (SAC) explained simply refers to the tendency of sites situated close together to be more similar in their characteristics than those situated some distance apart; i.e. the lack of independence between pairs of observations at given spatial intervals (Diniz-Filho et al. 2003). It is a common phenomenon in ecology (Dormann 2007), and ecologists have been aware of it for some time (Legendre 1993; Sokal and Oden 1978). Some researchers have suggested that SAC, if not explicitly accounted for in analyses, has the potential to distort analytical outcomes (Fortin et al. 2002; Kühn 2007; Lennon 2000). More recent work however suggests that whilst SAC has an impact on model accuracy, explicitly addressing it in spatial models has at best a moderate impact on model accuracy (Diniz-Filho et al. 2003; Dormann 2007). Indeed, SAC may be representing information in the model that should not be 'corrected for', and it may make more sense for the model to directly address the environmental factors influencing SAC, e.g. dispersal and competition (Austin 2002; Dormann 2007).

1.9 Summary

A number of possibilities for further research arise from this particular review of the state of urban bird ecology.

The first concerns the commonplace treatment of the urban matrix as almost universally hostile to (native) birds and only irregularly dotted with remnant native vegetation refugia, versus the concept of it being a landscape of interconnected and continuous bird habitats of varying quality and suitability for different kinds of birds.

The nature of how or why some birds become urbanised whilst others remain marginalised, and the extent to which the drivers are environmental and/or behavioural, in urban landscapes is still very much open for debate and substantial elaboration.

Lastly, the notion of objective classification of birds into urban tolerant or intolerant assemblages is still relatively uncommon in the discipline, and the extent to which subjective or objective classifications influence the dominant narrative in urban ecology is unclear.

"... Well,
then men and women came
and took my simple materials ...
and with such ordinary things
constructed walls, floors and dreams ..."

'Ode to criticism'
Pablo Neruda 'Elemental Odes' (1952–1957)

CHAPTER 2:

THE STUDY

2.1   Thesis aims and objectives

The overarching objective of this research is to study the patterns of occurrence, relative abundance (= incidence) and habitat preference of urban birds across the gradient of urbanisation, from urban through to peri-urban, but at a landscape scale across the whole of the metropolitan Melbourne area. Secondly, it is proposed to take ecological results and interpretation about settlement patterns which support varying complements of urban bird diversity, behavioural traits which may convey urban adaptiveness, and develop a more nuanced understanding of the nature of what defines an urban bird than already seen in the literature. The proposal is to deconstruct what it is to be urban, and take the birds-eye view.

2.2   Thesis structure

The core of this thesis is presented in the form of published manuscripts. Chapters 3, 4 and 5 have already been published in international, peer-reviewed journals, and Chapter 6 has been submitted for publication in a journal of the same standing.

Individual published papers have embedded references, but a single consolidated reference list (including both those in thesis text and published papers) is provided at end of this thesis.

An early point of distinction for this project was the development of a methodology for objective classification of urban birds based on primary data analysis, rather than subjective application of criteria from other studies as is more commonly seen. This is explored in detail in Chapter 3 (Conole and Kirkpatrick 2011). Taking the groupings of urban birds thrown up by the classification exercise, it is then intended that correlative studies of assemblage distribution and abundance against a range of environmental and human demographic factors be undertaken. The objective of this exercise is to reveal mechanistic processes underlying urban preference, related to fundamental ecological processes of foraging, nesting and dispersal. This is also investigated in detail in Chapter 3 (Conole and Kirkpatrick 2011). Assumptions about the universality or otherwise of the action of these factors on birds which are indigenous in the region or are introduced from other parts of the world are examined in Chapter 4 (Conole 2011). Included in this strand is an examination of the extent to which introduced birds are synathropic. The next research strand investigates the different responses of urban exploiter and urban adapter bird assemblages to intensity of urbanisation, and tests the relationship with habitat-of-origin as a determinant of adaptability; presented as Chapter 5 (Conole 2014). Chapter 6 (Conole in prep.) investigates the significance of fear of predation in conferring adaptive advantages to some birds over others in urban environments.

2.3   Research significance

To the best of my knowledge this whole-of-landscape approach to urban bird ecological research has not been attempted previously on the scale that Melbourne offers; though several authors have recognised the need for such an approach to add to the existing knowledge gained from fine-grained studies of local impacts (Donnelly and Marzluff 2006; Miller *et al.* 2001). Landscape scale thresholds for extinction have only comparatively recently been demonstrated empirically for woodland birds in a rural landscape (Radford *et al.* 2005), but previous hybrid local/landscape research models in urban areas have only been able to infer that regional

attributes may be significant for urban birds by extrapolating to the general (landscape) from the particular (patch) (Drinnan 2005). Previous research has also not investigated the ecological equivalkence of exotic and indigenous birds in the urban context (John Marzluff, University of Washington, pers. comm., February 2015).

The existence of a datset of some 220,000 bird records from within the urban area of Metropolitan Melbourne (Barrett et al. 2003) along with a corresponding set of environmental and demographic parameters (Hahs and McDonnell 2006) offers a unique opportunity to robustly interrogate a large dataset and test a number of hypotheses about how and why birds are distributed in a large diverse city. The ecological aspects of this proposed research are of intrinsic scientific interest, but there is also a genuine opportunity to discover if any universal urban landscape ecology principles exist which can be codified into policy and decision making tools for use in urban design and planning practices. The novel aspect of the urban design/planning dimension of this research is the intention to produce generalisable principles of appropriate scale and relevance for urban biodiversity planning.

2.4   Research ethics

The research that was proposed did not involve any direct use of birds or other animals, as was working entirely from existing compiled datasets. Therefore, there are no animal ethics implications. The raw secondary data that I proposed to use were in the public domain, and did not identify the data collectors. Furthermore, I did not require knowledge about the originators of individual data points in order to use them for my research. Therefore, there are no privacy issues with the bird and landscape data proposed for use in this research. Therefore, my research did not constitute an ethics risk level greater than the lowest formal ranking.

2.5   The study area

The study area is metropolitan Melbourne; capital city of the State of Victoria in coastal south-eastern Australia, within a 50 km radius of its Central Business District (37°49'S 144°58'E) (Figure 2.1). The study area excludes Port Phillip Bay waters, but includes areas not yet urbanised. In 2007 the total area of metropolitan Melbourne (equivalent to the Melbourne statistical division) was *circa* 8,100km² with a population in 2007 of approximately 3.8 million (Australian Bureau of Statistics 2009).

Suburbs, with detached single dwellings in gardens dominated by plant species exotic to Melbourne, cover most of the study area. Semi-natural remnants of native vegetation are scattered within the bounds of the urban area, which also contains many parks and gardens planted with exotic plant species. Trees are planted in most streets; these tend to be native to Australia, but not to the Melbourne region (Frank *et al.* 2006). The original vegetation of Melbourne and the native vegetation that survives on its margins is highly varied, this variation being related to soils, which range from highly fertile black, cracking clays to highly infertile, deep, leached sands, and annual rainfall which ranges between 540–1,000mm from west to east.
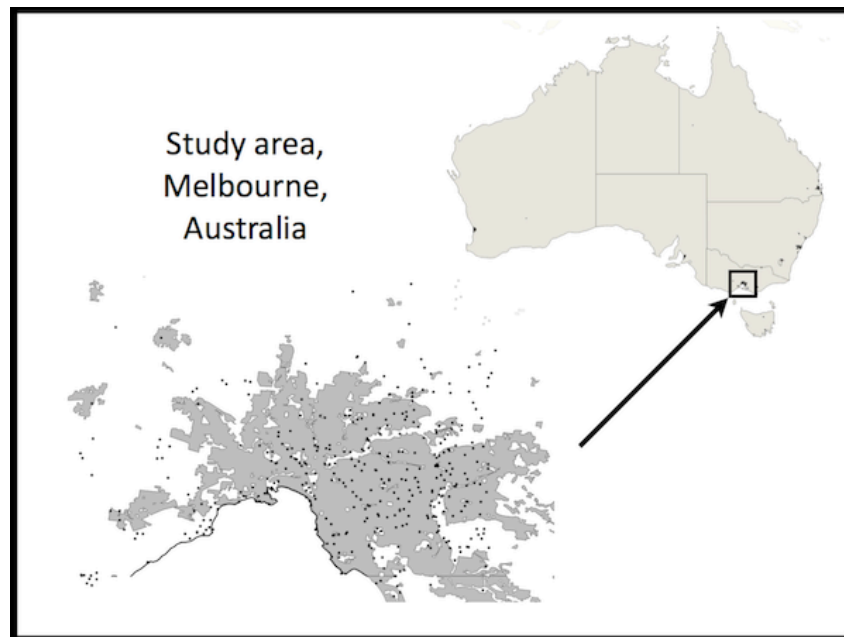
Figure 2.1: The study area — Melbourne, Victoria, Australia
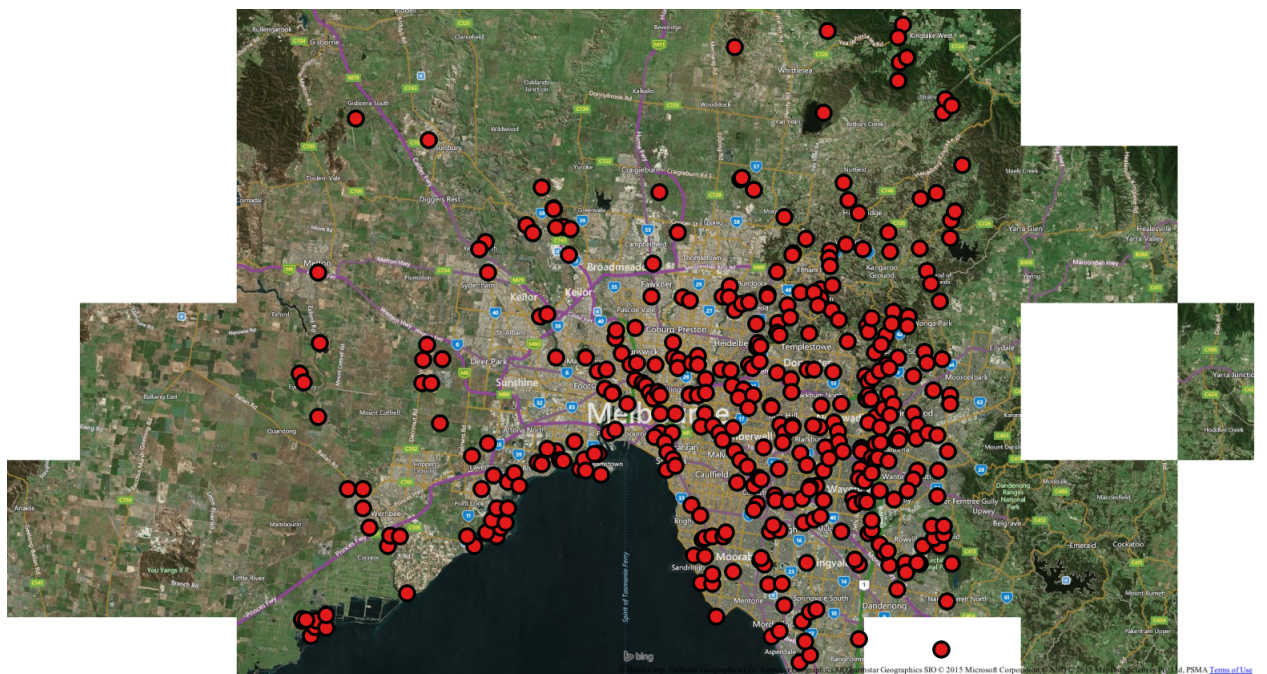
Figure 2.2: The study area showing study sites and landscape context (© Microsoft Bing Maps)
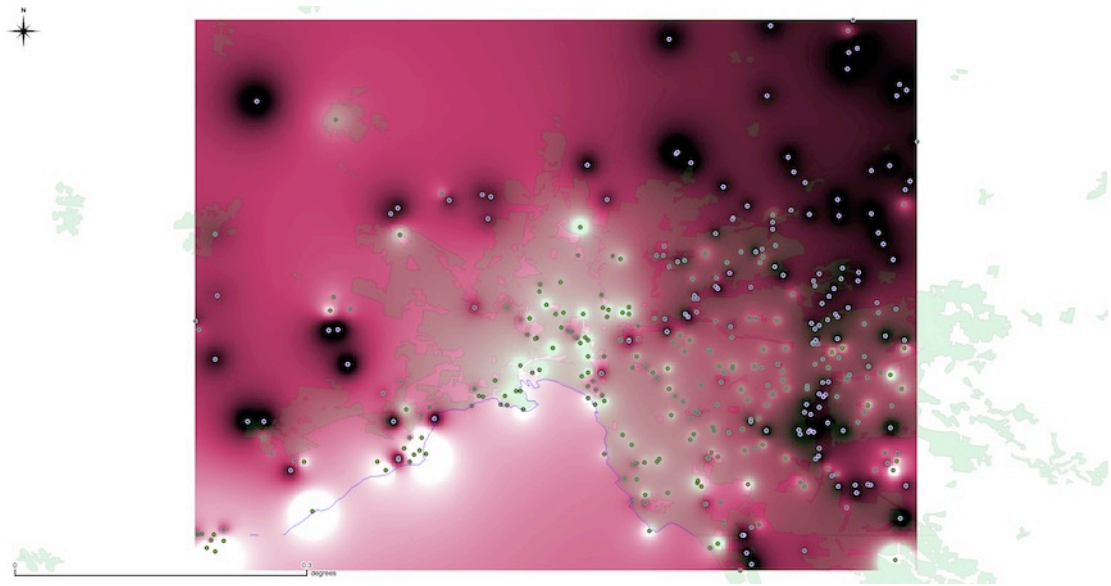
Figure 2.3: Interpolated Frequency Greenspace map of Melbourne. Pale areas around the study site dots show lower values for Frequency Greenspace and darker areas show higher Frequency Greenspace. Pale green background shows built-up areas of Melbourne.
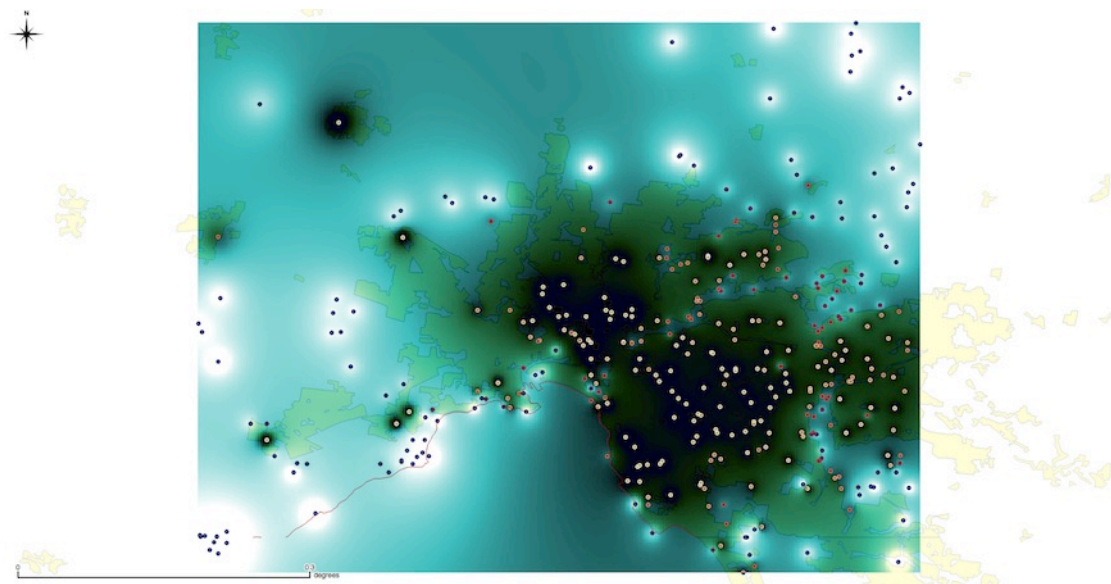
Figure 2.4: Interpolated $Index_{Combined}$ map of Melbourne. Pale areas around the study site dots show lower values for $Index_{Combined}$ and darker areas show higher $Index_{Combined}$. Pale green background shows built-up areas of Melbourne.

2.6 Methods and materials

2.6.1 Data handling

Data acquisition, preparation and analysis to produce the objectively classified urban bird assemblages is described in detail in Chapter 3 (Conole and Kirkpatrick 2011), and the process is summarised briefly below.

Approximately 220,000 records of 292 species of birds from 11,434 surveys were extracted from the Birds Australia New Atlas of Australian Birds project database (hereafter the Atlas) (Barrett et al. 2003).

The Atlas database contains four types of record: 2–ha search for 20 minutes; small area search (within 500m of a central point); large area search (within 5 km of a central point); and, incidental observations of individual species from a single point (Barrett et al. 2003). Each survey represents a list of species for a defined area and time (ranging from 20 minutes to one month), with geographic co-ordinates. All data were collected between 1998 and 2002.

Data initially extracted for this study included 4,221 2–ha searches, 4,993 small area searches, 793 large area searches, and 1,427 incidental observations, and were compiled in a matrix as species and their relative abundance (number of surveys in which a species was recorded in a cell divided by the total number of surveys conducted in the cell) by site. Using ArcMap GIS, a 1 x 1 km grid based on that developed by the Australian Research Centre for Urban Ecology (ARCUE) (Hahs and McDonnell 2007) was intersected with Atlas records to produce a matrix of grid cells by species presence/absence. All surveys were assigned to the grid cell in which the central geographic coordinates fell, regardless of survey spatial or temporal scale. It was assumed that most large area searches (6.9% of the surveys in the unfiltered data set) referred to areas of between 500–2,000 m diameter, and therefore could reasonably be assigned to 1 x 1 km grid cells within which the central coordinates fell.

As there is a likelihood that less abundant species may be missed where sampling effort is lower, leading to uneven representation of species (Watson 2004), a measure of estimated sampling completeness was calculated for each of the grid cells. This enabled an assessment of the evenness of sampling, and for unrepresentative samples to be removed from the data to be analysed.

Several assumptions were made about species to be excluded from analyses, and species were not included in grid cell totals and were eliminated from further analyses if any of the following exclusion criteria were met: (i) constituted fewer than five records in the total dataset; (ii) was an irregular or vagrant species to the area or feral species not yet naturalised, determined from the literature (Barrett et al. 2003); or, (iii) were seabird, waterbird, and nocturnal species (except the readily observed Tawny Frogmouth *Podargus strigoides*) from the orders or families: Anseriformes, Podicipediformes, Strigiformes, Eurostopodidae, Aeogothelidae, Procellariformes, Spenisciformes, Phalacrocaraciformes, Ciconiiformes, Gruiformes, Charadriiformes (*sensu* Christidis and Boles 2008). A final list of 141 species (hereafter the filtered species list) was retained for further analysis.

Grid cells were eliminated from further analyses if any of the following exclusion criteria were met:

- 0–1 surveys in the cell;

- %*Completeness* < 50%;

- land area < 25% of the cell; or

- a high proportion of singleton records (>50%) and/or no doubleton records (indicating skewed data collection, e.g. single-species or other narrowly targeted surveys).

A final list of 390 grid cells was retained for further analysis (Figure 2.2).

Bird species were classified into foraging guilds using a modified scheme for southern Victorian species (Mac Nally 1994). Mac Nally's (1994) 'Hawker' and 'Sweeper' categories were combined to make 'Hawker/Sweeper', 'Wood Searcher' and 'Bark Prober' combined to make 'Wood Searcher/Bark Prober', and the categories of 'Raptor' and 'Frugivore' were added. Species not classified by Mac Nally (1994) were classified according to data contained in the '*Handbook of Australian, New Zealand and Antarctic Birds*' (hereafter referred to as HANZAB) (Davies et al. 1991; Higgins and Davies 1996; Higgins and Peter 2003; Higgins et al. 2001; Higgins et al. 2006; Higgins 1999; Marchant et al. 1994). Nest substrate and dispersal groupings were also assigned from data contained in HANZAB. Data on bird size was tabulated as maximum mass (in grams [g]) from HANZAB. Systematics and nomenclature of birds follow Christidis and Boles (2008).

Spatial data on the degree of urbanization of the study area employed in this study were developed at ARCUE and are discussed in detail by Hahs & McDonnell (2006); a brief summary follows. People per square kilometre (People km^{-2}) is the total number of people in census collection districts. Dwellings per square kilometre (Dwellings km^{-2}) is the total number of dwellings in census collection districts. Frequency Greenspace is the reciprocal of the average amount of impervious surface calculated at the sub-pixel level from the impervious surface fraction image created during the spectral mixture analysis of the 2000 Landsat ETM+ image (Hahs & McDonnell 2006). Combined index ($Index_{combined}$) is the average value of $Index_{image}$ and $Index_{census}$; where $Index_{image}$ is calculated from fraction images produced by the spectral mixture analysis of the 2000 Landsat ETM+ image, and $Index_{census}$ = the total number of people multiplied by the proportion of males employed in non-agricultural work, as enumerated in the 2001 Australian census (Hahs and McDonnell 2006). Combined index was found to be a useful measure for determining the level of urbanization represented by a combination of demographic and spatial data (Hahs & McDonnell 2006). Metrics were calculated for all cells in the 65 x 66 km ARCUE grid (Hahs & McDonnell 2006; Amy Hahs pers. comm., 25 May 2007).

Interpolated maps showing the distribution of Frequency Greenspace and $Index_{combined}$ and within the elbourne area are shown as Figures 2.3 and 2.4, and photographic examples of points on the urbanisation gradient as Figures 2.5–2.8.

2.6.2   Data analysis

I performed all statistical analyses in the R-framework (R Development Core Team 2009–2010), using core functions and procedures from the community ecology package 'vegan' (Oksanen et al. 2008). The data for cluster analysis consisted of a standard 'r x c' array, with sites as rows, species as columns, and relative abundance (% incidence in surveys conducted in each cell) data for species occurring in each grid cell. I prepared a Bray-Curtis distance matrix, and formed groups of species were by hierarchical agglomerative clustering using Wards algorithm performed on the distance matrix, as a function of their similarity in distribution and relative

abundance. Following González–Oreja et al. (2007), an assemblage is a cluster of species separated from all other such clusters by an ecological distance greater than the greatest distance between the two most disparate members of the clade. Where significant sub-structuring in the dendrogram coincided with diagnosable trends in the environmental and demographic data, I recognised sub-assemblages. I named assemblages using a version of Blair's (1996) standard nomenclature, in keeping with its wide use in the urban bird ecology literature (Chace and Walsh 2006). I ordinated the species and grid cells by global non-metric multidimensional scaling (NMDS) methods, using the 'vegan' package. I chose a two-dimensional solution using the Wisconsin square-root transformation and Bray-Curtis coefficients as a measure of dissimilarity in species composition between the sample plots. I fitted vectors for seven variables to both the species and grid cell two-dimensional ordination space using the procedure, 'envfit', in 'vegan', and plotted the species ordination space. Each grid cell was attributed to the bird cluster that had the highest proportion of its total number of species within it, except for 13 cells out of 390 (3.3%), which had equal numbers of cluster 2a and 2b species present.

I used a Kruskal-Wallis test to test whether these five groups of grid cells differed in a simple measure of urbanization intensity, People km^{-2}. I also used a Kruskal-Wallis test to test whether these five groups of grid cells differed in longitude (indicating their position on a west to east environmental gradient in Melbourne), and to test whether bird mass differed significantly between the five groups. I used the the Mann-Whitney U-test to determine which means were significantly different from others. As the principal interest was in the comparisonwise error rate rather than the 'experimentise error rate', an α correction (such as Bonferroni) for multiple comparison testing was judged to be unnecessary (Bender and Lange 2001).

The assemblage members were then allocated to the categories of 'urban exploiter', 'suburban adapter', or 'urban avoider' (Blair 1996) on the basis of their membership of the clusters associated with different levels of urbanisation intensity. This process differs from the method employed in some other studies, in which the urban bird classes were aligned *a priori* with predetermined classes of urbanization intensity (e.g. White *et al.* 2005, Croci *et al.* 2006). For most analyses and discussion, the exploiter and adapter groups are pooled as urban tolerant. A Pearsons Chi-square test was used to determine whether particular functional and size classes deviated from expected distributions between urban tolerant and urban avoider birds.

2.6.3 Subsequent data handling and analyses

More targeted analyses are presented in Chapters 4 (Conole 2011), 5 (Conole 2014) and 6 (Conole in prep.).

(a) Aerial

(b) Street view

Figure 2.5: Human population density range 0–255 people/km². © Google Earth.

(a) Aerial

(b) Street view

Figure 2.6: Human population density range 700–1,100 people/km². © Google Earth.

(a) Aerial

(b) Street view

Figure 2.7: Human population density range 4,000–5,200 people/km². © Google Earth.

(a) Aerial
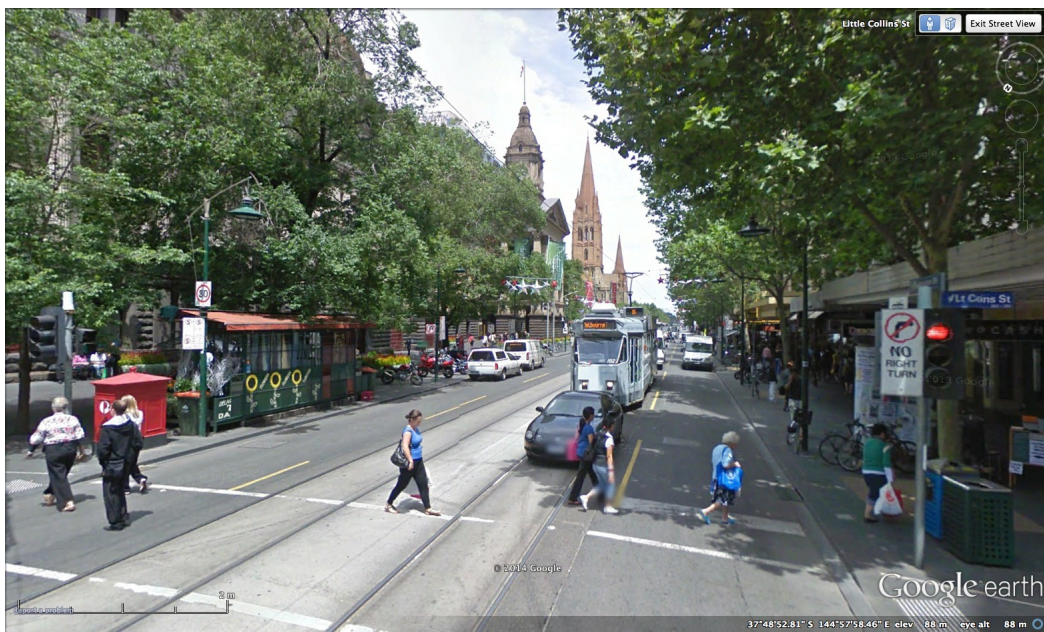
(b) Street view

Figure 2.8: Human population density range 5,200–8,300 people/km². © Google Earth.

*"... Even if what youre working on doesnt go anywhere, it
will help you with the next thing you're doing ..."*

Attributed to Cormac McCarthy

CHAPTER 3:

FUNCTIONAL AND SPATIAL DIFFERENTIATION OF URBAN BIRD ASSEMBLAGES AT THE LANDSCAPE LEVEL

Chapter 3

Abstract

We studied the diversity and distribution of diurnal birds in a large city in south-eastern Australia. Approximately 220,000 bird records were extracted from the Atlas of Australian Birds project (1998–2002) for Melbourne, and filtered on the basis of representativeness in surveys. The filtered data for 141 species were subjected to cluster analysis to recognise assemblages, and ordination and guild analysis to determine spatial and functional organisation. Measures of the intensity of urbanisation and environmental characteristics of Melbourne were used to test the separation of the avifauna into broad urban tolerant and urban avoider assemblages and sub-assemblages. Distribution and relative abundance of urban tolerant birds were found to be positively associated with areas of higher urban intensity, while urban avoiders were associated with areas of lower urban intensity in natural areas within the urban matrix or along its periphery. Urban tolerant species are medium-sized, generalist foragers, which use cavities and canopy sites for nesting, while urban avoiders are either small or very large, foraging specialists (particularly insectivores), which nest on or near the ground as well as in the canopy or shrub layer. Our study confirms that cities do include habitats that are important for a number of urban adapted birds, and suggests ways in which conserving bird diversity can be accommodated in urban planning frameworks.

Status

Attribution statement

The paper was co-authored with Distinguished Professor Jamie Kirkpatrick (School of Land and Food (Geography and Environmental Studies), University of Tasmania, Private Bag 78, Sandy Bay, Tasmania 7001, Australia)

I conducted the literature review, formulated the research questions, undertook the analyses, and wrote the paper. Professor Kirkpatrick contributed to the processes of refining the research direction, and interpretation of results.

This article has been removed for copyright or proprietary reasons.

"... Familiar things are strange
While strangers play upon the lawn ..."

'Native born'
Archie Roach 'Charcoal Lane' (1990)

CHAPTER 4:

DIVERSE RESPONSES OF EXOTIC BIRDS TO URBANISATION

Chapter 4

Supplementary material appended here as Appendix 2:

Abstract

Exotic bird species are prominent members of urban avifaunas in many areas of the world, and much has been generalised about their distribution, abundance and undesirability in urban habitats. Less attention has been given to the spatial and functional responses of exotics to the urban environment. This study tests the hypothesis that exotic birds exhibit responses to environmental factors that are similar to those of local native birds. Exotics group with natives in generalist urban tolerant and specialised urban avoider assemblages, and their species richness and site similarity are broadly proportional with those of natives. Urban tolerant exotics are significantly larger than avoiders, as with native birds. Habitat filtering is occurring to create unique urban bird assemblages, acting differentially on all species according to their ecology and biology, regardless of origin.

Status

Published in July 2011 in *Natureza & Conservação*; which is a peer-reviewed, Open Access journal in English devoted to improving theoretical, methodological and practical aspects of conservation science. Formerly known as *'Brazilian Journal of Nature Conservation'*, *'Natureza & Conservação'* (literally *'Nature & Conservation'*) was published by the Brazilian Association for Ecology and Conservation (Associação Brasileira de Ciência Ecológica e Conservação — ABECO), with substantial support from the Boticário Foundation. Now published by Elsevier. Impact factor (2015): 1.327.

www.abeco.org.br/volume-9-numero-1

Diverse Responses of Exotic Birds to Urbanization

Lawrence Edwin Conole*

School of Geography and Environmental Studies, University of Tasmania, Tasmania, Australia

Abstract

Exotic bird species are prominent members of urban avifaunas in many areas of the world, and much has been generalized about their distribution, abundance and undesirability in urban habitats. Less attention has been given to the spatial and functional responses of exotics to the urban environment. This study tests the hypothesis that exotic birds exhibit responses to environmental factors that are similar to those of local native birds. Exotics group with natives in generalist urban tolerant and specialized urban avoider assemblages, and their species richness and site similarity are broadly proportional with those of natives. Urban tolerant exotics are significantly larger than avoiders, as with native birds. Habitat filtering is occurring to create unique urban bird assemblages, acting differentially on all species according to their ecology and biology, regardless of origin.

Key words: Urban, Exotic, Birds, Spatial Distribution, Functional Responses.

Introduction

Exotic bird species are prominent members of urban avifaunas in many areas of the world (Blair 2001). An exotic species is defined as one that has established a reproductive population in an area not part of its natural range (Long 1981); the 'passive colonists' of Catterall (2009). Exotic bird species do not always establish self-sustaining populations in the locations to which they are introduced, despite sometimes considerable support and repeated attempts; they also suffer extinctions as well as going on to establish in new locations (Long 1981). Most exotic species also have extensive non-urban distributions in countries of introduction (Long 1981), and are not exclusively synanthropic.

Much has been generalized about the distribution, abundance and undesirability of exotic birds in general, including in urban habitats, particularly in the popular literature (Rolls 1969; Low 2002). For instance, it has been asserted that they reduce food production, compete with native species for resources and disperse invasive plants (Long 1981; Hart & Bomford 2006). Despite a bad press, little empirical research has been published which specifically targets the effects of exotic birds in urban systems (Chace & Walsh 2006; White *et al.* 2009), or their responses to environmental or habitat factors. In one of the few relevant studies, direct negative impacts of the Common Myna (*Sturnus tristis*) on native birds through competition for nest sites have

been demonstrated in Australia (Pell & Tidemann 1997), though the same species' foraging strategy was found not to overlap with native species (Crisp & Lill 2006). Recher (2006) suggested that most exotic birds in urban habitats are essentially benign, and are cherished by many city dwellers for '… *colour, movement and song* …' in otherwise bland urban landscapes.

By their very presence, exotic species homogenize global urban avifaunas (McKinney 2006), but their distributions may not be homogeneous within cities (Natuhara & Hashimoto 2009). Exotic species are often present in urban native vegetation remnants, but at lower levels of abundance than in surrounding built-up areas (Catterall 2009; Antos *et al.* 2006). Global 'ubiquitists' were found only to dominate 'bare' suburbs in subtropical Brisbane (Catterall 2009), and the same is true for temperate Melbourne (Conole & Kirkpatrick 2011) and many other cities (*e.g.* Hugo & Van Rensburg 2009; Croci *et al.* 2008; van Heezik *et al.* 2008; Kark *et al.* 2007; Chace & Walsh 2006). In studies of the distributions of plants it has been common to find that exotic species are as closely related to environmental variation as native plants (*e.g.* Fensham & Kirkpatrick 1989; McKinney 2004).

There have been assumptions made more widely that as many exotic bird species are at least in part synanthropic (Johnston 2001), that this conveys a competitive advantage in urban environments. An unstated assumption of this generalization is that exotic bird species introduced into urban habitats will be free of the environmental constraints operating on the range of formerly occurring and colonizing

*Send correspondence to: Lawrence Edwin Conole
School of Geography and Environmental Studies,
University of Tasmania,
Private Bag 72, Sandy Bay, Tasmania 7002, Australia
E-mail: lconole@gmail.com

native bird species. The distributions of native and exotic birds in Melbourne are intermixed (Conole & Kirkpatrick 2011), suggesting that any presumed freedom from urban environmental constraints for exotics may be in error at least for this city, and therefore worthy of exploration.

At the time of writing, Melbourne had 13 established non-native bird species present within its terrestrial bird assemblages (Conole & Kirkpatrick 2011). Most species are long established in Melbourne, having been introduced since the mid to late nineteenth century. This well-established and diverse exotic avifauna has parallels elsewhere in the temperate zones of the world, particularly in New Zealand, Western Europe and North America (Long 1981).

In this paper the hypothesis is advanced that exotic and native urban tolerant species are similar in their range of spatial and functional responses to urbanization; in other words, environmental filters operating on the natives will also act on exotics. As subsets of the main hypothesis it is theorized that i) most exotic species will be urban tolerant, but some more specialized species will be urban avoiders; ii) exotic species diversity will vary proportionally with overall bird species diversity; and, iii) most exotic species will be least abundant in areas of low urbanization intensity and higher native species richness.

Material and Methods

Detailed descriptions of the study area and methodology used to derive the urban bird assemblages can be found in the Supplementary Material[*], and in Conole & Kirkpatrick (2011). A brief summary follows below.

Study area and data handling

The study area is metropolitan Melbourne; capital city of the State of Victoria in coastal south-eastern Australia, within a 50 km radius of its Central Business District (37° 49' S and 144° 58' E). Approximately 220,000 records of birds were extracted from the Birds Australia 'New Atlas of Australian Birds' project database and intersected with 1×1 km grid cells (Hahs & McDonnell 2007) to produce a matrix of grid cells by species presence/absence. Species and sites were filtered out according to criteria for representativeness to arrive at a final list of 141 species and 390 cells (Figure 1).

Environmental and demographic indices

$Index_{combined}$, representing urbanization intensity by a combination of demographic and spatial data; is derived from $Index_{image}$ = spectral mixture analysis of the 2000 Landsat ETM+ image, and $Index_{census}$ = the total number of people multiplied by the proportion of males employed in non-agricultural work (Hahs & McDonnell 2006).

Data analysis

A Bray-Curtis distance matrix was prepared, and groups of species (assemblages) were formed by hierarchical

agglomerative clustering using Ward's algorithm performed on the distance matrix, as a function of their similarity in distribution and relative abundance (Conole & Kirkpatrick 2011). Jaccard's Index of similarity was calculated for exotic (JI_{exotic}) and native (JI_{native}) species by site (390 sites, 75844 pairwise comparisons). A ratio (JI_{exotic}/JI_{native}) served as a relative metric indicating whether grid cells showed a tendency to share exotic species to a greater (ratio > 1) or lesser extent (ratio < 1) than native species (McKinney 2004).

Results

Species richness of exotic birds in Melbourne is proportional to total bird species richness ($R^2 = 0.213$) (Figure 2). The Jaccard's Index of similarity among sites for exotic and native species ($R^2 = 0.187$) (Figure 2) follows the species richness trend; in other words, sites that share many native species also share many exotic species, and *vice versa*. However, relative abundance (incidence in surveys) of individual exotic species is broadly inversely proportional to native bird species richness (Figures 3, S2). In all cases the Jaccard's Index ratio between exotic and native birds exceeded one (>1).

Melbourne has 13 established exotic bird species present within its terrestrial bird assemblages (excluding waterbirds). All non-Australian species are from the Old World; either Eurasian or S-SE Asian in origin (Long 1981). Of the 13 species, eight are urban exploiters distributed widely in the urban area and either universally or locally abundant (Conole & Kirkpatrick 2011) (Table 1). The other five species are urban avoiders, and are either habitat or foraging specialists abundant only in non-urbanised habitats, or are rare with localized occurrences (Conole & Kirkpatrick 2011) (Table 1).
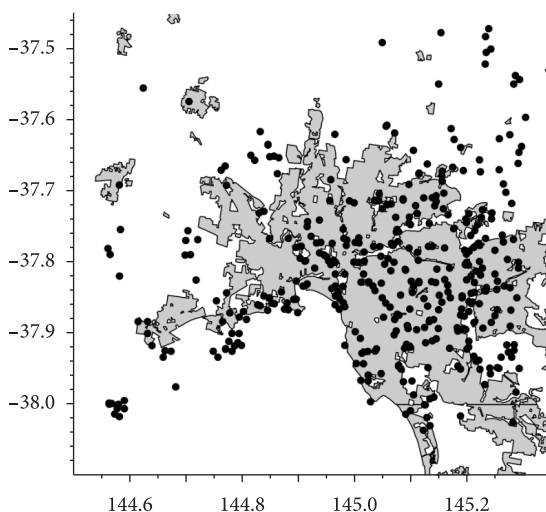
Figure 1. Spatial plot of filtered grid cells (black circles) over the Melbourne study area (built-up areas shaded grey) (x = longitude, y = latitude; decimal degrees).
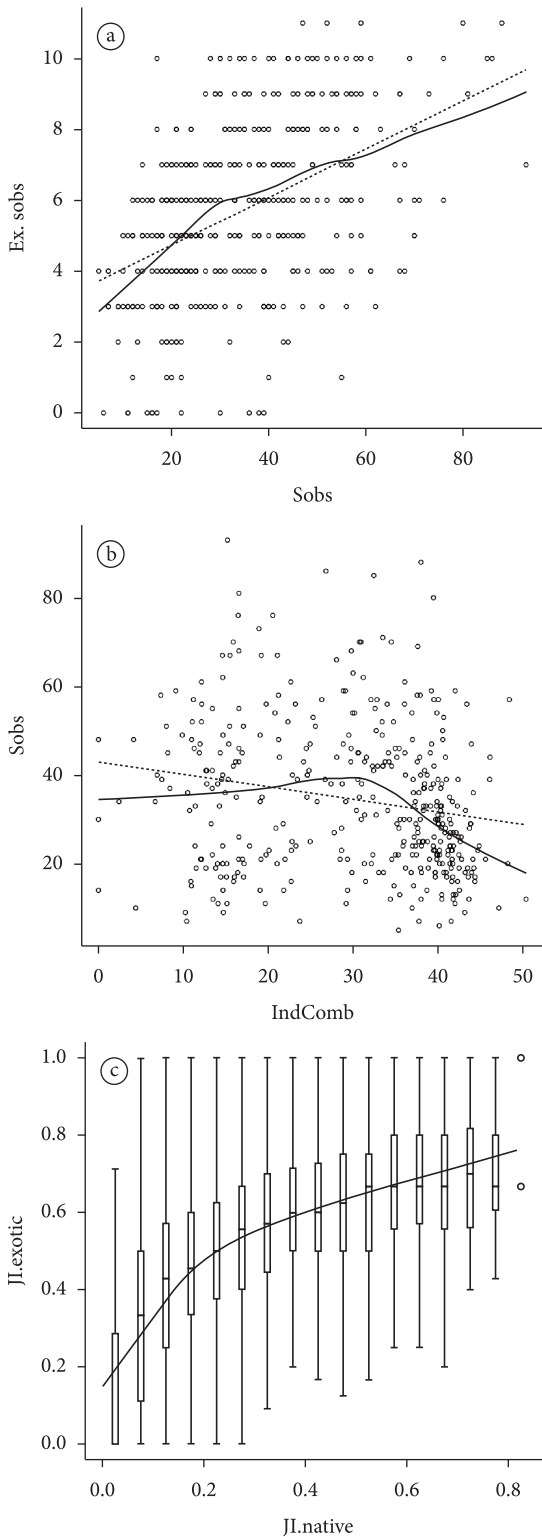
Figure 2. a) Exotic bird species richness (S_{exotic}) (y axis) plotted as a function of total bird species richness (S_{obs}) (x axis) (R^2 = 0.213). Regression line and Lowess curve shown; b) All bird species richness (S_{obs}) plotted as a function of a measure of urbanization intensity ($IndComb$). (R^2 = 0.037). Regression line and Lowess curve shown; c) Jaccard's Index (JI_{exotic}) for exotic bird species shared between sites (y axis), plotted against Jaccard's Index (JI_{native}) for all native species (x axis) (R^2 = 0.187). Lowess curve shown.

The most widespread species, occurring at over 80% of the 390 grid cells, were respectively Common Myna, Common Blackbird, Common Starling and Spotted Dove (Table 1). The incidence in surveys of these species is proportional to urbanization intensity (Figure 3, S1). The other nine species occurred in 1.8-62.1% of sites (Table 1).

The general trend for all exotics at the landscape scale is that they peak in relative abundance as a measure of urban intensity ($Index_{combined}$) increases, and then decline at the highest values of $Index_{combined}$ (*e.g.* Figure 2, S1). The corollary of this is that individual exotic species relative abundance declines as overall bird species richness increases (Figure 3, S2). In other words, exotics are least diverse in areas that are least urbanised and with greater diversity of all bird species.

Following the patterns established earlier for the entire urban avifauna (Conole & Kirkpatrick 2011), body mass of urban exploiters amongst the exotic birds is significantly greater than for urban avoiders (Student's *t*-test: p = 0.033) (Figure 4). Likewise, the only ground-nesting, frugivorous and nectarivorous exotics are urban avoiders (Table 1).

Discussion

It has already been demonstrated in earlier work that most exotic species in Melbourne are urban tolerant (Green 1986), but this is not universal, and some more specialized species are urban avoiders: Eurasian Skylark, Common Greenfinch, European Goldfinch, Red-whiskered Bulbul and Scaly-breasted Lorikeet (Conole & Kirkpatrick 2011). The first three exotic species fit with a suite of native bird species which characterize the assemblage as one largely of coastal areas, grassland, and wetland margins, whilst the latter two fit with the range of rare and range-restricted species in the largest of Melbourne's urban bird assemblages (Conole & Kirkpatrick 2011). The remaining eight species are classic urban exploiters, being widespread and at times abundant in a range of more intensively urbanised sites (Conole & Kirkpatrick 2011).

The sorting of exotic species into three of Melbourne's four urban bird assemblages, exhibiting similar functional and spatial responses to urbanization as for the natives, gives the first indication that both native and exotic species are filtered by habitats (Conole & Kirkpatrick 2011). The size differential between urban exploiter and urban avoider exotic birds matches that in native urban birds (Figure 4), as do the nest substrate and foraging profiles (Table 1, this paper; Conole & Kirkpatrick 2011).

The results of investigations conducted for the present paper indicate that exotic species richness and the extent to which sites share exotic species, are broadly proportional with those same variables in native urban birds. In the case of individual species trends, it is also clear that there are several responses at the highest level of urban intensity. Some species more typical of suburban habitats such as

Table 1. List of exotic bird species analyzed in this study, arranged by assemblage with proportion of cells occupied, taxonomic family, assemblage guild membership categories and biogeographic origin shown.

Percentage (%) of cells	Family	Common name	Scientific name	Urban status	Assemblage	Mass (g)	Foraging	Nest substrate	Dispersal	Biogeographic origin
87.7	Turdidae	Common Blackbird	*Turdus merula*	Exploiter	2b	89	Ground Carnivore	Shrub	Sedentary	Eurasia
23.1	Fringillidae	Common Greenfinch	*Chloris chloris*	Avoider	3	25	Granivore	Shrub	Sedentary	Eurasia
89.5	Sturnidae	Common Myna	*Sturnus tristis*	Exploiter	2b	116	Ground Carnivore	Other Cavity	Sedentary	South Asia
83.6	Sturnidae	Common Starling	*Sturnus vulgaris*	Exploiter	2b	78	Ground Carnivore	Other Cavity	Sedentary	Eurasia
17.7	Alaudidae	Eurasian Skylark	*Alauda arvensis*	Avoider	3	35	Ground Carnivore	Ground	Sedentary	Eurasia
13.6	Passeridae	Eurasian Tree Sparrow	*Passer montanus*	Exploiter	2b	24	Granivore	Other Cavity	Sedentary	Eurasia
42.1	Fringillidae	European Goldfinch	*Carduelis carduelis*	Avoider	3	16	Granivore	Shrub	Sedentary	Eurasia
62.1	Passeridae	House Sparrow	*Passer domesticus*	Exploiter	2b	27	Granivore	Other Cavity	Sedentary	Eurasia
1.8	Pycnonotidae	Red-whiskered Bulbul	*Pycnonotus jocosus*	Avoider	4	32	Frugivore	Shrub	Sedentary	South – South-east Asia
46.4	Columbidae	Rock Dove	*Columba livia*	Exploiter	2b	300	Granivore	Cliff/ledge/building	Sedentary	Eurasia
3.6	Loriidae	Scaly-breasted Lorikeet	*Trichoglossus chlorolepidotus*	Avoider	4	86	Nectarivore	Tree Hollow	Sedentary	Eastern Australia
19.0	Turdidae	Song Thrush	*Turdus philomelos*	Exploiter	2b	83	Ground Carnivore	Shrub	Sedentary	Eurasia
82.1	Columbidae	Spotted Dove	*Streptopelia chinensis*	Exploiter	2b	158	Granivore	Shrub	Sedentary	South Asia
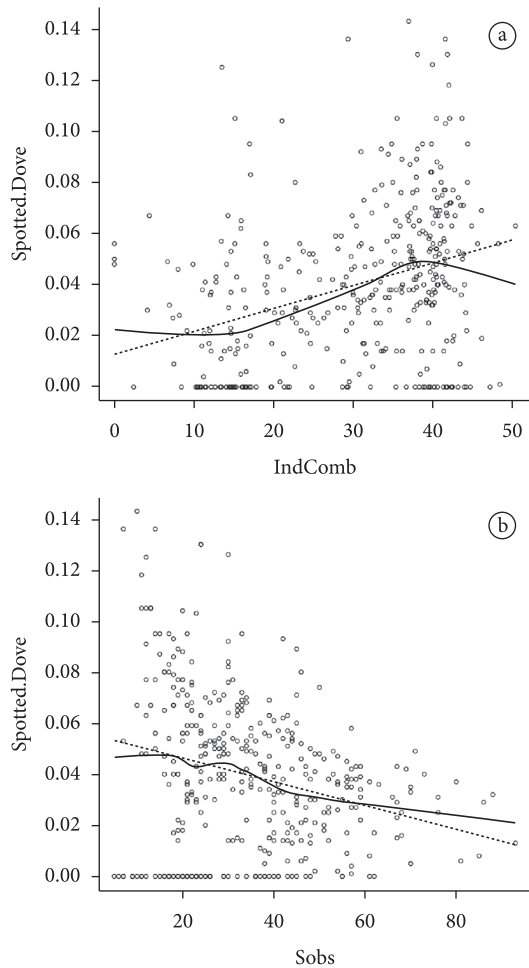
Figure 3. a) Spotted Dove incidence in surveys (y axis) plotted against a measure of urbanization intensity ($Index_{combined}$) (x axis) ($R^2 = 0.117$). Regression line and Lowess curve shown; b) Spotted Dove incidence in surveys (y axis) plotted against species richness of all birds (S_{obs}) (x axis) ($R^2 = 0.153$). Regression line and Lowess curve shown.
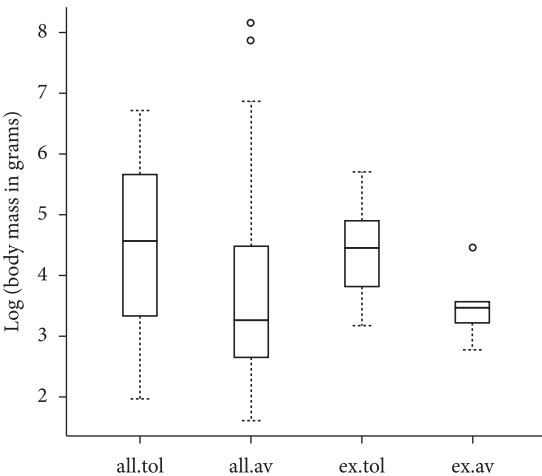
Figure 4. Body mass (g, log transformed) of urban tolerant and urban avoider birds in Melbourne, for all species (all.tol, all.av) and exotic species (ex.tol, ex.av).

the Spotted Dove and Common Blackbird (Conole & Kirkpatrick 2011) (Figures 3, S1) show a terminal decline in incidence, whereas more broadly based urban exploiters such as Common Myna, Common Starling and House Sparrow (Figure S1) show a terminal upward trend. There is not a generic response by exotic birds to urbanization intensity.

In all cases the Jaccard's Index ratio between exotics and natives was greater than one ($JI_{exotic}/JI_{native} > 1$), indicating that across all sites the tendency was for more sharing of exotic than native species, or that some exotics showed a tendency to be evenly distributed throughout the urban area. The hypothesis that environmental and other filters operating on the native avifauna also act on exotic species is compelling, based on these data.

Individual exotic bird species relative abundance shows a clear trend of decline for all species as total bird species richness (S_{obs}) rises (Figure S2). Most decline uniformly across the range of S_{obs}, whilst others (Red-whiskered Bulbul, Scaly-breasted Lorikeet) decline from a mid-point to higher S_{obs}, or are slightly bimodal (Common Blackbird, Common Starling and House Sparrow) (Figure S2). The Spotted Dove (Figure 3), Common Starling and House Sparrow (Figure S2) show a much flatter declining trend than other common exotic species, and this reflects the extent to which these species occur across the urban habitat spectrum, including the propensity to invade areas of higher native vegetation integrity with accompanying higher native bird S_{obs} (L.E. Conole, pers. obs.). These trends are broadly consistent with that observed by Antos *et al.* (2006), that exotic bird species were less abundant in native vegetation remnants than in surrounding suburbs in Melbourne, but not strongly for all species. The hypothesis subset that most exotic species reach their lowest relative abundance in areas of low urban intensity with high diversity of native birds is supported.

Biomass of exotic bird species often significantly exceeds that of native species in intensively urbanized habitats (Blair 2001), and examinations of species richness alone do not address this apparent imbalance. It is generally assumed that this imbalance is an adverse outcome of competition between exotic and native species. However, the conceptual model created from earlier work on these data (Conole & Kirkpatrick 2011) and supported again here, suggests that it may also be possible that species-poor subsets of urban tolerant bird assemblages (including a small number of exotic and native species) prosper at sites that are at the extremes of urban habitat gradients. Such highly urbanised sites are species poor for both native and exotic bird species (Figure 2). Exotic bird dominance may therefore be a marker of particular urban habitat types where overall bird species richness and individual native species abundance is low (Figures 2 and 3).

The data and analyses presented here and by others (Conole & Kirkpatrick 2011; Croci *et al.* 2008; Kark *et al.* 2007) suggest that habitat filtering is occurring to create unique

urban bird assemblages, acting differentially on all species according to their ecological traits, regardless of whether they are exotic or native.

Acknowledgements

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*"... Nothing's measured
by what it needs ..."*

'Already Dead'
Beck Hansen 'Sea Change' (2002)

CHAPTER 5:

DEGREE OF ADAPTIVE RESPONSE IN URBAN TOLERANT BIRDS SHOWS INFLUENCE OF HABITAT-OF-ORIGIN

Chapter 5

Conole, L. E. (2014). Degree of adaptive response in urban tolerant birds shows influence of habitat-of-origin. *PeerJ* 2: e306.

`doi:10.7717/peerj.306`

Supplementary material attached here as Appendix 3.

Also available from: `https://peerj.com/articles/306/#supp-1`

`doi:10.7717/peerj.306/supp-1`

Pre-print

Conole, L. E. (2013). Habitat-of-origin predicts degree of adaptation in urban tolerant birds. *PeerJ PrePrints* 2: e156v3.

`doi:10.7287/peerj.preprints.156v3`

Abstract

Urban exploiters and adapters are often coalesced under a term of convenience as 'urban tolerant'. This useful but simplistic characterisation masks a more nuanced interplay between and within assemblages of birds that are more or less well adapted to a range of urban habitats. I test the hypotheses that objectively-defined urban exploiter and suburban adapter assemblages within the broad urban tolerant grouping in Melbourne vary in their responses within the larger group to predictor variables, and that the most explanatory predictor variables vary between the two assemblages. A paired, partitioned analysis of exploiter and adapter preferences for points along the urban-rural gradient was undertaken to decompose the overall trend into diagnosable parts for each assemblage. In a similar way to that in which time since establishment has been found to be related to high urban densities of some bird species and biogeographic origin predictive of urban adaptation extent, habitat origins of members of bird assemblages influence the degree to which they become urban tolerant. Bird species that objectively classify as urban tolerant will further classify as either exploiters or adapters according to the degree of openness of their habitats-of-origin.

Status

Submitted to the pre-print server *PeerJ PrePrints* on 16 December 2013. After revisions, subsequently submitted to the companion journal *PeerJ* for publication. Accepted by editor for review on 19 December 2013; accepted for publication on 18 February 2014; published online 13 March 2014.

PeerJ provides academics with two Open Access publication venues: *PeerJ* (a peer-reviewed academic journal) and *PeerJ Pre-Prints* (a pre-print server). Both are focused on the Biological and Medical Sciences. *PeerJ* had an Impact Factor of 2.1 in June 2015.

`http://peerj.com/articles/306.pdf`

PeerJ

Degree of adaptive response in urban tolerant birds shows influence of habitat-of-origin

Lawrence E. Conole

School of Geography and Environmental Studies, University of Tasmania, Sandy Bay, Tasmania, Australia

ABSTRACT

Urban exploiters and adapters are often coalesced under a term of convenience as 'urban tolerant'. This useful but simplistic characterisation masks a more nuanced interplay between and within assemblages of birds that are more or less well adapted to a range of urban habitats. I test the hypotheses that objectively-defined urban exploiter and suburban adapter assemblages within the broad urban tolerant grouping in Melbourne vary in their responses within the larger group to predictor variables, and that the most explanatory predictor variables vary between the two assemblages. A paired, partitioned analysis of exploiter and adapter preferences for points along the urban–rural gradient was undertaken to decompose the overall trend into diagnosable parts for each assemblage. In a similar way to that in which time since establishment has been found to be related to high urban densities of some bird species and biogeographic origin predictive of urban adaptation extent, habitat origins of members of bird assemblages influence the degree to which they become urban tolerant. Bird species that objectively classify as urban tolerant will further classify as either exploiters or adapters according to the degree of openness of their habitats-of-origin.

INTRODUCTION

The community of ecologists studying urban bird ecology has to a large extent converged on *Blair*'s (*1996*) typology of 'urban exploiters', 'suburban adapters' and 'urban avoiders', defined by the bird assemblages' biological and behavioural traits (*Chace & Walsh, 2006*; *González-Oreja et al., 2007*; *Kark et al., 2007*; *Croci, Butet & Clergeau, 2008*). Such assemblages as described here are elsewhere sometimes characterised as 'response guilds' (*Leveau, 2013*). Exploiters and adapters are often coalesced under a term of convenience as 'urban tolerant'. Such a useful but simplistic characterisation of the urban tolerant subset may mask a more nuanced interplay between and within groups of birds that are more or less well adapted to a range of urban habitats, ranging from the intensely urbanised 'down town' areas of the inner city, out through a fluctuating gradient of generally decreasing urbanisation intensity through the suburbs to the urban fringe. That there are identifiable

How to cite this article Conole (2014), Degree of adaptive response in urban tolerant birds shows influence of habitat-of-origin. **PeerJ** 2:e306; DOI 10.7717/peerj.306

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'exploiters' and 'adapters' in addition to the 'avoiders' suggests further targeted testing of the urban tolerant grouping may be fruitful in understanding some underlying processes in urban bird ecology.

A humped distribution of bird species richness has been observed in a number of urban studies, with highest values recorded in the intermediate urbanisation intensity range on the rural–urban gradient (*Tratalos et al., 2007*; *Luck & Smallbone, 2010*; *Shanahan et al., 2014*). This pattern has been shown to hold true for all species, but also for urban tolerant species as a subset (*Shanahan et al., 2014*). However, results of earlier data analyses of Melbourne birds suggest that the two assemblages within the urban tolerant group may not show the uniform response to urbanisation as has been shown for other cities (*Conole, 2011*; *Conole & Kirkpatrick, 2011*).

Gradient analysis (*Ruszczyk et al., 1987*) has been broadly applied in urban ecological studies over the past two decades (*McDonnell & Hahs, 2008*), and much longer in ecology more generally (*Whittaker, 1967*). It is intuitively compatible with a landscape ecology perspective (*Snep, Timmermans & Kwak, 2009*), and despite criticisms of the limitations of gradient analysis as an approach for studying urban ecology (*Catterall, 2009*; *Ramalho & Hobbs, 2012a*), the potential remains for this approach to be the 'scaffolding' upon which deeper investigations are built (*McDonnell, Hahs & Pickett, 2012*; *Ramalho & Hobbs, 2012b*). In taking the assemblages identified through gradient analysis (*Conole & Kirkpatrick, 2011*) as the basis for the present study, I acknowledge the reality that the urban–rural gradient is not simplistically linear (*Ramalho & Hobbs, 2012a*) or neatly concentric around the 'down town' centre (*Catterall, 2009*). The reality of non-concentricity does not limit the usefulness of gradient analysis in understanding complexity and nuance in urban bird ecology. While acknowledging the utility of the urban exploiter/adapter typology, I seek in this paper to deconstruct the concept of 'urban tolerance' for birds, and test the hypothesis which contends that 'urban tolerance' is not monolithic, but multifaceted.

The urban tolerance status of birds included in many published studies has been applied *a priori*, based on work of others in geographically related systems (such as *Kark et al., 2007*), or compiled from secondary or tertiary descriptive sources (such as *Bonier, Martin & Wingfield, 2007*, but see *González-Oreja et al., 2007*). It is also the case that many urban bird studies are largely descriptive or narrowly site-specific (*Marzluff, Bowman & Donnelly, 2001*; *McDonnell & Hahs, 2013*), lacking either a theoretical underpinning or focus (*Scheiner, 2013*), and there have been calls to formulate research questions designed to develop a greater mechanistic understanding of the underlying ecological processes operating in urban landscapes (*Shochat et al., 2006*; *McDonnell & Hahs, 2013*), and move towards generalisable concepts (*Mac Nally, 2000*).

Part of the process of moving towards generalisable concepts in urban bird ecology involves gaining a better understanding of the extent to which the degree of adaptation to urban environments progresses from intolerance to the high level of adaptation that characterises exploiters. How similar are the responses of the adapters and exploiters to different aspects of the urban–rural gradient?

The data in this paper are focused on two assemblages characterised by the author as urban exploiters and suburban adapters from Melbourne, Australia (Fig. S1) (*Conole & Kirkpatrick, 2011*). The present study departs from the approach taken in many others of similar kind in that urban bird assemblages that form the basis of the work were objectively classified at the landscape scale from direct data analyses (*Conole & Kirkpatrick, 2011*) rather than indirect inference or *a priori* assignment. I attempt a paired, partitioned analysis of exploiter and adapter preferences for points along the urban–rural gradient to decompose the overall trend into diagnosable parts for each assemblage, in a way not previously seen in the literature.

I test the hypotheses that the distinct urban exploiter and suburban adapter assemblages within the broad urban tolerant grouping in Melbourne vary in their responses to predictor variables. I also test the hypothesis that habitat-of-origin has predictive utility in determining which urban tolerant birds become exploiters or adapters.

MATERIALS & METHODS

Detailed descriptions of the study area and methodology used to derive the urban bird assemblages can be found in *Conole & Kirkpatrick (2011)*, and are summarised in the Supplemental Text.

Study area and data handling

The study area is metropolitan Melbourne; capital city of the State of Victoria in coastal southeastern Australia, within a 50 km radius of its Central Business District (Fig. S1) (37°49′S and 144°58′E).

Approximately 220,000 records of birds were extracted from the Birds Australia 'New Atlas of Australian Birds' database (*Barrett et al., 2003*), and intersected with a 1×1 km grid (*Hahs & McDonnell, 2006*) to produce a matrix of grid cells by species presence/absence. Species and sites were filtered out according to criteria for representativeness (see Supplemental Text) to arrive at a final list of 141 species and 390 cells (*Conole & Kirkpatrick, 2011*).

Environmental and demographic indices

Spatial data on the degree of urbanisation of the study area employed in this study were developed at ARCUE and are discussed in detail by *Hahs & McDonnell (2006)*; a brief summary of the two selected factors follows.

Frequency Greenspace (hereafter greenspace) is the reciprocal of the average amount of impervious surface calculated at the sub-pixel level from the impervious surface fraction image created during the spectral mixture analysis of the 2000 Landsat ETM + image (*Hahs & McDonnell, 2006*).

Combined index ($Index_{Combined}$) is the average value of $Index_{Image}$ and $Index_{Census}$; where $Index_{Image}$ is calculated from fraction images produced by the spectral mixture analysis of the 2000 Landsat ETM + image, and $Index_{Census}$ = the total number of people multiplied by the proportion of males employed in non-agricultural work, as enumerated in the 2001 Australian census (*Hahs & McDonnell, 2006*).

Other environmental factors considered in analyses included PC_URB (percent cover of urban landform), People per square kilometre (People/km^2—the total number of people in census collection districts) and Dwellings per square kilometre (Dwellings/km^2—the total number of houses in census collection districts) (*Hahs & McDonnell, 2006*; *Conole & Kirkpatrick, 2011*).

Data analysis

Statistical analyses were performed in R (*R Core Team, 2013*) using base R functions and procedures from the R-packages 'vegan' (*Oksanen et al., 2013*) and 'bayespref' (*Fordyce et al., 2011*). Figures were drawn using R base graphics, R-packages 'vegan' and 'ggplot2' (*Wickham, 2009*; *Oksanen et al., 2013*), and QGIS (*QGIS Development Team, 2013*).

An earlier assemblage analysis (*Conole & Kirkpatrick, 2011*) was the basis for partitioning the total bird datasets for this study; detailed methodology is described therein. Adapter and exploiter species were further partitioned into two new matrices for this study, and separate non-metric multidimensional scaling (NMDS) ordinations performed for each (see Supplemental R Script #1). Only factors for which $p \leq 0.01$ were considered further in analyses, and where a choice between the overlapping PC_URB and Index$_{Combined}$ factors was required, the recommendation of *Hahs & McDonnell (2006)* for Index$_{Combined}$ was adopted.

Boxplots of species richness of the two urban tolerant assemblages were made, binned by an index of urbanisation intensity (Index$_{Combined}$—hereafter urbanisation index) and cover of vegetation (greenspace) (see Supplemental R Script #2).

Species richness of exploiter and adapter species was enumerated for each of 390 grid cells (*Conole & Kirkpatrick, 2011*), along with the index of urbanisation intensity and cover of vegetation. Data were then modelled as hierarchical Bayesian models using R-package 'bayespref' (*Fordyce et al., 2011*) to test the preferences of exploiters and adapters for partitioned urban habitats. Model parameters were estimated using a Markov Chain Monte Carlo (MCMC) approach, with 10,000 MCMC steps following a burn-in of 1,000 generations. The parameters estimated in this way are intended to directly address the hypothesis (*Fordyce et al., 2011*), namely that adapter and exploiter bird assemblages show preferences for urban habitat characterised by differing levels of urbanisation intensity or vegetation cover. The hierarchical Bayesian approach has the advantage of directly estimating the parameter of interest (in this case preference for levels of urbanisation or green space by urban tolerant bird assemblages), and models the uncertainty around those parameters as well as allowing comparisons between *a priori* identified groups, in contrast to methods such as ANOVA or *t*-tests, which assess whether the mean difference is different from zero (*Fordyce et al., 2011*). The estimates are population-level preferences (*Fordyce et al., 2011*).

Within 'bayespref' a facility for assessing model convergence (indicated by MCMChain mixing) by plotting MCMC steps against population level preferences is available (*Fordyce et al., 2011*). A well-mixed chain is one characterised by a broad scatter of data points in the scatterplot without obvious clumping (Figure SR4 in Supplemental R Script #3), whereas clumping of data points indicates poorly-mixed chains. Although a subjective

visual measure, it is sufficient to identify satisfactory MCMChain mixing, and this method was used here to determine when satisfactory model convergence had been achieved.

Proposal distance in the MCMC is set by the 'bayespref' switch 'dirvar'; usually at the default setting of 2. Runs of 'bayespref' with a 'dirvar' value of 2, 5, 10 and 20 were executed, to determine whether optimal mixing of the MCMChains influenced the overall trends in habitat preference (see Supplemental R Script #3), but the gross trends were unchanged. Nonetheless, results cited in this paper use the highest tested proposal distance ('dirvar' = 20) to ensure thoroughly mixed MCMC chains.

Outputs from the 'bayespref' analysis were plotted, with base R functions, as binned median preference with 95% confidence intervals (see Supplemental R Script #4).

Adapter and exploiter species' habitats-of-origin were determined by reference to the literature (*Marchant & Higgins, 1993*; *Higgins & Davies, 1996*; *Higgins, 1999*; *Schodde & Mason, 1999*; *Higgins, Peter & Steele, 2001*; *Higgins & Peter, 2002*; *Higgins, Peter & Cowling, 2006*), and shown in Table 1. Habitat-of-origin is used here to mean the primary natural (pre-urbanisation) habitats that species are known to have occupied. The data for cluster analysis consisted of a standard array, with species as rows and habitat-of-origin as columns (forest, woodland, heath, scrub, urban, farm, air). A Bray-Curtis distance matrix was prepared, and groups of species were formed by hierarchical agglomerative clustering using Ward's algorithm performed on the distance matrix, using core R-function 'hclust' (*R Core Team, 2013*) (see Supplemental R Script #5).

RESULTS AND DISCUSSION

Results

In an earlier ordination of all bird species from the Melbourne study, urban exploiters and adapters are shown as overlapping but distinct clusters in ordination space (Fig. S2) (*Conole & Kirkpatrick, 2011*). When the exploiters and adapters were partitioned from the avoiders and run as separate ordinations, different pictures of response to urban environmental factors became apparent (Figs. 1 and 2).

For exploiters the observed species richness vector (S_{obs}) was orthogonal with both greenspace and the urbanisation index (Fig. 2). The equivalent vector for adapters (Fig. 1) was orthogonal with the urbanisation index, but almost aligned with that for greenspace (Fig. 2). Greenspace and the urbanisation index were chosen as representative of structural and demographic aspects of urbanisation intensity even though other parameters were included in the initial analyses, and further analyses were limited to these two factors.

The same data plotted as binned boxplots showed that adapter species richness was positively associated with increasing greenspace, but exploiter species richness was flat across the range (Fig. 3). Whilst broadly similar trends were evident for both groups as binned boxplots plotted against the urbanisation index (Fig. 4), adapters trended to zero species richness at the highest levels, whilst 10–15 species of exploiters persisted at the same level. Peak species diversity of urban adapter birds occurred in the middle of the range of urbanisation intensity (Fig. 4). Adapter richness peaked at approximately 0.8 frequency green-space; exploiters at around 0.55 (Fig. 3).

Table 1 List of bird species analysed in this study.

Common name	Scientific name	Family	Urban adapter	Urban exploiter	Habitat-of-origin
White-browed Scrubwren	*Sericornis frontalis*	Acanthizidae	Y		Forest, woodland, heath, scrub
Brown Thornbill	*Acanthiza pusilla*	Acanthizidae	Y		Forest, woodland, heath, scrub
Yellow-tailed Black-Cockatoo	*Calyptorhynchus funereus*	Cacatuidae	Y		Forest, woodland, heath
Gang-gang Cockatoo	*Callocephalon fimbriatum*	Cacatuidae	Y		Forest, woodland
Sulphur-crested Cockatoo	*Cacatua galerita*	Cacatuidae	Y		Forest, woodland
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	Campephagidae	Y		Forest, woodland
Common Bronzewing	*Phaps chalcoptera*	Columbidae	Y		Forest, woodland, scrub
Australian Raven	*Corvus coronoides*	Corvidae	Y		Forest, woodland
Grey Butcherbird	*Cracticus torquatus*	Artamidae	Y		Forest, woodland
Pied Currawong	*Strepera graculina*	Artamidae	Y		Forest, woodland
Grey Currawong	*Strepera versicolor*	Artamidae	Y		Forest, woodland, heath
Laughing Kookaburra	*Dacelo novaeguineae*	Halcyonidae	Y		Forest, woodland
Rainbow Lorikeet	*Trichoglossus haematodus*	Loriidae	Y		Forest, woodland, heath
Superb Fairy-wren	*Malurus cyaneus*	Maluridae	Y		Forest, woodland, heath, scrub
Eastern Spinebill	*Acanthorhynchus tenuirostris*	Meliphagidae	Y		Forest, woodland, heath, scrub
Bell Miner	*Manorina melanophrys*	Meliphagidae	Y		Forest, woodland, scrub
Noisy Miner	*Manorina melanocephala*	Meliphagidae	Y		Forest, woodland
Spotted Pardalote	*Pardalotus punctatus*	Pardalotidae	Y		Forest, woodland
Tawny Frogmouth	*Podargus strigoides*	Podargidae	Y		Forest, woodland
Crimson Rosella	*Platycercus elegans*	Psittacidae	Y		Forest, woodland
Eastern Rosella	*Platycercus eximius*	Psittacidae	Y		Forest, woodland
Grey Fantail	*Rhipidura albiscapa*	Rhipiduridae	Y		Forest, woodland
Silvereye	*Zosterops lateralis*	Timaliidae	Y		Forest, woodland, heath, scrub
Brown Goshawk	*Accipiter fasciatus*	Accipitridae		Y	Forest, woodland
Galah	*Eolophus roseicapillus*	Cacatuidae		Y	Woodland, grassland
*Rock Dove	*Columba livia*	Columbidae		Y	Grassland
*Spotted Dove	*Streptopelia chinensis*	Columbidae		Y	Forest, woodland
Crested Pigeon	*Ocyphaps lophotes*	Columbidae		Y	Woodland, grassland
Little Raven	*Corvus mellori*	Corvidae		Y	Woodland, grassland
Australian Magpie	*Cracticus tibicen*	Artamidae		Y	Woodland, grassland
Australian Hobby	*Falco longipennis*	Falconidae		Y	Forest, woodland, heath, scrub
Welcome Swallow	*Hirundo neoxena*	Hirundinidae		Y	Aerial
Musk Lorikeet	*Glossopsitta concinna*	Loriidae		Y	Forest, woodland
Little Lorikeet	*Glossopsitta pusilla*	Loriidae		Y	Forest, woodland
White-plumed Honeyeater	*Lichenostomus penicillatus*	Meliphagidae		Y	Forest, woodland
Little Wattlebird	*Anthochaera chrysoptera*	Meliphagidae		Y	Forest, woodland, heath, scrub
Red Wattlebird	*Anthochaera carunculata*	Meliphagidae		Y	Forest, woodland, heath, scrub
Magpie-lark	*Grallina cyanoleuca*	Monarchidae		Y	Woodland, grassland
*House Sparrow	*Passer domesticus*	Passeridae		Y	Urban, farm
*Eurasian Tree Sparrow	*Passer montanus*	Passeridae		Y	Urban
Red-rumped Parrot	*Psephotus haematonotus*	Psittacidae		Y	Woodland, grassland
Willie Wagtail	*Rhipidura leucophrys*	Rhipiduridae		Y	Woodland, grassland

(continued on next page)

Table 1 (*continued*)

Common name	Scientific name	Family	Urban adapter	Urban exploiter	Habitat-of-origin
[*]Common Starling	*Sturnus vulgaris*	Sturnidae		Y	Urban, farm, woodland, heath, scrub
[*]Common Myna	*Sturnus tristis*	Sturnidae		Y	Urban, farm, woodland
[*]Common Blackbird	*Turdus merula*	Turdidae		Y	Forest, woodland, heath, scrub, urban
[*]Song Thrush	*Turdus philomelos*	Turdidae		Y	Urban

Notes.

Habitat data from *Marchant & Higgins (1993)*, *Higgins & Davies (1996)*, *Higgins (1999)*, *Schodde & Mason (1999)*, *Higgins, Peter & Steele (2001)*, *Higgins & Peter (2002)* and *Higgins, Peter & Cowling (2006)*.

[*] Feral species are denoted with an asterisk.
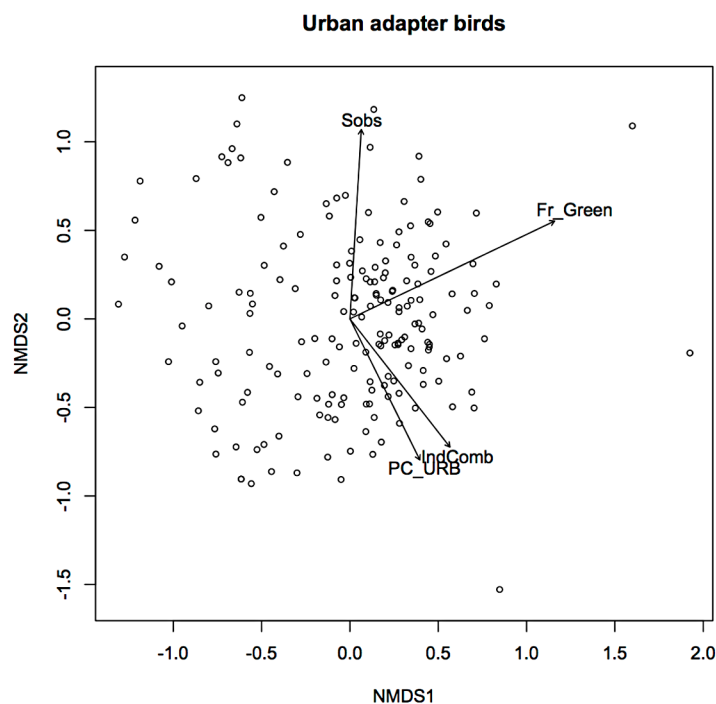
Figure 1 **Non-metric multidimensional scaling (NMDS) ordination; urban adapters—fitted vectors for which $p \leq 0.01$.**

The hierarchical Bayesian models for greenspace showed a relatively flat preference by urban exploiters across the range; though increasing preference by urban adapters for higher levels of greenspace (median = 0.46; credible intervals 0.424–0.494) almost match exploiter preference (0.54; 0.506–0.576) in the highest bin (Fig. 5; Table S1). Even allowing for high levels of variance in the lower bins where data points were more scarce, the preferences of urban exploiters and adapters did not overlap in any of the greenspace bins.

Hierarchical Bayesian models for the combined index showed a joint preference by urban adapters and exploiters in the middle of the range of the urbanisation index (20.0–29.9). Areas of low (0–19.9) and high (30.0–50.0) urbanisation index were strongly preferred by urban exploiters but not adapters (Fig. 6; Table S2).

Urban exploiter birds
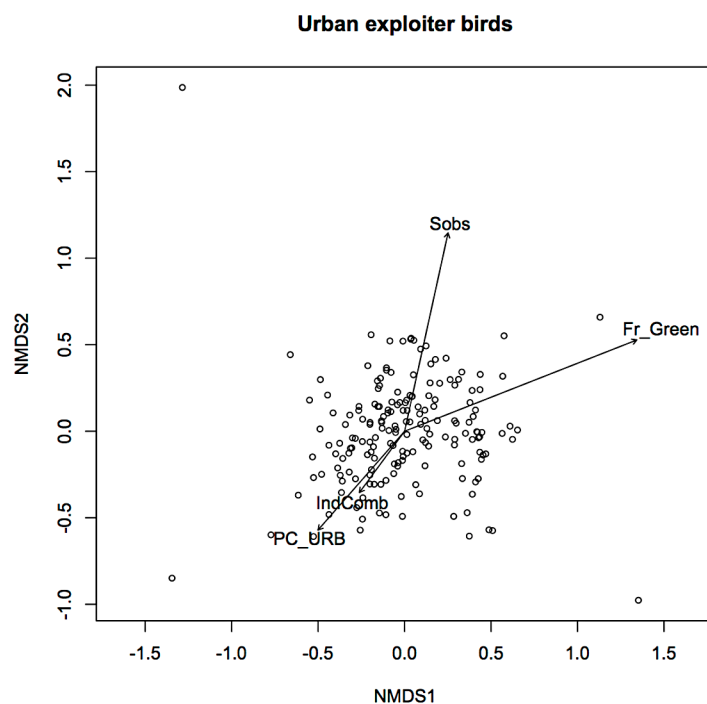
Figure 2 Non-metric multidimensional scaling (NMDS) ordination; urban exploiters—fitted vectors for which $p \leq 0.01$.
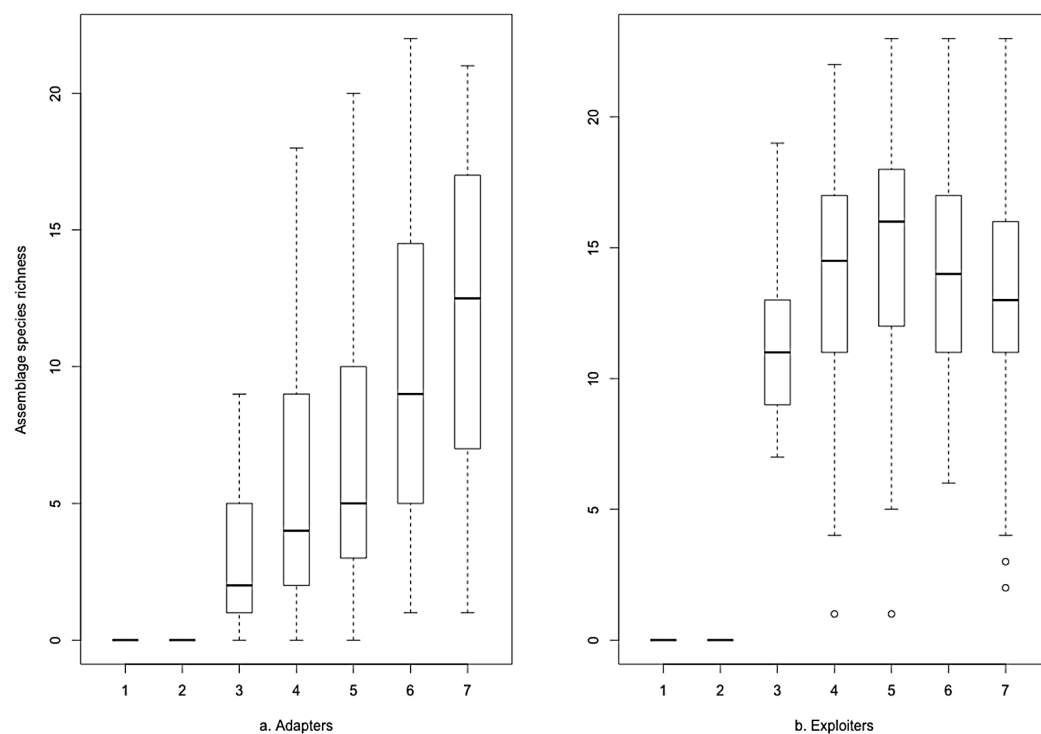
Figure 3 Species richness of (A) urban adapter and (B) urban exploiter bird species binned by the proportion of Frequency Greenspace at urbanised sites.
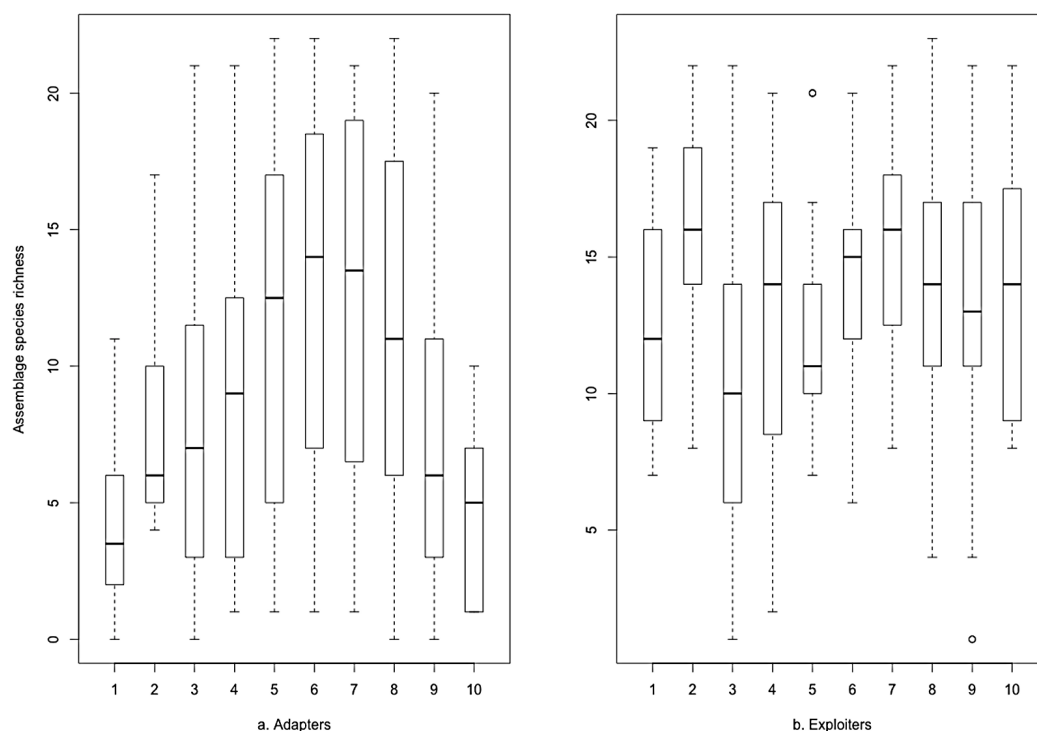
Figure 4 Species richness of (A) urban adapter and (B) urban exploiter bird species binned by urbanisation intensity (Index_Combined) at urbanised sites.

The cluster analysis of adapters and exploiters by habitat of origin returned a dendrogram showing two clear major clusters. All of the adapters clustered together in a woody vegetation habitat group, along with a group of exploiters; five indigenous nectarivores (Red Wattlebird *Anthochaera carunculata* (Shaw, 1790), Little Wattlebird *A. chrysoptera* (Latham, 1802), White-plumed Honeyeater *Lichenostomus penicillatus* (Gould, 1837), Musk Lorikeet *Glossopsitta concinna* (Shaw, 1791), Little Lorikeet *G. pusilla* (Shaw, 1970)), two indigenous avivorous raptors (Australian Hobby *Falco longipennis* Swainson, 1837, Brown Goshawk *Accipiter fasciatus* (Vigors and Horsfield, 1827)) and two exotic species which are not exclusively synanthropic (Common Blackbird *Turdus merula*, Linnaeus, 1758, Common Starling *Sturnus vulgaris* Linnaeus, 1758) (*Conole, 2011*). The cluster of exclusively exploiter species were characterised by those originating from open grassy or urban habitats.

The boxplots (Figs. 3 and 4) and the hierarchical Bayesian models (Figs. 5 and 6) showed clear but distinct trends of urban habitat preference by urban exploiter and adapter bird assemblages against these two representative urban habitat measures. The landscape scale preferences of urban adapters and urban exploiters for levels of greenspace never overlap, though they come close to each other at the highest values as exploiter preference declines and adapter preference increases. In contrast, landscape preferences for urbanisation intensity measured by the urbanisation index overlap strongly in the middle of the range but are strongly divergent at the lowest and highest values.
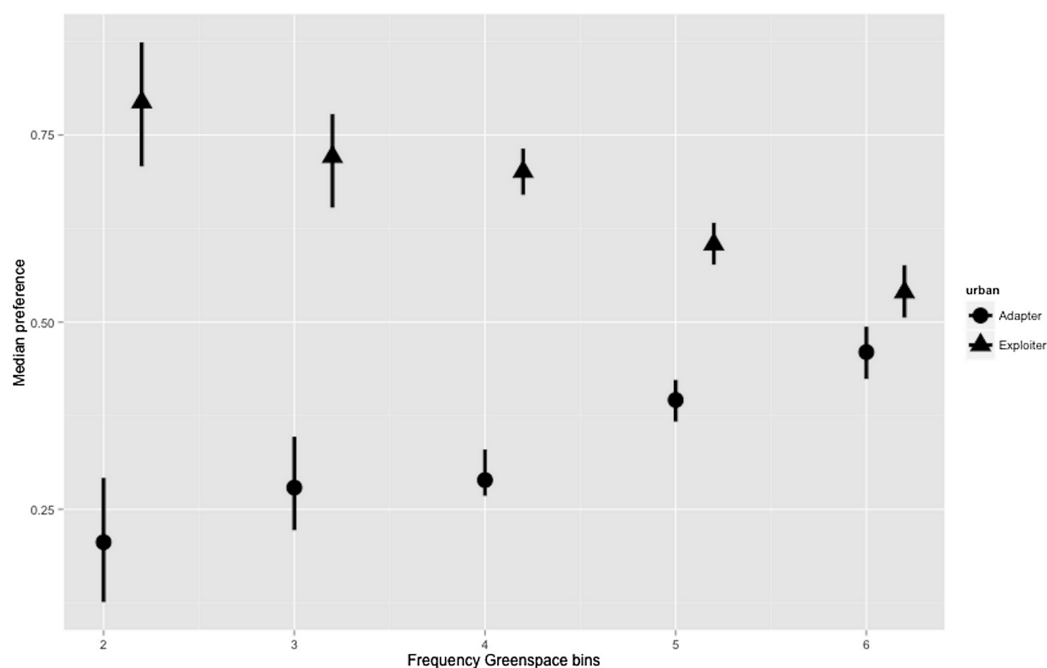
Figure 5 Posterior density for landscape-scale preferences of urban adapter and exploiter bird assemblages (median preference and 95% credible intervals) binned by Frequency Greenspace at urbanised sites.
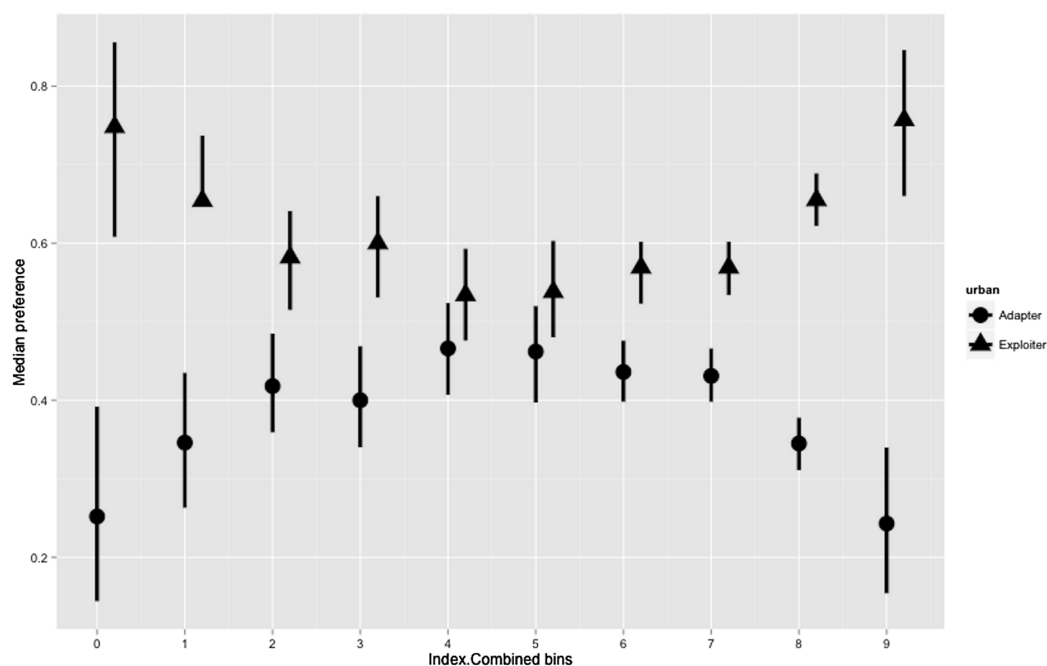
Figure 6 Posterior density for landscape-scale preferences of urban adapter and exploiter bird assemblages (median preference and 95% credible intervals) binned by urbanisation intensity at urbanised sites.

Discussion

The diversity of urban adapters on the gradient of urban intensity follows a humped distribution (Fig. 4); the trend even more strongly humped when viewed as landscape scale preference (Fig. 6). This is consistent with the trend seen for urban tolerant birds in other studies (*Marzluff & Rodewald, 2008*; *Tratalos et al., 2007*), and for bird species richness in response to several environmental factors at a landscape scale (*Bar-Massada et al., 2012*). The inverted, humped curve for exploiters is not consistent with the trends for urban tolerant bird species richness seen in other studies (*Tratalos et al., 2007*; *Luck & Smallbone, 2010*; *Shanahan et al., 2014*), and this marks a strong divergence in response by exploiters and adapters to urbanisation intensity.

This quadratic trend in diversity also resembles that described by the Intermediate Disturbance Hypothesis (IDH), where diversity peaks at a midpoint along a gradient of disturbance (*Catford et al., 2012*; *Fox, 2013*). The urban–rural gradient is, however, not a true analogue of a disturbance gradient. Suburban areas are more stable habitats than either the developing fringe or the intensely re-shaped core of the city, and so disturbance itself shows a quadratic distribution along the urban–rural gradient. Also implicit within IDH is a notion of competition/colonisation trade-off amongst species more or less adapted to disturbed environments, and at least for urban adapted birds it has been suggested that competition is not important (*Mikami & Nagata, 2013*) except for specific cases such as the 'despotic' Noisy Miner (*Manorina melanocephala*) (*Kath, Maron & Dunn, 2009*; *Maron et al., 2013*; *Robertson et al., 2013*).

The zone of overlap in habitat preference along the human demographic gradient accords broadly with the inner ring of suburbs in Melbourne; long established and heavily vegetated (*Hahs & McDonnell, 2006*). At the extremes of this gradient lie the new suburbs/exurbia at the fringe, and the central business districts ('down town') at various central locations—either lightly vegetated or with largely treeless vegetation (lawns and pasture) (*Hahs & McDonnell, 2006*). The overlap represents depressed preference by exploiters coincident with greatest preference shown by adapters.

The response of urban tolerant birds to increasing Frequency Greenspace is consistent with wider trends in other cities (*Chace & Walsh, 2006*), and closely mirrors the relationship observed between bird species richness and foliage height diversity observed in a non-urban landscape (*Bar-Massada & Wood, 2014*). Increasing foliage height diversity is a marker of established suburbs versus the developing fringe in Melbourne (*Hahs & McDonnell, 2006*). The distinct responses between adapters and exploiters is also less marked with respect to greenspace than urbanisation intensity.

The responses of the two assemblages to two simple measures of urban habitat character were divergent, consistent with the study's main hypothesis. Though the larger group of urban tolerant bird species may occasionally be treated as one entity, it is clear from this study and others (*Croci, Butet & Clergeau, 2008*; *Catterall, 2009*; *Conole, 2011*; *Conole & Kirkpatrick, 2011*) that the two groups within it are sufficiently distinct in their responses to urbanisation to caution against using pooled data for urban tolerant species in future studies.

The response of urban adapter species to the urbanisation index is consistent with what we broadly understand them to be; adapted to suburbanisation (*Blair & Johnson, 2008*). Greenspace typically increases in old suburbs versus the exurban fringe or downtown areas (*Hahs & McDonnell, 2006*). The strong depression in exploiter preference for mid-range urbanisation intensity (versus the extremes) is less expected. At least with the Melbourne data, there is not a single generalised urban tolerant group of birds. The adapters and exploiters share ecological traits with each other but also with avoiders (*Conole & Kirkpatrick, 2011*).

In part the contemporary avifauna of an urbanised area is a legacy of the species present in the former landscape, rather than solely being the product of invasion or colonisation (*sensu Møller et al., 2012*). As urban areas progressively come to resemble woodland, structurally if not floristically (*Kirkpatrick, Daniels & Zagorski, 2007*), it makes sense that the urban tolerant bird species are likely to include legacy woodland-adapted species. Despite the findings of *Blair & Johnson (2008)* in North American urban areas, it does not appear that suburban areas within a previously forested landscape in Melbourne are loci for indigenous woodland bird extirpation or exotic bird invasion (*Conole & Kirkpatrick, 2011*). Instead the reverse seems to be true. They are sites for colonisation and expansion of some indigenous woodland birds (adapters) and places where exotic exploiters are less abundant.

Exploiters are mostly indigenous species derived from open environments such as grassland and grassy open-woodland (*Møller et al., 2012*), with a small cohort of synanthropic exotic species and indigenous dietary specialists (avivorous raptors, nectarivores) more typical of forest/woodland habitats (Table 1; Fig. 7) (*Conole & Kirkpatrick, 2011*). Adapters as a group are all indigenous species of forest, woodland and riparian scrub origins (Table 1; Fig. 7), and they have closer affinities with the riparian and bush remnant urban avoiders than the exploiters (*Conole & Kirkpatrick, 2011*). It is therefore remnants of the former indigenous avifauna of wooded parts of Melbourne that are the source of the emerging group of urban adapted species, though none are yet as successful as the aptly named urban exploiters. The adapters are essentially the vanguard of a group of semi-specialised bird species that utilise particular niches of greater foliage height diversity within urban matrix habitats, but are not yet ubiquitous across the matrix in the way of exploiters.

The responses observed here of each group to both degree of urbanisation and greenspace are largely explained by their ecological histories. The exploiters are able to use disturbed habitats across the matrix analogous to their original habitats, and many of them were established in Melbourne during the early stages of urban expansion and consolidation of the city. As suburban parts of the city became more heavily vegetated and less open, a group of species from analogous riparian/forest habitats became increasingly well established in parts of the city proximate to their source natural habitats. Many parts of the urban matrix are now at or close to the point of saturation with members of the exploiter assemblage due to their ubiquity, but the number of adapter species contributing to bird species richness at points across the matrix is likely to increase on a site by site basis as the process of afforestation of the older suburbs continues. It follows then that the
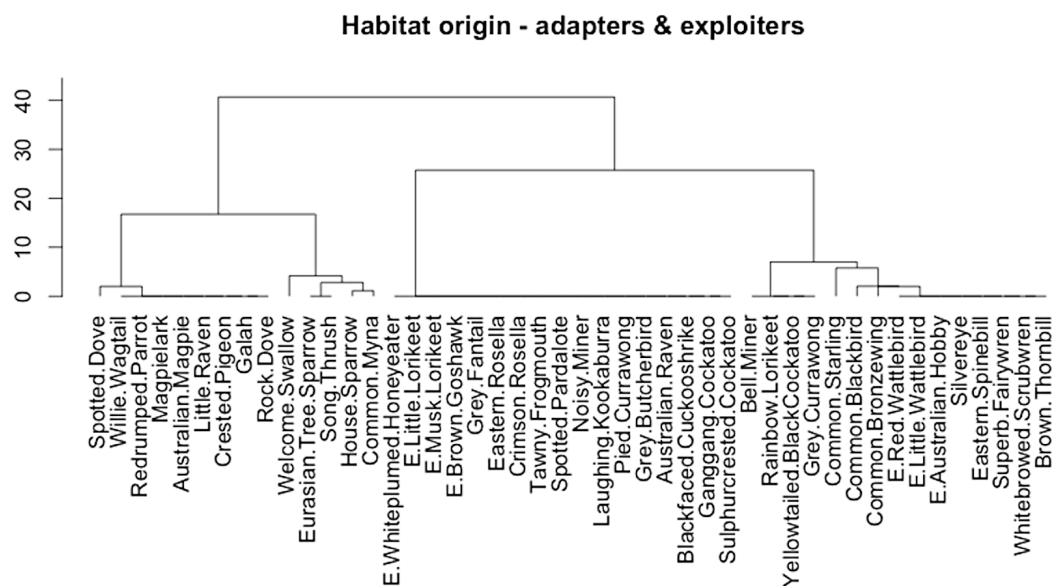
Figure 7 Cluster dendrogram (Ward method) of adapters and exploiters by habitat-of-origin. Exploiters that cluster within the adapters are prefixed with the letter "E".

distribution of exploiter species may decline in more established suburban parts of the city over time, though expanding in range and continuing to dominate in developing areas of the city at or near the fringe. Clues to this trend can be found in studies that model the trajectory of abundance for open habitat, ground feeding specialists (such as the Crested Pigeon *Ocyphaps lophotes* GR Gray, 1842) declining as those habitats become denser with woody vegetation (*Kutt & Martin, 2010*).

CONCLUSION

The partitioning of adapters and exploiters within the urban tolerant grouping in this study reveals the possible pitfall in assuming uniformity of response of all 'urban tolerant' species, that otherwise might result in the overlooking of a key to understanding how habitat origins may be important for understanding bird species' adaptation to urban environments. Other workers have examined the importance of a variable suite of physiological and behavioural traits that may predispose birds to urban adaptability (e.g., *Kark et al., 2007*; *Møller, 2009*; *Evans et al., 2010*). This study has examined the higher order habitat filtering mechanism that may be influential in this regard, and more broadly generalisable as a conceptual model at the scale of the landscape and the assemblage.

In a similar way to that in which time since establishment has been found to be related to high urban densities of some bird species (*Møller et al., 2012*), or biogeographic origin predictive of urban adaptation extent (*González-Oreja, 2011*), spatial and habitat origins of members of bird assemblages influence the degree to which they become urban tolerant; ranging from not at all through to ubiquitous. Bird species that classify as urban tolerant will further classify as either exploiters or adapters according to the degree of openness of their habitats-of-origin.

ACKNOWLEDGEMENTS

ADDITIONAL INFORMATION AND DECLARATIONS

Author Contributions

- Lawrence E. Conole conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.306.

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"... The story isn't true of how he came to fall down
The sun was never that hot
He was shot from the ground ..."

'Icarus Missed'
The Verlaines 'Bird Dog' (1987)

CHAPTER 6:

ON FEARFULNESS AND PATTERNS OF BIRD URBANISATION IN AN AUSTRALIAN METROPOLIS

Chapter 6

Conole, L. E. (2015). On fearfulness and patterns of bird urbanisation in an Australian metropolis. Submitted to *Behavioral Ecology*.

Abstract

I have utilised an assemblage of 91 bird species, their urban tolerance status objectively classified, with data on bird flight initiation distance (FID), to test questions of the importance of birds' fearfulness of humans in determining urban tolerance or intolerance in the metropolis of Melbourne, Australia. While several studies have shown that mean FID for bird species (m_{FID}) differs between rural and urban populations of bird species, stronger predictive ability is shown by variability in FID (cv_{FID}) in modelling urban invasiveness. I test two hypotheses. Firstly, that m_{FID} will be shorter in urban exploiter bird species than urban adapters and avoiders. Secondly that cv_{FID} is positively correlated with bird incidence at the landscape scale in Melbourne. Relatively weak explanatory power of cv_{FID} found in this study suggest that environmental and behavioural factors acting in concert better explain the urban tolerance of bird species and assemblages, rather than fearfulness alone.

Status

On fearfulness and patterns of bird urbanisation in an Australian metropolis

Lawrence E. Conole

School of Land and Food, University of Tasmania, Private Bag 78, Hobart 7001, Tasmania, Australia. `lconole@utas.edu.au`

ABSTRACT

I have utilised an assemblage of 91 bird species, their urban tolerance status objectively classified, with data on bird flight initiation distance (FID), to test questions of the importance of birds' fearfulness of humans in determining urban tolerance or intolerance in the metropolis of Melbourne, Australia. While several studies have shown that mean FID for bird species (m_{FID}) differs between rural and urban populations of bird species, stronger predictive ability is shown by variability in FID (cv_{FID}) in modelling urban invasiveness. I test two hypotheses. Firstly, that m_{FID} will be shorter in urban exploiter bird species than urban adapters and avoiders. Secondly that cv_{FID} is positively correlated with bird incidence at the landscape scale in Melbourne. Relatively weak explanatory power of cv_{FID} found in this study suggest that environmental and behavioural factors acting in concert better explain the urban tolerance of bird species and assemblages, rather than fearfulness alone. *Key words:* Fearfulness, flight initiation distance, urbanisation, birds.

INTRODUCTION

Uʀʙanisation has been widely written about as one of the most pervasive and important modern forms of land-use modification. By 2014, 54% of the world's human population lived in urban areas, with the expectation that this proportion will continue to grow (United Nations 2014). Thus, impacts on biodiversity from urban expansion may also be expected to continue growing rapidly (Grimm et al. 2008; Seto et al. 2012).

Studies of urban biodiversity seek to understand the underlying mechanisms by which species either succeed or fail in adapting to urban environments, whilst attempting to predict and provide insights for mitigating or managing deleterious impacts (Grimm et al. 2008). Biotic urbanisation is most commonly perceived as the process associated with invasion of urban areas by organisms, but it also the case that some biotic urbanisation is the consequence of adaptation by organisms which persist in the landscape as it is urbanised (Conole and

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28 Kirkpatrick 2011). As biodiversity loss in urban ecosystems is not random (Sol et al. 2015), it is therefore important to understand the variation in adaptations shown by species such as birds
30 if degrading processes are to be managed or mitigated.

Much urban ecology has been correlative, identifying relationships between observed
32 patterns of urban biodiversity in compositional, temporal and spatial contexts, in relation to a range of environmental factors associated with differing levels of urbanisation intensity
34 (McDonnell and Hahs 2013). Fewer studies have been directed at attempting to observe and understand behavioural responses of animal species to urbanisation, its novel habitats and
36 close proximity to large concentrations of humans (Weston et al. 2012).

The 'ecology of fearfulness' characterises disturbance responses to humans as a behavioural
38 syndrome. Birds are frequently used as model organisms (e.g. Blumstein 2006). The relevance of the concept in predicting urban fauna has been broadly investigated in Northern
40 Hemisphere Old World cities (Díaz et al. 2013; Møller 2008, 2009, 2010), and at least once in a Southern Hemisphere New World city (Carrete and Tella 2011). Fearfulness of humans as
42 potential predators of birds — more specifically variation in fearfulness — may filter the bird species in urban environments.

44 The term 'Flight Initiation Distance' (FID) — the distance at which birds flee from approaching humans — was conceived as a measurable indicator of fearfulness, and is
46 generally presented as species' mean FID (m_{FID}). Recent research has pointed to the stronger predictive ability of variation in m_{FID} in modelling urban invasiveness of bird species (Møller
48 2010), along with relative brain size (Carrete and Teller 2011). Variability in m_{FID} is shown generally as cv_{FID} — the Coefficient of Variation in m_{FID}.

50 Several authors have shown that m_{FID} was consistently lower in urban species cohorts than in their rural conspecifics, but that the m_{FID} of urban individuals was generally within the
52 lower-range distribution of their rural conspecifics (Carrete and Tella 2011; Møller 2008, 2010).

Although body size explained significant variation in birds' FID, and diet and sociality were
54 also important, many other potential correlates of FID remain to be investigated thoroughly (Blumstein 2006; Carrete and Tella 2011). Candidates include age, sex, morphology, study site
56 features such as distance from cover and the physical barriers such as fences, weather, and clothing colour (see Fernández-Juricic et al. 2006).

58 Environmental and behavioural factors acting in concert explain the urban tolerance of bird species and assemblages. In the present study I have utilised an assemblage of 91 bird species

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classified objectively for their urban tolerance status (Conole and Kirkpatrick 2011), and field-gathered data on bird FIDs summarised by Weston et al. (2012), to test questions of the role of fearfulness in urban tolerant and intolerant bird species in the metropolis of Melbourne, Australia.

I test two non-exclusive hypotheses which relate birds' fearfulness of humans to their degree of urban tolerance in the metropolis of Melbourne, Australia. If sensitivity to disturbance by humans mediates birds' tendency to occupy, and establish in, urbanised environments, it may follow that species with shorter FIDs are more likely to be successful urban species. The first hypothesis therefore is that m_{FID} will be shorter in urban exploiter bird species than urban adapters, and most particularly shorter than in urban avoiders. If higher variability in FID is more strongly predictive of urban invasiveness in birds, it may also logically follow that for successful urban invader species they will be in the upper range of a measure of relative abundance (incidence) and cv_{FID} in urbanised habitats, and low cv_{FID} in the lower range of relative abundance. Therefore, the second hypothesis being tested here is that variability in FID is positively correlated with relative abundance (incidence) in the urban avifauna of Melbourne.

MATERIAL AND METHODS

In earlier related work I conducted an objective classification of the urban tolerance status of the bird species of Melbourne, Australia (Conole and Kirkpatrick 2011). More detailed descriptions of the study area and methodology can be found in related publications (Conole 2011, 2014; Conole and Kirkpatrick 2011). A brief summary follows below.

Study area

The study area is metropolitan Melbourne; capital city of the State of Victoria in coastal south-eastern Australia, within a 50 km radius of its Central Business District (37°49'S 144°58'E) (Figure 1). The study area excludes the sea, but includes areas not yet urbanised. The total area of metropolitan Melbourne is approximately 880,000 ha, with a population in 2007 of approximately 3.8 million people (DPCD 2008). Suburbs, with detached single dwellings in gardens dominated by plant species exotic to Melbourne, cover most of the above area. Semi–natural remnants of native vegetation are scattered within the bounds of the urban area, which also contains many parks and gardens planted with exotic plant species. Trees are

planted in most streets; these tend to be native to Australia, but not to the Melbourne region
(Frank et al. 2006). The original vegetation of Melbourne and the native vegetation that
survives on its margins is highly varied, this variation being related to soils, which range from
highly fertile black, cracking clays to highly infertile deep leached sands, and annual rainfall,
which ranges from 540–1,000 mm from the west to the east.

Data management

In objectively classifying the urban tolerance status of birds in Melbourne, Australia, Conole
and Kirkpatrick (2011) extracted *circa* 220,000 records of 292 species of birds from 11,434
surveys from the BirdLife Australia 'New Atlas of Australian Birds' project database (hereafter
'the Atlas') (Barrett et al. 2003). Each survey represents a list of species for a defined area and
time (ranging from 20 min to one month), with geographic coordinates. All data were collected
between 1998 and 2002. As there is a likelihood that less abundant species may be missed
where sampling effort is lower, leading to uneven representation of species (Watson 2004), a
measure of estimated sampling completeness was calculated for each of the grid cells. This
enabled an assessment of the evenness of sampling, and for unrepresentative samples to be
removed from the data to be analysed. Species and sites were filtered out according to criteria
for representativeness to arrive at a final list of 141 species and 390 cells. Five assemblages of
bird species were objectively classified (Conole and Kirkpatrick 2011), namely: Clade 1 —
Urban Avoiders; Clade 2a — Urban Adapters; Clade 2b — Urban Exploiters; Clade 3 — Urban
Avoiders; Clade 4 — Urban Avoiders.

Data for m_{FID} and its standard deviation (σ) were extracted from Weston et al. (2012) and a
measure of m_{FID} variability (cv_{FID}) was derived as the Coefficient of Variation of m_{FID}. For this
paper, relevant data on 91 (out of 141 species earlier classified for urban tolerance status by
Conole and Kirkpatrick (2011) Australian birds' FID were available from the review conducted
by Weston et al. (2012). Except where explicitly indicated, these data report non-urban m_{FID}
data. This condition was confirmed where possible by reference to primary source (e.g.
Blumstein 2006). For the four species where both rural and urban m_{FID} were collated and
reported by Weston et al. (2012), rural data were used in the FID analyses here. Summary
graphical data for the four rural–urban species pairs (Willie Wagtail *Rhipidura leucophrys*,
Magpie-lark *Grallina cyanoleuca*, Australian Magpie *Cracticus tibicen*, and the introduced
Common Blackbird *Turdus merula*) are presented as Figure 6.

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As this study is principally a meta-analysis of extant data, it relied solely on rural (that is 'pre-urban' or 'non-urban') measures of FID, as summarised by Weston et al. (2012).

Statistical analyses

All statistical analyses in this current study were performed in R (R Core Team 2014), using core functions and procedures from the packages 'relaimpo' (Grömping 2006), 'multcompView' (Graves et al. 2015) and 'glmulti' (Calcagno and de Mazancourt 2010). Figures were drawn using R core functions, as well as 'ggplot2' (Wickham 2009), 'lattice' (Sarkar 2008), 'glmulti' (Calcagno and de Mazancourt 2010) and 'multcompView' (Graves et al. 2015) packages.

All bird species in this study (n = 91) were included in all analyses.

Exploratory analysis of the FID data included plotting the data (Figure 2) in order to identify basic patterning. Plotting of m_{FID} and cv_{FID}, as well as bird mass (g) was undertaken as 'lattice' strip plots to examine the distribution of values within each of the urban tolerance clades (bird assemblages). I produced a correlation matrix of the four predictor variables (m_{FID}, σ, Mass, cv_{FID}) included for further analyses (Table 1).

I tested the first hypothesis that m_{FID} would be shorter in urban exploiter bird species than urban adapters, and most particularly shorter than in urban avoiders, by conducting a Kruskal–Wallis rank order test to evaluate whether m_{FID}, cv_{FID} and bird mass (g) differed significantly between clades. I also summarised the multiple paired–comparisons of m_{FID} by clade (Figure 4).

In order to test the second hypothesis that cv_{FID} is positively correlated with relative abundance (incidence) in the urban avifauna of Melbourne, I first undertook an analysis of the relative importance of all four model terms with 'relaimpo' and 'glmulti'. Relative importance refers to the quantification of an individual regressor's contribution to a multiple regression model, and in dealing with a model where regressors are typically correlated, averaging over orderings (lmg) (Lindeman et al. 1980) and the proportional decomposition of variance method (pmvd) (Feldman 2005) are recommended (Grömping 2006). I included testing of whether the relative importance of a regressor differed if it were either the first or last added to the model. Following an infomation-theoretic approach (Burnhum and Anderson 2002; Garamszegi et al. 2009), I also conducted a model selection analysis including up to four of the predictor variables. As both hierachical partitioning and model–averaged relative importance testing confirmed the importance of cv_{FID} over other model terms, I regressed it against urban bird

incidence (relative abundance) (Figure 5).

RESULTS

152   Contrary to expectations, cv_{FID} was most constrained for the urban exploiters than in any of the other groups (Figure 2). Urban avoiders (clade 4) showed both the shortest and longest

154   measures of m_{FID} in this study (Figure 2). Exploiters and urban avoiders (clade 3) showed the least variability in bird mass (Figure 2).

156   Correlations between model terms (Table 1) indicated that cv_{FID} and m_{FID} were not strongly related, and that though m_{FID} and bird mass were strongly correlated, cv_{FID} and bird mass were

158   not.

      According to the relative importance of regressors analysis, the most important was cv_{FID}

160   (Table 2), and the best model was one that only included cv_{FID} (Table 2; Figure 3). The estimated importance of cv_{FID} measured by lmg was 70.0% and pmvd 94.0% (Table 3). If cv_{FID}

162   was last added to the model its importance was 87.6%, or first 68.9% (Table 2).

      A linear regression model of cv_{FID} as a function of Incidence showed a significant, positive

164   correlation (Figure 5) (R^2=0.1347, $F_{1,91}$=15.33, p=0.0002).

      Kruskal–Wallis rank sum testing of FID and bird mass across clades showed significant

166   differences for m_{FID} and cv_{FID}, but not bird mass (Table 2). Figure 4 illustrates that although Kruskal–Wallis results were significant at 95% (p = 0.03914), multiple paired comparisons of

168   m_{FID} did not show a significant or meaningful difference between clades.

      Linear modelling showed a positive relationship between cv_{FID} and bird incidence.

170   Kruskal-Wallis and multiple paired comparison difference testing failed to show a clear-cut distinction between FID of urban tolerant and urban intolerant species. Urban exploiters' cv_{FID}

172   and cv_{FID} were not clearly distinct from any of the urban avoider clades.

DISCUSSION

Support for the hypothesis that cv_{FID} is a strong predictor of urban invasiveness was equivocal

174   in this study. Despite cv_{FID} having the greater predictive utility of the measures of fearfulness in this study as elsewhere, it is still the case that the 'best' model explains a relatively small

176   component of the variation in urban bird relative abundance. Therefore in seeking to identify other measures to fill the gap in understanding, it is likely that natural history and

environmental factors identified as significant in Melbourne by Conole and Kirkpatrick (2011) and in many other world cities (Chace and Walsh 2006) acting in concert with behavioural syndromes provide the answer. Neither environmental (cf. Conole 2014; Conole and Kirkpatrick 2011) or behavioural flexibility (Møller 2008), or for that matter physiological plasticity (cf Carrete and Tella 2011), on its own consistently or best predicts which birds will become successful urban exploiters.

Difference testing also failed to distinguish the urban exploiters from any other clades, including urban adapters and urban avoiders, by the measure of m_{FID}. Therefore the hypothesis that exploiters will show shorter m_{FID} than avoiders is not proven. Counter–intuitively, the mean values for m_{FID} showed that despite there being no significant differences between clades, the mean values for urban exploiters and adapters were slightly higher than for any of the urban avoiders. The least urban tolerant birds of clade 4 showed the lowest values and group mean for m_{FID}. So, non-significantly, urban avoiders had slightly shorter m_{FID}, suggesting perhaps that allowing humans to get *too* close may be maladaptive for urbanisation purposes.

Contrary to expectations, cv_{FID} operated in a much tighter band for the urban exploiters compared to the other groups than expected (Figure 2b). The amplitude in interspecific variability seems to matter less for urban exploiters — their somewhat homogenous response to disturbance by humans around a central tendency little different to urban adapters and avoiders, perhaps indicates a successful behavioural syndrome for urbanisation in Melbourne, but one which is at odds with that suggested from studies elsewhere.

Despite the discounting of phenotypic sorting (Møller 2015), I nonetheless believe there may be a phylogenetic effect evident in these data. The close similarity in multiple paired-comparison values of m_{FID} for urban exploiters and clade three of the urban avoiders (Figure 4) is mirrored by a superficially similar phenotypic/phylogenetic structure. However, it is beyond the scope of this study to examine that aspect in any greater detail.

The utility of cv_{FID} for predicting urbanisation of birds has been demonstrated in old European cities (Møller 2010), by first establishing that urban bird populations generally have shorter m_{FID} than their rural conspecifics, and that rural species with greater cv_{FID} are more likely to go on to become urban 'invaders'. Comparative measures of rural or wildland FID with urban FID are scarce in Australian studies. Weston et al. (2012) in their wide-ranging review of the topic only uncovered four species for which such data exist, namely Willie Wagtail *Rhipidura leucophrys*, Magpie-lark *Grallina cyanoleuca*, Australian Magpie *Cracticus*

210 *tibicen*, and the introduced Common Blackbird *Turdus merula*. For the four examples where rural–urban species pair data exist, a summary plot (Figure 9) shows the trend observed

212 elsewhere in the world that urban populations demonstrate shorter and less variable FID than their rural conspecifics (lower and less variable values of both m_{FID} and cv_{FID} — Figure 6).

214   Carrete and Tella (2011) conducted their studies in a new city in Argentina; one in its first years of development, in response to Diamond's (1986) advice to study these phenomena in

216 places where the least subtle of impacts are recent and continuing. In so doing they attempted to avoid possible confounding effects of the long established trends and adaptations in bird

218 urbanisation that might be at play in older European cities — some entering their second millenium since establishment. Despite this, and in common with studies from the Old World,

220 they found that rural m_{FID} was not significantly related to birds' urban invasiveness, but cv_{FID} and relative brain size (RBS) were (Carette and Tella 2011).

222   Díaz et al. (2013) showed that m_{FID} decreases with increasing latitude in Europe, which they associated with a similar cline in an index of raptor abundance. In so doing they allowed for

224 bird body size and phylogenetic effects, but not for overall city size, which in Western Europe varies with latitude and other factors. Díaz et al. (2013) study sites included metropolitan areas

226 varying in human population from 11.2 million (Paris) to around 1.0–1.2 million such as Oslo in Norway (Brinkhoff 2015). The possibility that city size and density may confound other

228 observed effects cannot be discounted. It is perhaps worth noting that my study site, Melbourne, sits just below the middle of the Díaz et al. (2013) range in human population size,

230 and as a study-wide mean also approximately half-way along the range of m_{FID} reported by them. Melbourne's latitude between 37–38° S *versus* 37.5–65° N in Díaz et al. (2013) places

232 Melbourne at the bottom of the latitudinal range (in the opposite hemisphere) explored in their study. Without comparable studies from higher or lower latitudes in Australia, it is not possible

234 to draw further conclusions, other than that latitude may be valuable as a model term, but that metropolitan human population size should also be included.

236   Many authors in discussing birds' fear response behaviours and relating that to a propensity for urbanisation couch this in terms of birds' tendency for 'urban invasiveness'. I prefer to use

238 the term 'urban tolerance' (Conole and Kirkpatrick 2011; Conole 2011, 2014; Møller 2010) rather than urban invasion (*sensu* Carette and Tella 2011). Tolerance embraces a spectrum of

240 circumstances under which animal or plant species come to inhabit cities. Although biotic urbanisation is most commonly perceived as the process associated with invasion or

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colonisation of urban areas by animal and plant species, it also the case that at least some biotic urbanisation is as the consequence of adaptation by species which remain in the landscape as it is being urbanised, and indeed species which survive within the urban matrix have been identified as sources for the urban adapter assemblage (Conole 2014; Conole and Kirkpatrick 2011). The conceptualisation of urbanisation as a process of invasion rather than a combination of processes of colonisation, survival and adaptation tends to force thinking along particular lines, which may limit a broader understanding of how urbanisation comes about.

In Melbourne, an assemblage of urban exploiter bird species with both short m_{FID} and relatively homogenous cv_{FID}, include both species which are likely to have colonised the urban areas after their establishment — Brown Goshawk *Accipiter fasciatus*, Galah *Cacatua roseicapilla*, Crested Pigeon *Ocyphaps lophotes*, Australian Hobby *Falco longipennis*, Musk Lorikeet *Glossopsitta concinna*, Little Lorikeet *G. pusilla*, White-plumed Honeyeater *Lichenostomus penicillatus*, Little Wattlebird *Anthochaera chrysoptera*, Red Wattlebird *A. carunculata*, Red-rumped Parrot *Psephotus haematonotus* — as well as some species which in all likelihood were never absent from the developing and established city — Little Raven *Corvus mellori*, Australian Magpie *Cracticus tibicen*, Welcome Swallow *Hirundo neoxena*, Magpie-lark *Grallina cyanoleuca*, Willie Wagtail *Rhipidura leucophrys*. Yet others were deliberately introduced from outside Australia, and in the earliest days of the city's development — House Sparrow *Passer domesticus*, Eurasian Tree Sparrow *P. montanus*, Common Starling *Sturnus vulgaris*, Common Myna *S. tristis*, Common Blackbird, Song Thrush *Turdus philomelos*, Rock Dove (Feral Pigeon) *Columba livia* and Spotted Dove *Spilopelia chinensis* (Conole 2011).

In concluding, the data analysed in this study show again as elsewhere that birds' natural states of m_{FID} are poor predictors of urban tolerance. Also, as in studies elsewhere, cv_{FID} shows some predictive utility, but in the case of Melbourne explains relatively little of the variability in birds' urban tolerance. Environmental factors and bird functional traits identified in Melbourne (Conole and Kirkpatrick 2011; Conole 2011, 2014) and many other cities (summarised in Chace and Walsh 2006) offer more obviously explanatory factors for understanding urban tolerance. Future research should more deliberately integrate functional traits with behavioural and environmental factors as components of explanatory models to better understand the extent and complexity of interaction between these factors. As there may also be a phylogenetic effect operating on the tendency for bird species to become urbanised, I also recommend making any future analyses phylogenetically explicit.

ACKNOWLEDGMENTS

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Table 1: Correlation matrix — model terms.

Model term	m_{FID}	σ	Mass	cv_{FID}	Incidence
m_{FID}	1.0000	0.6718	0.4524	0.0496	0.0532
σ	0.6718	1.0000	0.2765	0.5649	0.2444
Mass	0.4524	0.2765	1.0000	0.0341	−0.0501
cv_{FID}	0.0496	0.5649	0.0342	1.0000	0.3797
Incidence	0.0532	0.2444	−0.0501	0.3797	1.0000

Table 2: Relative importance of model terms — `relaimpo` analysis. Proportion of variance explained by model = 15.32%

Predictor	lmg	pmvd	last	first
m_{FID}	0.034	0.022	0.021	0.014
σ	0.225	0.002	0.001	0.285
Mass	0.041	0.035	0.101	0.012
cv_{FID}	0.700	0.940	0.877	0.689

Table 3: Linear regression model selection output ranked by AIC_c — 10 best models.

Model	AIC_c	Weights
Incidence ~ 1 + cv_{FID}	−12.83351	0.370632
Incidence ~ 1 + cv_{FID} + Mass	−11.08297	0.154460
Incidence ~ 1 + cv_{FID} + σ	−10.79139	0.133506
Incidence ~ 1 + cv_{FID} + m_{FID}	−10.77713	0.132558
Incidence ~ 1 + cv_{FID} + m_{FID} + Mass	−9.39180	0.066311
Incidence ~ 1 + cv_{FID} + Mass + σ	−9.22691	0.061063
Incidence ~ 1 + cv_{FID} + m_{FID} + σ	−8.56658	0.043893
Incidence ~ 1 + cv_{FID} + m_{FID} + Mass + σ	−7.11281	0.021218
Incidence ~ 1 + m_{FID} + σ	−4.14785	0.004818
Incidence ~ 1 + σ	−4.08484	0.004669

Table 4: Kruskal-Wallis test results on FID and bird mass by clade

Variable	Kruskal-Wallis χ^2	DF	p–value
cv_{FID}	16.3065	4	0.0026
m_{FID}	10.0776	4	0.0391
Mass	6.6761	4	0.1540

Figure 1: : Study area — Melbourne, Australia
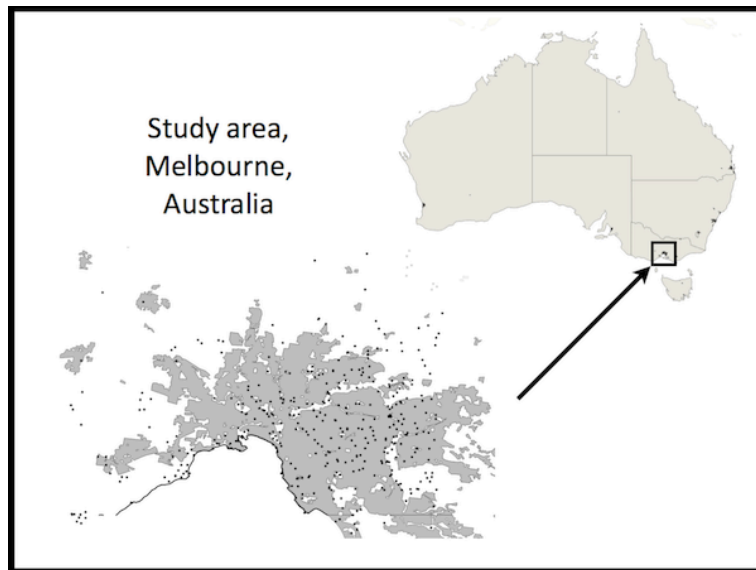
Figure 2: Strip plots of model term values
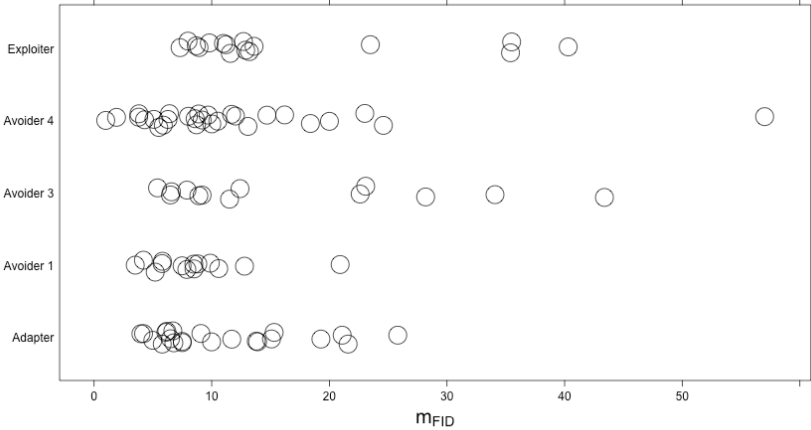
(a) Mean Flight Initiation Distance (m_FID) plotted by urban tolerance clade
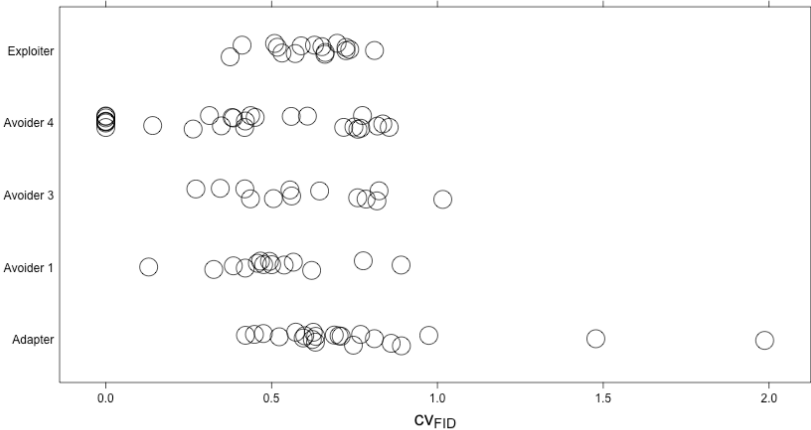
(b) Flight Initiation Distance Coefficient of Variation (cv_FID) plotted by urban tolerance clade
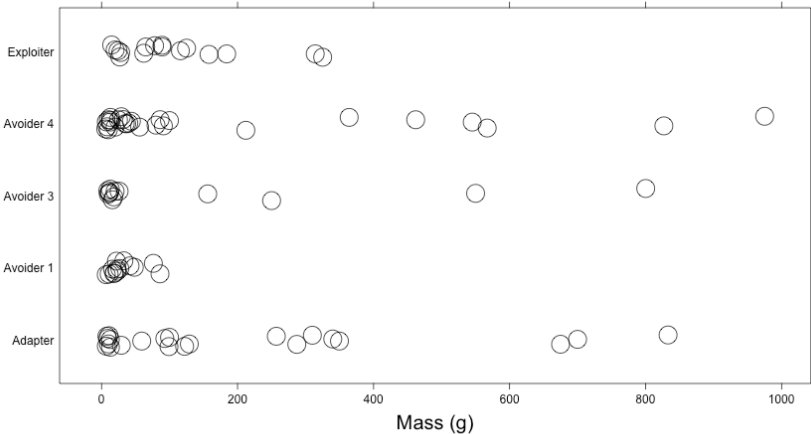
(c) Mass (g) plotted by urban tolerance clade

Figure 3: Relative importance of model terms (MFID = m_{FID}, SD = σ, Mass = bird mass (g), CVFID = cv_{FID}).
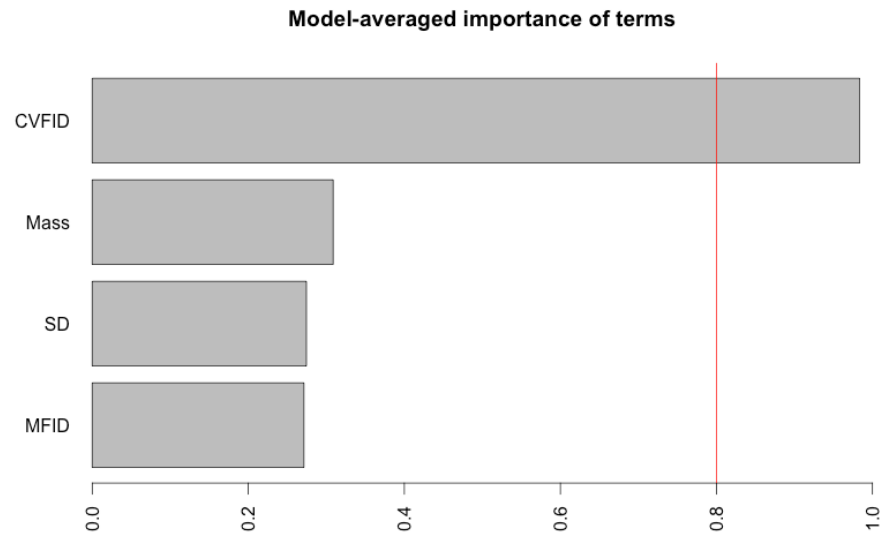
Figure 4: Summarised multiple paired comparisons of m_{FID} by Clade. Clades which share T-symbol do not significantly differ.
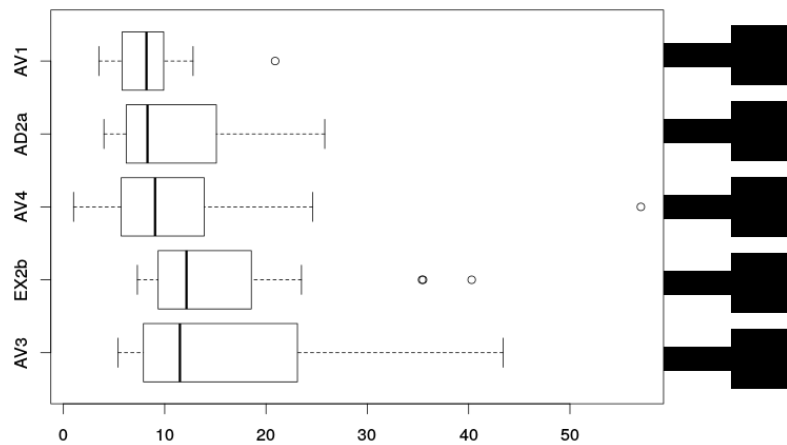
Figure 5: Positive correlation between the Coefficient of Variation of FID, cv_{FID} (= CVFID), and relative abundance (= INCIDENCE), R^2=0.1347, $F_{1,91}$=15.33, p=0.0002. Regression plot plus 95% confidence intervals.
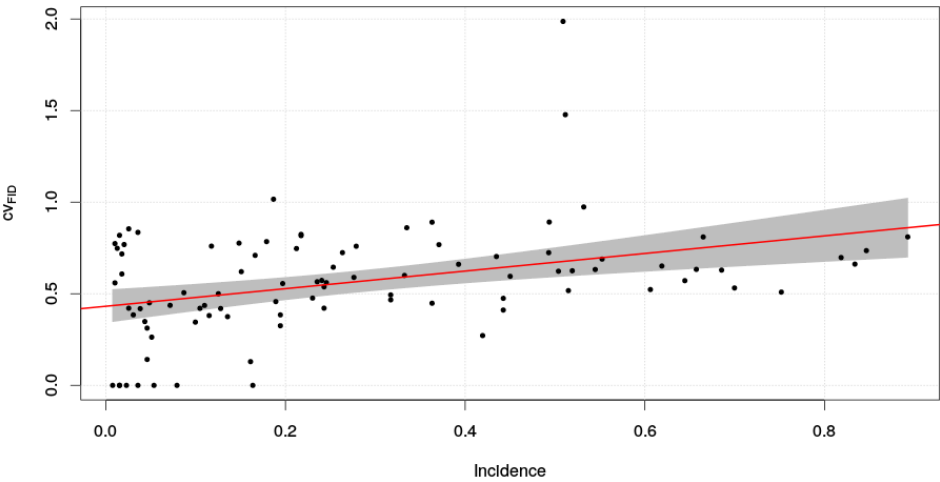
Figure 6: Rural–Urban species pairs, showing m_{FID} and one standard deviation.
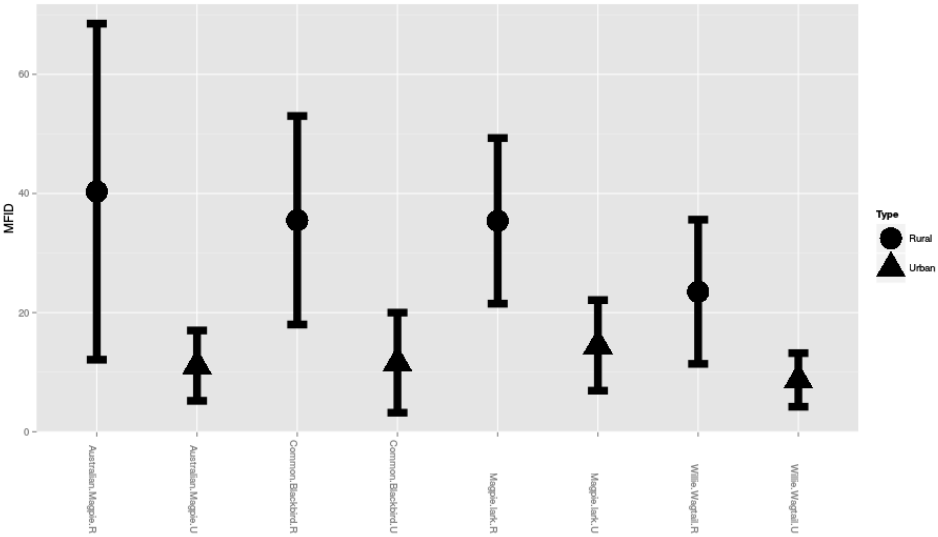
*"... We
papered the world
with numbers and names,
but things survived ..."*

'Ode to Numbers'
Pablo Neruda 'Elemental Odes' (1952–1957)

CHAPTER 7:

SUMMARY AND CONCLUSION

7.1 General discussion

The study presented here in Chapters 3–6 (Conole 2011, 2014, in prep.; Conole and Kirkpatrick 2011) presents a case to show that the urban bird assemblages of Melbourne are both broadly analogous in their organisation to those in other world cities, and also that they differ in ways that caution against broad generalisations of (i) what constitutes an urban bird, or (ii) where and how abundantly they occur within cities. Whilst others have examined a panoply of physiological and behavioural traits that may predispose birds to urban adaptation (e.g. Kark *et al.* 2007; Møller 2009; Evans *et al.* 2011), the present study has examined the higher order habitat filtering mechanisms that may be explanatory at a more fundamental mechanistic level, along with the adaptive significance of predator avoidance, and develops some broadly generalisable concepts at the scale of the landscape and the assemblage.

7.1.1 The birds

Melbourne's urban bird fauna was objectively classified into five assemblages, and a series of interpolated maps plotted by ordinary kriging (Nychka *et al.* 2014) are presented below to illustrate their spatial extent (Figure 7.1). Two urban tolerant assemblages contain the more commonly encountered bird species of Melbourne; exploiters (Assemblage 2b) occurred widely across the whole city but adapters (Assemblage 2a) mostly in the eastern suburbs (Figures 7.1 and 7.2). Three avoider assemblages occurred, specific to spatial and habitat nodes of the city. Assemblage 1 was characteristic of riparian and bush remnants of eastern Melbourne (Figures 7.1 and 7.2), Assemblage 3 was found mostly on wetland margins and in coastal vegetation (Figure 7.1), whilst Assemblage 4 comprised a group of rare and restricted forest and woodland birds found on the margins of the urban matrix or in larger remnant native vegetation patches within it (Figure 7.1).

Assemblage 4 species can also be interpreted as a group which are at heightened extinction risk within the broader Melbourne metropolitan area. Clustered as they are in widely spread, smaller pockets of natural habitats which are marginal and disappearing in greater Melbourne, Assemblage 4 is a 'watch list' for local extinction purposes.

As expected, moderate–high species richness (20–30 species) of urban tolerant assemblage species was broadly observed across Melbourne, while low species richness (<10 species) was more typical across the matrix for avoiders (Figure 7.1).

Bird body size differed significantly between assemblages (Conole and Kirkpatrick 2011). Urban tolerant species (Assemblages 2a and 2b) were significantly larger in body size than urban avoiders of Assemblages 1 and 4. Assemblage 3 substantially overlapped 2a and 2b, and while the difference between them is not statistically significant, the median for Assemblage 3 is notably lower than either 2a or 2b (Figure 7.2).

Certain combinations of foraging and nest substrate guild membership were exclusively urban avoiders, and characterised largely by the tendency to either nest on the ground or to be gleaning species or frugivores, or to be specialists such as brood-parasitic cuckoos (Conole and Kirkpatrick 2011) (Figures 7.2 and 7.2). In contrast, other combinations that were exclusively urban tolerant included many that utilised cavities for nesting (including those in buildings) in combination with being omnivorous or granivorous ground feeders. Nectarivores were often urban tolerant, whereas most raptors were not. All spring migrants were avoiders (except for the

partial spring migrant Black-faced Cuckoo-shrike, which was an adapter), as were 73.6% of winter migrants, 59.5% of sedentary species, and 63.2% of nomadic species (all greater than expected) (Figure 7.2).

The conceptual model which incorporates the above-mentioned characteristics (see Section 4.2) of successful urban adapter and exploiter bird species also allows the identification of candidate species which may become part of Melbournes future urban avifauna.

Candidate species for future incorporation into Melbourne's urban bird fauna include those that are:

- medium-bodied, cavity or canopy nesting,

- omnivorous, granivorous or nectarivorous, regionally resident or recorded but not yet established as part of Melbourne's urban avifauna,

- exotic urban ubiquitists such as such as the Barbary Dove (Columbidae: *Streptopelia risoria*), the Afro-Indian parakeets (Psittacidae: *Psittacula* species), the House Crow (Corvidae: *Corvus splendens*); or non-local Australian natives such as the Blue-faced Honeyeater (Meliphagidae: *Entomyzon cyanotis*).

Although earlier work showed that most exotic species in Melbourne are urban tolerant (Green 1986), this is not universally true, and five more-specialised species are urban avoiders (Eurasian Skylark *Alauda arvensis*, Common Greenfinch *Chloris chloris*, European Goldfinch *Carduelis carduelis*, Red-whiskered Bulbul *Pycnonotus jocosus* and Scaly-breasted Lorikeet *Trichoglossus chlorolepidotus* (Conole 2011; Conole and Kirkpatrick 2011). The eight other exotic species are urban exploiters distributed widely in the urban area and either universally or locally abundant (Conole and Kirkpatrick 2011). The exotic species sort into three of Melbournes five urban bird assemblages, and exhibit similar functional and spatial responses to urbanisation as natives. The size differential between urban exploiter and urban avoider exotic birds also mirrors that seen in native urban birds, as do the nest substrate and foraging profiles (Conole 2011), and this has not previously been demonstrated.

The conceptual model created from earlier work on these data (Conole and Kirkpatrick 2011) and supported again by the partitioned data on exotics (Conole 2011), suggests that it may be possible that species-poor subsets of urban tolerant bird assemblages prosper at sites that are at the extremes of urban habitat gradients. Such highly urbanised sites are depauperate for both native and exotic bird species, and therefore exotic bird dominance may simply be a marker of particular urban habitat types where overall bird species richness and individual native species abundance is low, rather than being sites where exotics displace natives from their niches.

The diversity of urban adapters along the gradient of urban intensity (measured by $Index_{Combined}$) follows a humped distribution, and the trend is more pronounced when viewed as landscape-scale preference for points on the gradient (Conole 2014). This resembles the trend seen for urban tolerant birds in other studies (Marzluff and Rodewald 2008; Tratalos *et al.* 2007), and for bird species richness in response to selected environmental factors at a landscape scale (Bar-Massada *et al.* 2012). The inverted, humped curve for exploiters is however not at all like trends for urban tolerant bird species richness seen in other studies (Tratalos *et al.* 2007; Luck and Smallbone 2010; Shanahan *et al.* 2014), and this marks a strong divergence in response by exploiters and adapters to urbanisation intensity. The response of urban tolerant birds to

increasing *Frequency Greenspace* resembles much more the broad trends observed in other cities (Chace and Walsh 2006), and closely mirrors the relationship observed between bird species richness and foliage height diversity observed in a non-urban landscape (Bar-Massada and Wood 2014).

The divergent responses of each group to urbanisation intensity are largely explained by their ecological histories. The exploiters are able to use disturbed habitats across the matrix analogous to their original habitats, and many of them were established in Melbourne during the early stages of urban expansion and consolidation of the city. As suburban parts of the city became more heavily vegetated and less open, a group of species from analogous riparian/forest habitats became increasingly well established in parts of the city proximate to their source natural habitats.

The data analysed in this study show again as elsewhere that birds non–urban Flight Initiation Distance (FID), as a measure of predation risk response to humans, is a poor predictor of urban tolerance. Also, as in studies elsewhere, variability in FID shows some predictive utility, but in the case of Melbourne explains relatively little of the variability in birds urban tolerance. Environmental factors and bird functional traits identified in Melbourne (Conole and Kirkpatrick 2011; Conole 2011, 2014) and many other cities (summarised in Chace and Walsh 2006) offer more obviously explanatory factors for understanding urban tolerance. Future research should more deliberately integrate functional traits with behavioural and environmental factors as components of explanatory models to better understand the extent and complexity of interaction between these factors.

7.1.2   The urban matrix

Two environmental or demographic factors that best explained the spatial and community structure of urban bird assemblages were *Frequency Greenspace* (the reciprocal of impervious surface cover) (Figure 7.4) and $Index_{Combined}$ (a measure of the spectral mixture of the 2000 Landsat Enhanced Thematic Mapper Plus (ETM+) satellite image, and the proportion of people employed in non-agricultural, i.e. urban, work) (Figure 7.5) (Conole and Kirkpatrick 2011). The former reflected structural habitat characteristics of the urban habitat matrix, while the latter represented the matrix's human demographic attributes.

The urbanisation gradient described by *Frequency Greenspace* and $Index_{Combined}$ is exemplified, albeit coarsely, by the aerial and street-level photographic images shown in Figures 7.6–7.9. Human population density ranging from 0–8,300 people/km² was used as a proxy for the gradient from least to most strongly urbanised sites. At the lowest density of people/km² the sites are typically exurban and either rural or natural in character (Figure 6.6), whereas in the middle of the range the sites are typically suburban (Figures 7.7 & 7.8). Figure 7.9 shows the central business district of Melbourne and the most strongly urbanised of sites included in this study.

The spatial arrangement of most assemblages also showed a strong longitudinal gradient (Figure 7.2a).

(a) Assemblage 1 — urban avoiders of remnant native vegetation in the urban matrix (riparian zones, grassland, woodland)

(b) Assemblage 2a — urban adapters

(c) Assemblage 2b — urban exploiters

(d) Assemblage 3 — urban avoiders of wetland margins and coastal scrub

(e) Assemblage 4 — urban avoiders; localised and rare woodland and forest species

(f) Study area showing survey sites
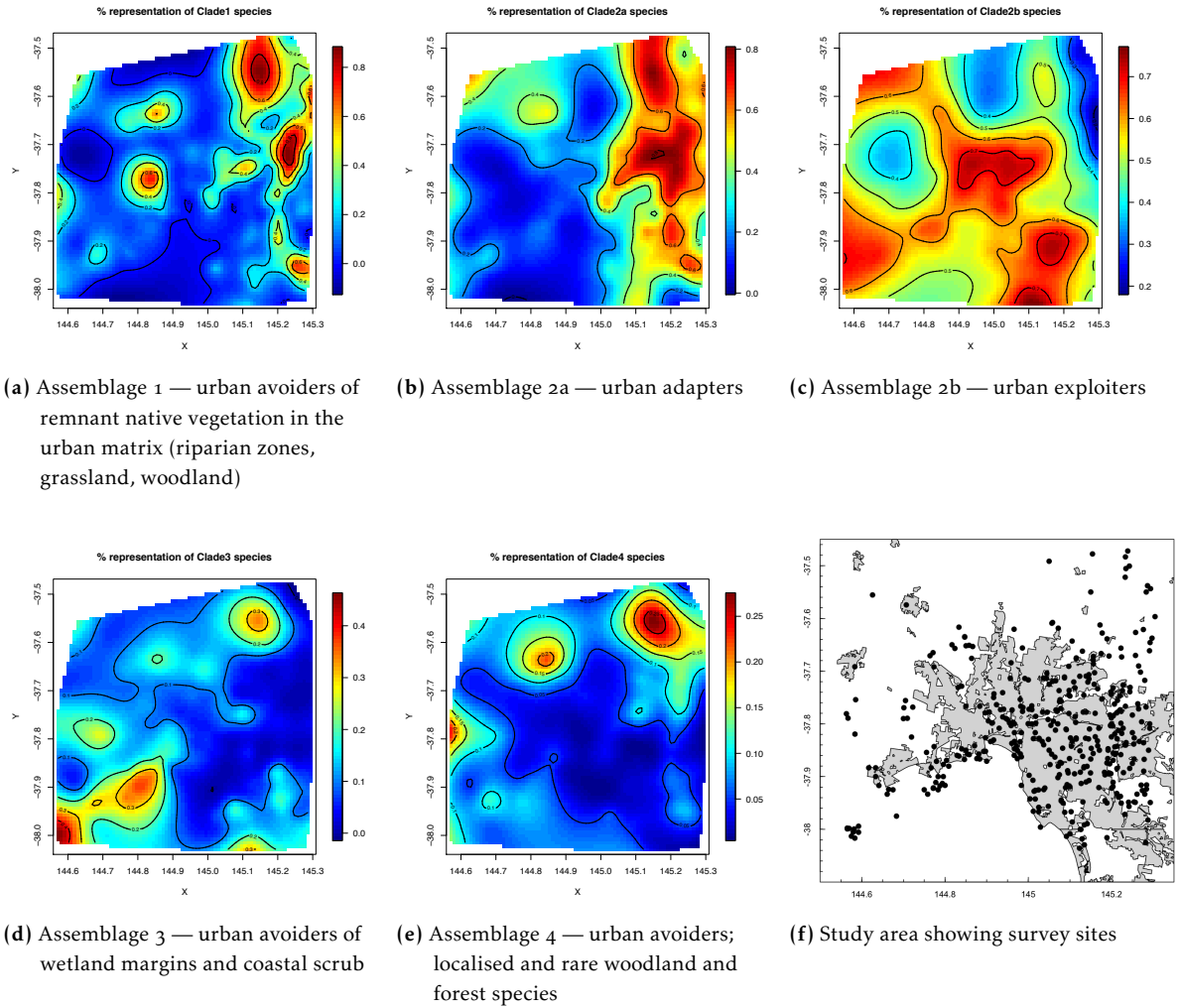
Figure 7.1: Interpolated maps (by kriging) of urban bird assemblage species richness in Melbourne.
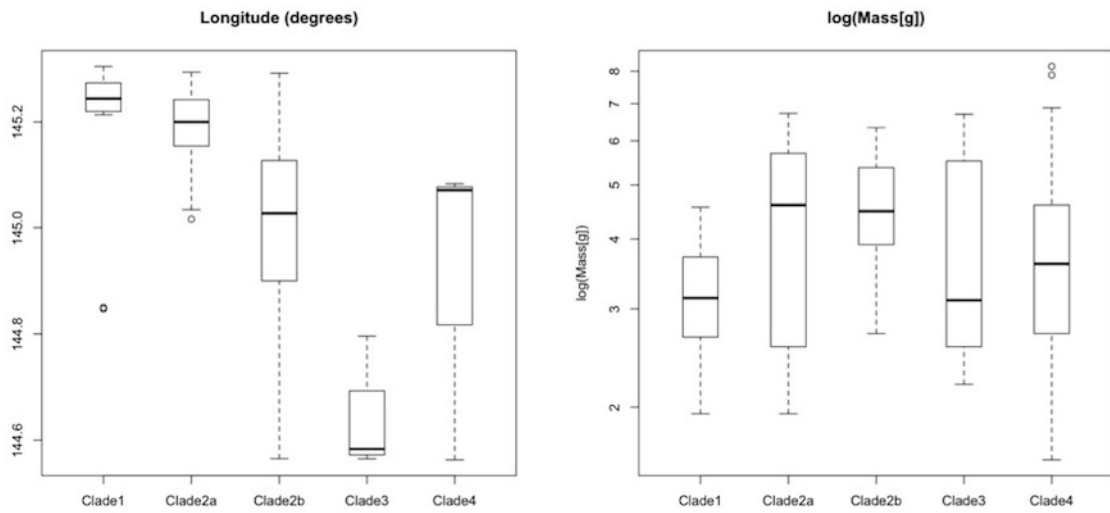
(a) East west gradient: boxplots of assemblage species richness **(b)** Mass of birds by assemblage, log(g) by longitude.
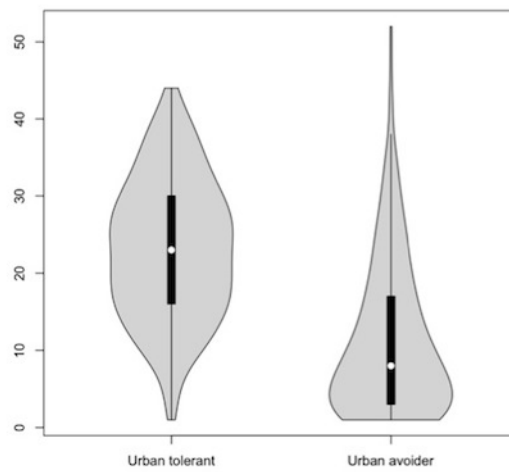
(c) Density plots of observed species richness at all sites across the Melbourne Metro area for urban tolerant species (assemblages 2a and 2b) and urban avoider species (assemblages 1, 3, 4).

Figure 7.2: Urban assemblage metrics
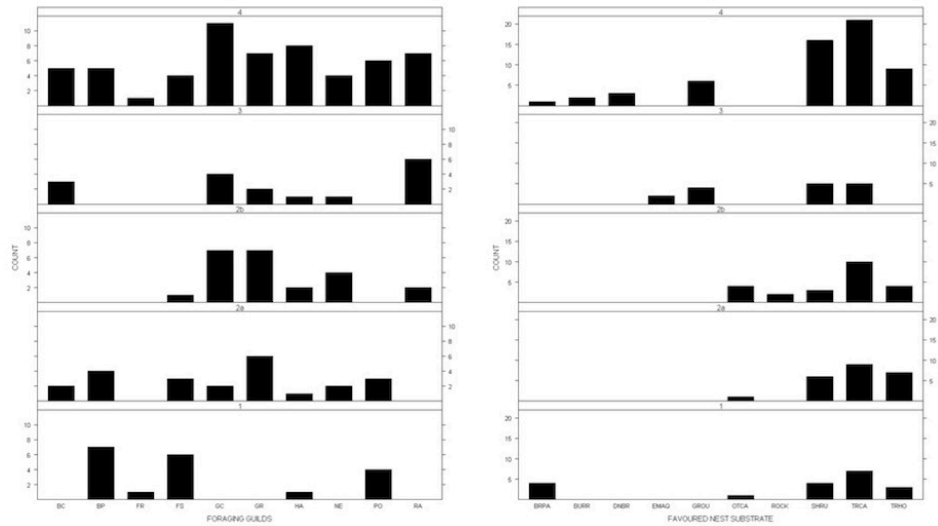
(a) Foraging guild membership of the assemblages. Assemblages numbered bottom to top — 1, 2a, 2b, 3, 4. In each facet the foraging guilds: BC (bush carnivore), BP (bark prober), FR (frugivore), GR (ground prober), HA (hawker/sweeper), NE (nectarivore), PO (pouncer), RA (raptor).

(b) Nest substrate classes of the assemblages. Assemblages numbered bottom to top — 1, 2a, 2b, 3, 4. In each facet the nest substrate classes: BRPA (brood parasite — cuckoos, order Cuculiformes), BURR (burrow), DNBR (do not breed in the study area), EMAQ (emergent aquatic), GROU (ground), ROCK (cliffs and ledges), SHRU (shrub), TRCA (tree canopy), TRHO (tree hollow).
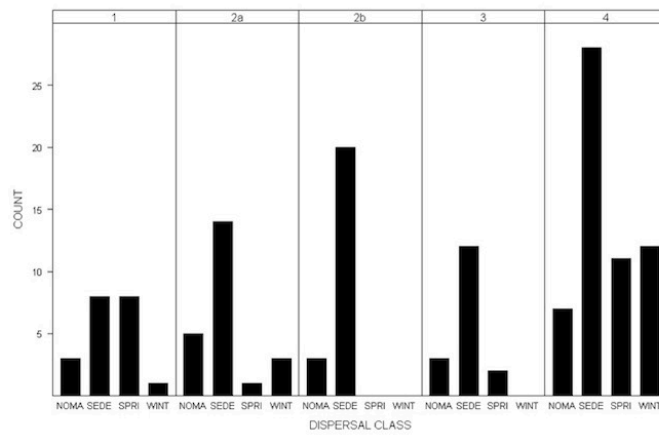
(c) Dispersal classes of the assemblages. Assemblages numbered left to right — 1, 2a, 2b, 3, 4. In each facet the dispersal classes: NOMA (nomadic/dispersive), SEDE (sedentary), SPRI (spring/summer migrant), WINT (winter/altitudinal migrant).

Figure 7.3: Guild structure of the assemblages

7.2 Discussion

In many ways the broad patterns observed in this study are not unique. They are repeated at least in part in global cities of the industrialised world (United States of America, Western Europe), and to some extent in the lesser studied cities of the developing world (South America, Asia, Africa). Patterns observed in Melbourne are however not mirror images of other large world cities, and important distinctions need to be made based on the research presented here. Differences are to be expected from cities on different continents with different patterns of human demography — some are due to differing environmental gradients in the city, as well as ecological idiosyncrasies of the pre-urban avifaunas.

Urban biodiversity research, particularly that targeting birds, has shown that species richness tends to decline along a gradient of increasing urbanisation (Clergeau et al. 2006; Faeth et al. 2005; Marzluff et al. 2001; McKinney 2006; Shochat 2004). Other work has also shown that species richness reaches a maximum in areas of intermediate urbanisation (Blair 1996, 1999; Crooks et al., 2004; see also Shochat et al., 2006). A repeated pattern in many parts of the world is one where a relatively small number of species well-adapted to anthropogenic landscapes, thereby replacing a wider range of native species or utilising habitats that native species find inhospitable, has been termed biotic homogenization (Blair 2001; Lockwood & McKinney, 2002; Crooks et al., 2004). So it is in broad terms in Melbourne (Conole and Kirkpatrick 2011; section 7.1.1 above).

Chace and Walsh (2006) in summarising the literature available at that time concluded that ifferences in nesting and feeding may also play a role in urban exploitation and adaptation. In the research presented here, combinations of preference for foraging and nesting substrates were found to characterise birds' urban tolerance accurately (Conole and Kirkpatrick 2011).

In some other studies, migrants decreased in occurrence with increasing intensity of urbanisation (e.g. Kark et al. 2007), reflecting the importance of sedentariness as a factor determining whether a species develops urban tolerance. In the research presented here, the same trend was observed, and all migratory species were urban avoiders (Conole and Kirkpatrick 2011)

The ecological equivalence of exotic species with indigenous species has not been explicitly addressed in other research, though it has been examined implicitly by the inclusion of native and non-native bird species in most other studies. The conclusions drawn here (Conole 2011), coming as they do without clear precedent, are novel.

Behavioural flexibility, adaptation and plasticity have been invoked to explain the stratification in birds' responses to urbanisation, allowing some species to prosper in cities while others remain at low numbers or disappear (Chace and Walsh 2006). Traits such as lower levels of fear of humans or reduced responses to disturbance by humans (in its most developed form known as commensalism), low or reduced levels of resource investment in territory maintenance, and gregarious behaviour (Mills et al. 1989), and sedentariness (Chace and Walsh, 2006; Díaz et al. 2013; Jokimäki and Suhonen 1998) have also been invoked. The extent to which behavioural flexibility, measured in this case by the flight initiation distance (FID) as a measure of fearfulness of humans, plays a significant role has been shown relatively strongly in Europe (Díaz et al. 2013; Møller 2008, 2010), but the evidence from Melbourne is at best equivocal. As elsewhere (Carrete and Tella 2011; Møller 2008, 2010), the variability in FID (cv_{FID}) in Melbourne showed limited explanatory capacity. I have concluded above that a combination of

behavioural traits and responses to environmental factors best explains birds' adaptations to urbanisation in Melbourne.

Species of the same family may show similar life-history, morphological and behavioural traits (Bennett and Owens 2002; Kark et al. 2007). It is therefore possibly the case that results produced elsewhere, and here, may be impacted by phylogenetic factors.

7.3 Conclusion

Whilst on one hand heeding the advice of Mac Nally (2000) on the desirability of working towards generalisable concepts, but with Watson and Herring's (2014) clarion warning to see the forest **and** the trees ringing in my ears, and the difficulties of generalising about urban areas in any global sense (Shwarz *et al.* 2014), I advance bravely towards the bigger picture items that can be generalised from the site- and species-specific analyses undertaken here on the urban birds of Melbourne.

Adapter is not the most accurate term to describe the group that classifies this way (*sensu* Blair 1996). It is nearly right, insofar as that the species have adapted to some suburban areas close to the woodland habitats and pre-urban assemblages they derived from. However, in their spatial and community organisation, and habitats of origin, they have a close affinity with Assemblage 1 urban avoiders. In the future, species that become urban exploiters may be as likely to come from one of the groups currently identified as avoiders as well as, or instead of, the adapters.

Many parts of the urban matrix must now be nearly saturated with the current cohort of urban exploiters due to their ubiquity, but the number of adapter species (either the current adapter cohort, or other species which may join that category in future) contributing to bird species richness at points across the matrix is likely to increase as the process of afforestation of the older suburbs continues. It follows also that distribution of exploiter species may decline in more established suburbs over time — though expanding in range and continuing to dominate in developing areas of the city at or near the fringe. Clues to this trend can be found in studies that model the trajectory of abundance for open habitat, ground feeding specialists (such as the Crested Pigeon *Ocyphaps lophotes*) which decline as those habitats accumulate denser woody vegetation (Kutt and Martin 2010).

In their behavioural responses to humans, measured by the distance at which they flush when approached (mean flight initiation distance, m_{FID}), urban birds of Melbourne showed no clear, significant distinction between urban tolerant and intolerant assemblages of species. Even the generally more informative measure of the variability in fear response (coefficient of variation of flight initiation distance, cv_{FID}) in the case of Melbourne explained very little of the urbanisation tolerance of species.

The partitioning of adapters and exploiters within the urban tolerant grouping in this study gives reason to be cautious in assuming uniformity of response of all 'urban tolerant' species. We might otherwise overlook the importance of habitat origins for understanding bird species' adaptation to urban environments. Similarly to the way in which time since establishment has been found to be related to high urban densities of some bird species (Møller *et al.* 2012), and biogeographic origin predictive of urban adaptation extent (González-Oreja 2011), spatial and habitat origins of members of bird assemblages influence the degree to which they become urban tolerant — ranging from not at all through to ubiquitous. Thus, bird species that classify

as urban tolerant will tend to become either exploiters or adapters according to the degree of openness of their habitats-of-origin.

7.4   Recommendations

Implementation of urban planning measures which prioritise amongst other things a notion of functional diversity of the biota, and not just species diversity, will take account of the subtleties evident in the objective classification of Melbourne's birds into five distinct assemblages. Whilst the ongoing presence of species from assemblages 2a and 2b, the urban tolerant groups, is easy to regard as a certainty, the survival of habitat specialists from the three urban avoider assemblages (1, 3, and 4) is less assured. Even urban tolerant species occur at much reduced species richness and relative abundance in the least hospitable zones of the city. Retention of a range of bird species (and other biota for which birds act as surrogates or indicator species) will require that structurally diverse habitats are retained or created throughout the urban matrix, at a spatial grain that allows for interaction and connection.

Assemblage 4 species can also be interpreted as a group which are at heightened extinction risk within the broader Melbourne metropolitan area. Clustered as they are in widely spread, smaller pockets of natural habitats which are marginal and disappearing in greater Melbourne, Assemblage 4 is a 'watch list' for local extinction purposes. Targeted measures to address the potential loss of these species from the study area are required — more specialised variants of that proposed in the first recommendation — if their retention is judged to be a priority.

Future community ecology research in urban areas should treat exotic species as ecological equivalents, and in some cases as preferential study subjects. The ubiquity of some species makes them readily accessible, and the extent to which they respond to environmental factors as indigenous species do, makes them ideal study subjects. Their exotic pest status perhaps allows more readily for manipulative field experiments involving the control of numbers or biomass of some species.

The differential responses to environmental factors in urban areas of the two urban tolerant assemblages, exploiters and adapters, suggests that future studies should respect the distinction, and design research questions which can further explore the implications of the differences.

Future behavioural ecology research on predator avoidance in the urban context should more deliberately integrate functional traits with behavioural and environmental factors as components of explanatory models to better understand the extent and complexity of interaction between these factors. As there may also be a phylogenetic effect operating on the tendency for bird species to become urbanised, I also recommend finding ways of making future analyses phylogenetically explicit.

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APPENDICES

Appendix 1: List of conference papers.

Appendix 2: Supplementary material from Chapter 4 (Conole, L. E. 2011. Diverse Responses of Exotic Birds to Urbanization. *Natureza & Conservação*, 9(1), 99–104)

Appendix 3: Supplementary material from Chapter 5 (Conole, L. E. 2014. Degree of adaptive response in urban tolerant birds shows influence of habitat-of-origin. *PeerJ 2*: e306.)

Appendix 4: Correlation matrix for remotely-sensed environmental factors used throughout this thesis.

APPENDIX 1

Conference Papers arising from research conducted for this thesis.

- Conole, L. E. (2007). Using Bayesian Belief Networks to model urban bird macroecology. Presented to the School of Geography and Environmental Studies Conference Program, October 2007, Hobart.

- Conole, L. E. (2008). Urban birds in Melbourne — diversity, distribution and community ecology. Presented to the School of Geography and Environmental Studies Conference Program, October 2008, Hobart.

- Conole, L. E. (2010). How are urban bird assemblages organised in Metro Melbourne? Poster paper. Birds Australia 2010 Conservation Forum, University of Melbourne.

- Conole, L. E. (2010). Homogenisation of suburban bird assemblages: an Australian perspective. Presented at the 25th International Ornithological Congress, Campos do Jordão, Brazil.

- Conole, L. E. (2010). Homogenisation of suburban bird assemblages: an Australian perspective. Presented to the Departmento do Ecologia, Instituto de Biociências da Universidade de São Paulo, Brazil.

- Conole, L.E. (2011). Theres nothing really special about urban birds, is there? Poster paper. Ecological Society of Australia Conference, Hobart, November 2011.

APPENDIX 2

Supplementary material from Chapter 4 (Conole, L. E. 2011. Diverse Responses of Exotic Birds to Urbanization. *Natureza & Conservação* 9, 99–104)

SUPPLEMENTARY MATERIAL

Study area

The study area is metropolitan Melbourne; capital city of the State of Victoria in coastal south-eastern Australia, within a 50 km radius of its Central Business District (37°49'S 144°58'E). The study area excludes the sea, but includes areas not yet urbanised. The total area of metropolitan Melbourne is approximately 880,000 ha, with a population in 2007 of approximately 3.8 million people (DPCD, 2008). Suburbs, with detached single dwellings in gardens dominated by plant species exotic to Melbourne, cover most of the above area. Semi-natural remnants of native vegetation are scattered within the bounds of the urban area, which also contains many parks and gardens planted with exotic plant species. Trees are planted in most streets; these tend to be native to Australia, but not to the Melbourne region (Frank et al., 2006). The original vegetation of Melbourne and the native vegetation that survives on its margins is highly varied, this variation being related to soils, which range from highly fertile black, cracking clays to highly infertile deep leached sands, and annual rainfall, which ranges from 540-1,000 mm from the west to the east.

Atlas data

Approximately 220,000 records of 292 species of birds from 11,434 surveys were extracted from the Birds Australia 'New Atlas of Australian Birds' project database (hereafter 'the Atlas') (Barrett et al., 2003). The Atlas database contains four types of record: 2-ha search for 20 minutes; small area search (within 500 m of a central point); large area search (within 5 km of a central point); and, incidental observations of individual species from a single point (Barrett et al., 2003). Each survey represents a list of species for a defined area and time (ranging from 20 minutes to one month), with geographic co-ordinates. All data were collected between 1998 and 2002. Data initially extracted for this study included 4,221 2-ha searches, 4,993 small area searches, 793 large area searches, and 1,427 incidental observations, and were compiled in a matrix as species and their relative abundance (number of surveys in which a species was recorded in a cell divided by the total number of surveys conducted in the cell) by site.

Using ArcMap GIS, a 1 x 1 km grid based on that developed by the Australian Research Centre for Urban Ecology (ARCUE) (Hahs and McDonnell, 2007) was intersected with Atlas records to produce a matrix of grid cells by species presence/absence (Figure 1). All surveys were assigned to the grid cell in which the central geographic coordinates fell, regardless of survey spatial or temporal scale. It was assumed that most large area searches (6.9% of the surveys in the unfiltered data set) referred to areas of between 500 – 2,000 m diameter, and therefore could reasonably be assigned to 1 x 1 km grid cells within which the central coordinates fell.

Estimated sampling completeness

As there is a likelihood that less abundant species may be missed where sampling effort is lower, leading to uneven representation of species (Watson, 2004), a measure of estimated sampling completeness was calculated for each of the grid cells. This enabled an assessment of the evenness of sampling, and for unrepresentative samples to be removed from the data to be analysed.

First, the predicted number of species (S_{Chao2}) was calculated for each cell in a 66 km x 65 km grid, using the Chao$_2$ formula (Chao, 1987) (Formula 1), where S_{obs} equals the number of species observed, Q_1 the number of unique records (species observed once at a site during surveys), and Q_2 the number of doubletons (species observed twice). S_{Chao2} is the estimated total number of species present at survey sites, including those not found during surveys.

$$S_{Chao2} = S_{Obs} + \frac{Q_1^2}{2Q_2}$$

Formula 1: Chao2

From these calculations a standardized measure of sampling completeness (%Completeness) was also calculated for each grid cell, with observed species richness (S_{obs}) as a proportion of predicted species richness (S_{Chao2}) (Peterson and Slade, 1998).

Data organisation

Several assumptions were made about species to be excluded from analyses, and species were not included in grid cell totals and were eliminated from further analyses if any of the following exclusion criteria were met: (i) constituted fewer than five records in the total dataset; (ii) was an irregular or vagrant species to the area or feral species not yet naturalised, determined from the literature (Barrett et al., 2003); or, (iii) were seabird, waterbird, and nocturnal species, except the Tawny Frogmouth *Podargus strigoides*, from the orders or families: Anseriformes, Podicipediformes, Strigiformes, Eurostopodidae, Aeogothelidae, Procellariformes, Spenisciformes, Phalacrocaraciformes, Ciconiiformes, Gruiformes, Charadriiformes (sensu Christidis and Boles 2008). A final list of 141 species (hereafter 'the filtered species list') was retained for further analysis.

Grid cells were eliminated from further analyses if any of the following exclusion criteria were met: (i) ≤ 1 surveys in the cell; (ii) %Completeness < 50%; (iii) land area < 25% of the cell; or (iv) a high proportion of singleton records (>50%) and/or no doubleton records (indicating skewed data collection, e.g. single-species or other narrowly targeted surveys). A final list of 390 grid cells was retained for further analysis.

Bird species were classified into foraging guilds using a modified scheme for southern Victorian species (Mac Nally, 1994). Mac Nally's (1994) 'Hawker' and 'Sweeper' categories were combined to make 'Hawker/Sweeper', 'Wood Searcher' and 'Bark Prober' combined to make 'Wood Searcher/Bark Prober', and the categories of 'Raptor' and 'Frugivore' were added. Species not classified by Mac Nally (1994) were classified according to data contained in the 'Handbook of Australian, New Zealand and Antarctic Birds' (HANZAB) (Davies et al., 1991; Higgins and Davies, 1996; Higgins and Peter, 2003; Higgins et al., 2001; Higgins et al., 2006; Higgins, 1999; Marchant et al., 1994). Nest substrate and dispersal groupings were also assigned from data contained in HANZAB. Data on bird size was tabulated as maximum mass (in grams) from HANZAB. Systematics and nomenclature of birds follow Christidis and Boles (2008).

Spatial data on the degree of urbanisation of the study area employed in this study were developed at ARCUE and are discussed in detail by Hahs and McDonnell (2006); a brief summary follows. People per square kilometre (People km^{-2}) is the total number of people in census collection districts (Australian Bureau of

Statistics, 2003). Dwellings per square kilometre (Dwellings km^{-2}) is the total number of dwellings in census collection districts (Australian Bureau of Statistics, 2003). Frequency Greenspace is the reciprocal of the average amount of impervious surface calculated at the sub-pixel level from the impervious surface fraction image created during the spectral mixture analysis of the 2000 Landsat ETM+ image (Hahs and McDonnell, 2006). Combined index (Indexcombined) is the average value of $Index_{image}$ and $Index_{census}$; where $Index_{image}$ is calculated from fraction images produced by the spectral mixture analysis of the 2000 Landsat ETM+ image, and $Index_{census}$ = the total number of people multiplied by the proportion of males employed in non-agricultural work, as enumerated in the 2001 census (Hahs and McDonnell, 2006). Combined index was found to be a useful measure for determining the level of urbanisation represented by a combination of demographic and spatial data (Hah and McDonnell, 2006).

Metrics were calculated for all cells in the 65 x 66 km ARCUE grid (Hahs and McDonnell, 2006; Amy Hahs pers. comm, 25 May 2007).

Data analysis

All statistical analyses were performed in R (R Development Core Team, 2009), using core functions and procedures from the community ecology package 'vegan' (Oksanen et al., 2008). Figures were drawn using R core functions, and the 'PBSmapping' (Schnute et al., 2008) and 'sp' (Bivand et al., 2008) packages.

The data for cluster analysis consisted of a standard 'r x c' array, with sites as rows, species as columns, and relative abundance (% incidence in surveys conducted in each cell) data for species occurring in each grid cell. A Bray-Curtis distance matrix was prepared, and groups of species were formed by hierarchical agglomerative clustering using Ward's algorithm performed on the distance matrix, as a function of their similarity in distribution and relative abundance. Following González Oreja et al., (2007), an assemblage is a cluster of species separated from all other such clusters by an ecological distance greater than the greatest distance between the two most disparate members of the clade (Figure 2). Where significant sub-structuring in the dendrogram (Figure 2) coincided with diagnosable trends in the environmental and demographic data, sub-assemblages were recognized. Assemblages were named using Blair's (1996) standard nomenclature, in keeping with its wide use in the urban bird ecology literature (Chace & Walsh, 2006).

The species and grid cells were ordinated by global non-metric multidimensional scaling (NMDS) methods, using the 'vegan' package. A two-dimensional solution using the Wisconsin square-root transformation and Bray-Curtis coefficients as a measure of dissimilarity in species composition between the sample plots was chosen. Vectors for seven variables (Table 2) were fitted to both the species and grid cell two-dimensional ordination space using the procedure, 'envfit', in 'vegan', and the species ordination space was plotted in an ordination graphic (Figure 3).

Each grid cell was attributed to the bird cluster that had the highest proportion of its total number of species within it, except for 13 cells out of 390 (3.3%), which had equal numbers of cluster 2a and 2b species present. A Kruskal-Wallis test was used to test whether these five groups of grid cells differed in a simple measure of urbanisation intensity, People km-2. A Kruskal-Wallis test was also used to test whether these five groups of

grid cells differed in longitude (indicating their position on a west to east environmental gradient in Melbourne), and to test whether bird mass differed significantly between the five groups. The Mann-Whitney U-test was used to determine which means were significantly different from others. As we were principally interested in the 'comparisonwise error rate' rather than the 'experimentise error rate', an α correction (such as Bonferroni) for multiple comparison testing was judged to be unnecessary (Bender and Lange, 2001).

The assemblage members were then allocated to the categories of urban exploiter, suburban adapter, or urban avoider (Blair, 1996) on the basis of their membership of the clusters associated with different levels of urbanisation intensity. This process differs from the method employed in some other studies, in which the urban bird classes were aligned a priori with predetermined classes of urbanisation intensity (e.g. White et al., 2005, Croci et al., 2006).

For most analyses and discussion, the exploiter and adapter groups are pooled as urban tolerant. A Pearson's Chi-square test was used to determine whether particular functional and size classes deviated from expected distributions between urban tolerant and urban avoider birds.

Proportions of urban tolerant or urban avoider species occurring in foraging, nest substrate dispersal and size classes were converted to simple probabilities. Joint probabilities of all extant foraging and nest substrate combinations were obtained by multiplying simple probability pairings. Odds Ratios were also calculated for all these combinations. The Odds Ratio is a measure of effect size, and is a way of comparing whether the probability of a certain event is the same for two groups (Rita and Komonen, 2008). An odds ratio of 1 implies that the event is equally likely in both groups, an odds ratio greater than one implies that the event is more likely in the first (focal) group, or an odds ratio less than one (indicated by negative index -1) implies that the event is less likely in the first (focal) group. Where the focal proportion is p, and the reference proportion r, the Odds Ratio is calculated by dividing the odds of an event happening (p) by the odds of it not happening (r) (McCarthy 2007). The Odds Ratio is suitable for measuring both the size and direction of the difference between proportions in ecology (Rita and Komonen, 2008).

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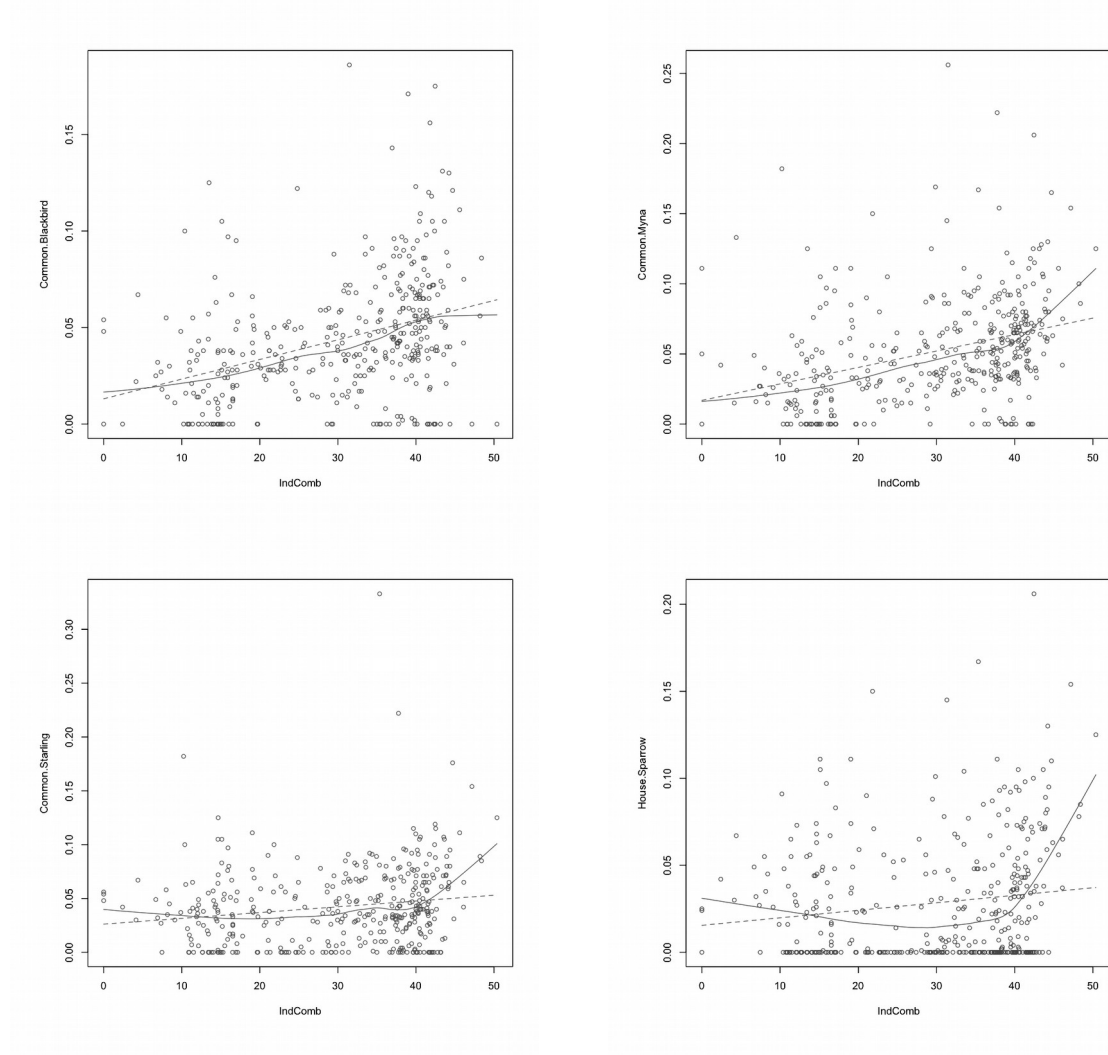
Figure S1: Incidence in surveys (y axis) of the second to fifth most abundant and widespread exotic species (Common Blackbird, Common Myna, Common Starling and House Sparrow) plotted against a measure of urbanization intensity ($Index_{combined}$) (x axis). Regression line and Lowess curve shown.
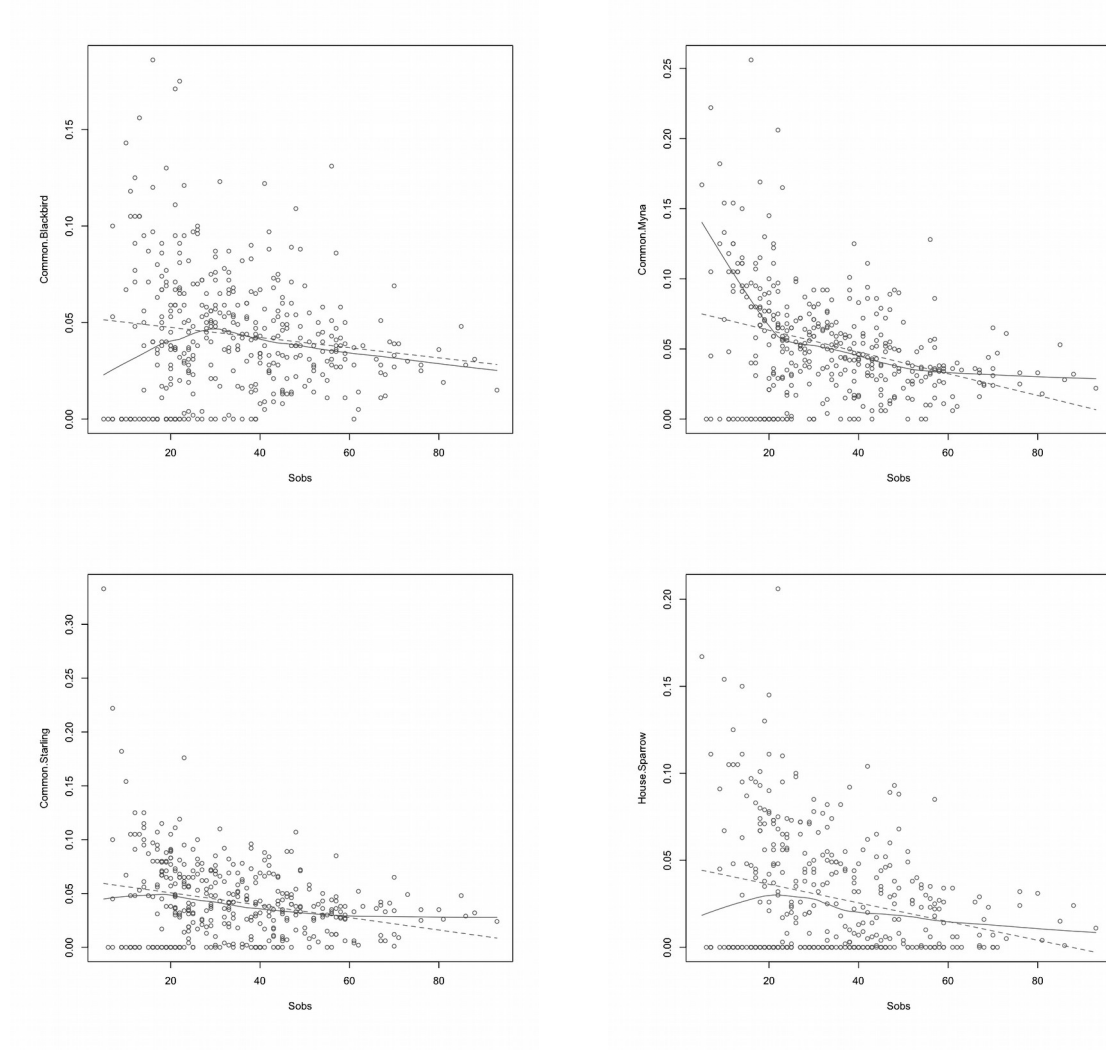
Figure S2: Incidence in surveys (y axis) of the second to fifth most abundant and widespread exotic species (Common Blackbird, Common Myna, Common Starling and House Sparrow) plotted against species richness of all birds (S_{obs}) (x axis). Regression line and Lowess curve shown.

APPENDIX 3

Supplementary material from Chapter 5 (Conole, L. E. 2014. Degree of adaptive response in urban tolerant birds shows influence of habitat-of-origin. *PeerJ* 2: e306.)

SUPPLEMENTARY TEXT FOR:

Degree of adaptive response in urban tolerant birds shows influence of habitat-of-origin

Lawrence E. Conole [1,2]

1. School of Geography and Environmental Studies, University of Tasmania, Private Bag 72, Sandy Bay, Tasmania 7002, Australia.

2. Current address: 7 Maxwell Street, Tylden, Victoria 3444, Australia. lconole@gmail.com

The data sets that were utilised in (Conole, 2013) were derived and refined as described below. Most of these procedures were initially carried out to support analyses reported in Conole and Kirkpatrick (2011).

Study area

The study area is metropolitan Melbourne; capital city of the State of Victoria in coastal southeastern Australia, within a 50 km radius of its Central Business District (37°49'S 144°58'E). The study area excludes the sea, but includes areas not yet urbanised. The total area of metropolitan Melbourne is approximately 880,000 ha, with a population in 2007 of approximately 3.8 million people (DPCD 2008). Suburbs, with detached single dwellings in gardens dominated by plant species exotic to Melbourne, cover most of the above area. Semi-natural remnants of native vegetation are scattered within the bounds of the urban area, which also contains many parks and gardens planted with exotic plant species. Trees are planted in most streets; these tend to be native to Australia, but not to the Melbourne region (Frank, Waters, Beer, & May, 2006). The original vegetation of Melbourne and the native vegetation that survives on its margins is highly varied, this variation being related to soils, which range from highly fertile black, cracking clays to highly infertile deep leached sands, and annual rainfall, which ranges from 540 to 1,000 mm from the west to the east.

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$$S_{Chao2} = S_{Obs} + \frac{Q_1^2}{2Q_2}$$

Supplementary Formula 1: Chao2

From these calculations a standardized measure of sampling completeness (%Completeness) was also calculated for each grid cell, with observed species richness (S_{obs}) as a proportion of predicted species richness (S_{Chao2}) (Peterson & Slade, 1998).

Data organisation

Several assumptions were made about species to be excluded from analyses, and species were not included in grid cell totals and were eliminated from further analyses if any of the following exclusion criteria were met: (i) constituted fewer than five records in the total dataset; (ii) was an irregular or vagrant species to the area or feral species not yet naturalised, determined from the literature (Barrett et al., 2003); or, (iii) were seabird, waterbird, and nocturnal species, except the Tawny Frogmouth *Podargus strigoides*, from the orders or families: Anseriformes, Podicipediformes, Strigiformes, Eurostopodidae, Aeogothelidae, Procellariformes, Spenisciformes, Phalacrocaraciformes, Ciconiiformes, Gruiformes, Charadriiformes (sensu Christidis & Boles, 2008). A final list of 141 species (hereafter 'the filtered species list') was retained for further analysis.

Grid cells were eliminated from further analyses if any of the following exclusion criteria were met: (i) $\leq$ 1 surveys in the cell; (ii) %Completeness < 50%; (iii) land area < 25% of the cell; or (iv) a high proportion of singleton records (>50%) and/or no doubleton records (indicating skewed data collection, e.g. single-species or other narrowly targeted surveys). A final list of 390 grid cells was retained for further analysis.

Bird species were classified into foraging guilds using a modified scheme for southern Victorian species (Mac Nally, 1994). Mac Nally's (1994) 'Hawker' and 'Sweeper' categories were combined to make 'Hawker/Sweeper', 'Wood Searcher' and 'Bark Prober' combined to make 'Wood Searcher/Bark Prober', and the categories of 'Raptor' and 'Frugivore' were added. Species not classified by Mac Nally (1994) were classified according to data contained in the 'Handbook of Australian, New Zealand and Antarctic Birds' (HANZAB) (Higgins, 1999; Higgins & Davies, 1996; Higgins & Peter, 2002; Higgins, Peter, & Cowling, 2006; Higgins, Peter, & Steele, 2001; Marchant & Higgins, 1993). Nest substrate and dispersal groupings were also assigned from data contained in HANZAB. Data on bird size was tabulated as maximum mass (in grams) from HANZAB. Systematics and nomenclature of birds follow Christidis and Boles (2008).

Spatial data on the degree of urbanisation of the study area employed in this study were developed at ARCUE and are discussed in detail by Hahs and McDonnell (Hahs & McDonnell, 2006); a brief summary follows. People per square kilometre (People/km^2) is the total number of people in census collection districts (Australian Bureau of Statistics 2003). Dwellings per square kilometre (Dwellings/km^2) is the total number of dwellings in census collection districts (Australian Bureau of Statistics 2003). Frequency Greenspace is the reciprocal of the average amount of impervious surface calculated at the sub-pixel level from the impervious surface fraction image created during the spectral mixture analysis of the 2000 Landsat ETM+ image (Hahs & McDonnell, 2006). Combined index (Index$_{Combined}$) is the

average value of Index_{Image} and Index_{Census}; where Index_{Image} is calculated from fraction images produced by the spectral mixture analysis of the 2000 Landsat ETM+ image, and Index_{Census} = the total number of people multiplied by the proportion of males employed in non-agricultural work, as enumerated in the 2001 census (Hahs & McDonnell, 2006). Combined index was found to be a useful measure for determining the level of urbanisation represented by a combination of demographic and spatial data (Hahs & McDonnell, 2006).

Metrics were calculated for all cells in the 65 x 66 km ARCUE grid (Hahs & McDonnell, 2006) (Amy Hahs pers. comm, 25 May 2007).

Data analysis

All statistical analyses were performed in R (R Core Team, 2013), using core functions and procedures from the community ecology package 'vegan' (Oksanen et al., 2013). Figures were drawn using R core functions, and the 'PBSmapping' (Schnute et al., 2013) and 'sp' (Bivand, Pebesma, & Gómez-Rubio, 2013) packages.

The data for cluster analysis consisted of a standard row by column 'r x c' array, with sites as rows, species as columns, and relative abundance (% incidence in surveys conducted in each cell) data for species occurring in each grid cell. A Bray-Curtis distance matrix was prepared, and groups of species were formed by hierarchical agglomerative clustering using Ward's algorithm performed on the distance matrix, as a function of their similarity in distribution and relative abundance. Following González Oreja et al., (González-Oreja, Bonache-Regidor, Buzo-Franco, la Fuente Díaz Ordaz, & Hernández Satín, 2007), an assemblage is a cluster of species separated from all other such clusters by an ecological distance greater than the greatest distance between the two most disparate members of the clade. Where significant sub-structuring in the dendrogram coincided with diagnosable trends in the environmental and demographic data, sub-assemblages were recognized. Assemblages were named using Blair's (1996) standard nomenclature, in keeping with its wide use in the urban bird ecology literature (Chace & Walsh, 2006).

The species and grid cells were ordinated by global non-metric multidimensional scaling (NMDS) methods, using the 'vegan' package (Oksanen et al., 2013). A two-dimensional solution using the Wisconsin square-root transformation and Bray-Curtis coefficients as a measure of dissimilarity in species composition between the sample plots was chosen. Vectors for seven variables were fitted to both the species and grid cell two-dimensional ordination space using the procedure, 'envfit', in 'vegan', and the species ordination space was plotted in an ordination graphic.

Each grid cell was attributed to the bird cluster that had the highest proportion of its total number of species within it, except for 13 cells out of 390 (3.3%), which had equal numbers of cluster 2a and 2b species present.

A Kruskal-Wallis test was used to test whether these five groups of grid cells differed in a simple measure of urbanisation intensity, People/km^2. A Kruskal-Wallis test was also used to test whether these five groups of grid cells differed in longitude (indicating their position on a west to east environmental gradient in Melbourne), and to test whether bird mass differed significantly between the five groups. The Mann-Whitney U-test was used to determine which means were significantly different from others. As we were principally interested in the 'comparisonwise error rate' rather than the 'experimentise error rate', an α correction (such as Bonferroni) for multiple comparison testing was judged to be unnecessary (Bender & Lange, 2001).

The assemblage members were then allocated to the categories of urban exploiter, suburban adapter, or urban avoider (Blair, 1996) on the basis of their membership of the clusters associated with different levels of urbanisation intensity. This process differs from the method employed in some other studies, in which the urban bird classes were aligned a priori with predetermined classes of urbanisation intensity (Croci, Butet, & Clergeau, 2008; White, Antos, Fitzsimons, & Palmer, 2005).

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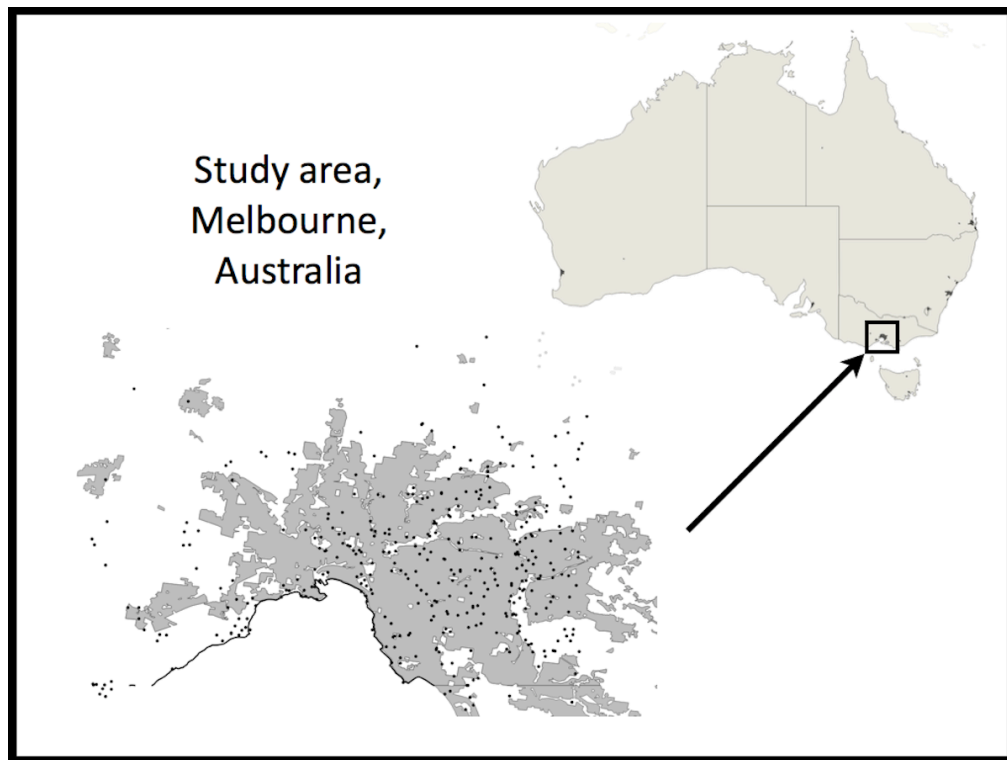
Supplementary Figure S1: Map of study area showing position within Australia and spread of study sites.
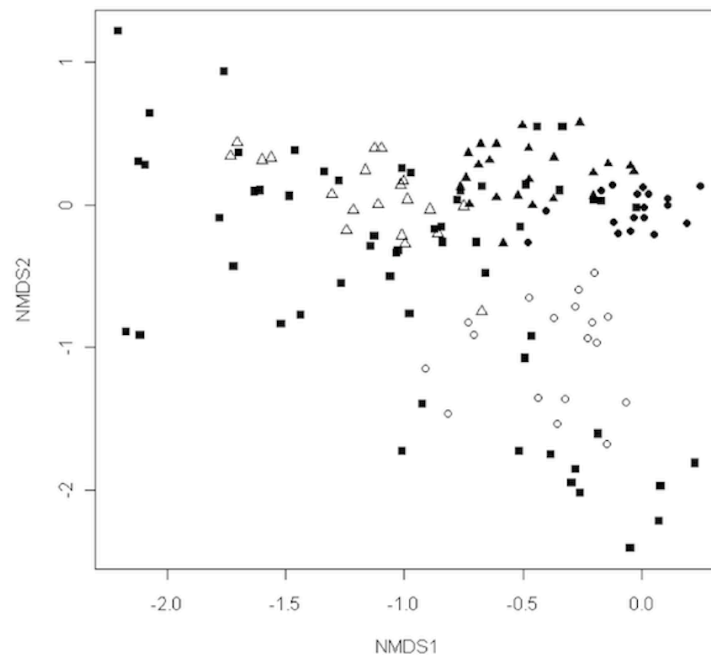
Supplementary Figure S2: Original non-metric multidimensional scaling (NMDS) ordination space for all five bird assemblages in urban Melbourne (from Conole and Kirkpatrick 2011).

Supplementary Table 1: Posterior density for landscape-level preferences of urban adapter bird assemblages (species richness) in Frequency Greenspace bins

Frequency Greenspace		Urban adapter		Urban exploiter	
Bin name	Range	Median preference	Credible intervals	Median preference	Credible intervals
2	20 – 29.9	0.206	0.126, 0.292	0.794	0.708, 0.874
3	30 – 39.9	0.279	0.222, 0.347	0.721	0.653, 0.778
4	40 – 49.9	0.289	0.268, 0.33	0.701	0.67, 0.732
5	50 – 59.9	0.396	0.367, 0.423	0.604	0.577, 0.633
6	60 – 69.9	0.46	0.424, 0.494	0.54	0.506, 0.576

Supplementary Table 2: Posterior density for landscape-level preferences of urban adapter bird assemblages (species richness) in Index$_{Combined}$ bins

Index$_{Combined}$		Urban adapter		Urban exploiter	
Bin name	Range	Median preference	Credible intervals	Median preference	Credible intervals
0	0 – 4.9	0.252	0.144, 0.392	0.748	0.608, 0.856
1	5.0 – 9.9	0.346	0.263, 0.435	0.654	0.565, 0.737
2	10 – 14.9	0.418	0.359, 0.485	0.582	0.515, 0.641
3	15 – 19.9	0.4	0.34, 0.469	0.6	0.531, 0.66
4	20 – 24.9	0.466	0.407, 0.524	0.534	0.476, 0.593
5	25 – 29.9	0.462	0.397, 0.52	0.538	0.48, 0.603
6	30 – 34.9	0.436	0.398, 0.476	0.569	0.523, 0.602
7	35 – 39.9	0.431	0.398, 0.466	0.569	0.534, 0.602
8	40 – 44.9	0.345	0.311, 0.378	0.655	0.622, 0.689
9	45 – 50	0.243	0.154, 0.34	0.757	0.66, 0.846

SUPPLEMENTARY R SCRIPT #1

Script for non-metric multidimensional scaling (NMDS) analysis of urban adapter bird data

This is an R Mardkown file which contains a 'vegan' script for a non-metric multidimensional scaling ordination for the urban adapter bird assemblage that I ran in:

Conole, L. E. (2013). Habitat-of-origin predicts degree of adaptation in urban tolerant birds. *PeerJ PrePrints.* doi:10.7287/peerj.preprints.156v2. https://peerj.com/preprints/156v2

```
library(vegan)
```

```
## Loading required package: permute
## Loading required package: lattice
## This is vegan 2.0-10
```

```
clade2a <- read.table("clade2a.RA.txt", header = T)
head(clade2a)
```

```
##      Australian.Raven Bell.Miner Blackfaced.CuckooShrike Brown.Thornbill
## AA45           0.0000          0                  0.0000               0
## AC44           0.0290          0                  0.0010               0
## AD36           0.0000          0                  0.0238               0
## AD46           0.0435          0                  0.0000               0
## AE45           0.0000          0                  0.0000               0
## AF34           0.0000          0                  0.0000               0
##      Common.Bronzewing Crimson.Rosella Eastern.Rosella Eastern.Spinebill
## AA45                 0               0               0                 0
## AC44                 0               0               0                 0
## AD36                 0               0               0                 0
## AD46                 0               0               0                 0
## AE45                 0               0               0                 0
## AF34                 0               0               0                 0
##      Grey.Butcherbird Grey.Currawong Grey.Fantail Laughing.Kookaburra
## AA45                0              0       0.0000                   0
## AC44                0              0       0.0290                   0
## AD36                0              0       0.0000                   0
## AD46                0              0       0.0000                   0
## AE45                0              0       0.0278                   0
## AF34                0              0       0.0000                   0
##      Noisy.Miner Pied.Currawong Rainbow.Lorikeet Silvereye
## AA45           0          0.000           0.0400     0.000
## AC44           0          0.001           0.0050     0.027
## AD36           0          0.000           0.0476     0.000
## AD46           0          0.000           0.0000     0.000
## AE45           0          0.000           0.0278     0.000
```

1

```
## AF34               0          0.000            0.0769       0.000
##      Spotted.Pardalote Sulphurcrested.Cockatoo Superb.Fairywren
## AA45             0.000                  0.0000           0.0400
## AC44             0.011                  0.0000           0.0390
## AD36             0.000                  0.0238           0.0238
## AD46             0.000                  0.0000           0.0000
## AE45             0.000                  0.0000           0.0833
## AF34             0.000                  0.0385           0.0000
##      Tawny.Frogmouth Whitebrowed.Scrubwren Yellowtailed.BlackCockatoo
## AA45               0                0.0000                          0
## AC44               0                0.0000                          0
## AD36               0                0.0238                          0
## AD46               0                0.0000                          0
## AE45               0                0.0000                          0
## AF34               0                0.0000                          0
##      Ganggang.Cockatoo
## AA45                 0
## AC44                 0
## AD36                 0
## AD46                 0
## AE45                 0
## AF34                 0
```

In the data frame 'clade2a', columns are species and rows are sites. The values in this 'r x c' frame are relative abundance of each species at each site.

This script runs a three dimensional NMDS ordination.

```
# run NMDS 3D
clade2a.mds <- metaMDS(clade2a, distance = "bray", k = 3, zerodist = "add",
    autotransform = TRUE, noshare = 0.1, wascores = TRUE, expand = TRUE, trace = 1,
    plot = FALSE)
```

```
## Zero dissimilarities changed into  0.02519
## Run 0 stress 0.1585
## Run 1 stress 0.1576
## ... New best solution
## ... procrustes: rmse 0.01035  max resid 0.1198
## Run 2 stress 0.1623
## Run 3 stress 0.1574
## ... New best solution
## ... procrustes: rmse 0.01515  max resid 0.1849
## Run 4 stress 0.16
## Run 5 stress 0.1585
## Run 6 stress 0.1585
## Run 7 stress 0.1588
## Run 8 stress 0.1575
## ... procrustes: rmse 0.01431  max resid 0.1854
## Run 9 stress 0.1648
```

2

```
## Run 10 stress 0.1616
## Run 11 stress 0.1603
## Run 12 stress 0.1574
## ... New best solution
## ... procrustes: rmse 0.01562  max resid 0.186
## Run 13 stress 0.1589
## Run 14 stress 0.1662
## Run 15 stress 0.1586
## Run 16 stress 0.1599
## Run 17 stress 0.1573
## ... New best solution
## ... procrustes: rmse 0.002593  max resid 0.02866
## Run 18 stress 0.1574
## ... procrustes: rmse 0.006134  max resid 0.06709
## Run 19 stress 0.1606
## Run 20 stress 0.1575
## ... procrustes: rmse 0.01537  max resid 0.1861
```

Plotting the first two axes.

```
# plot 2D NMDS - first 2 axes
ordiplot(clade2a.mds, type = "none", main = "Urban adapter birds - assemblage 2a")
points(clade2a.mds, "sites", pch = 21, col = "black", bg = "black")
text(clade2a.mds, "species", col = "blue", cex = 0.5)
```

A suite of environmental factors were fitted to the ordination. Columns in 'envar.clade2a' represent parameter names and rows represent sites. The values represented by column names are as follows:

- X = longitude in decimal degrees
- Y = latitude in decimal degrees (negative values indicate southern hemisphere)
- IndComb = the combined index, an index of urbanisation intensity
- Peop = density of people (per square kilometre)
- Dwell - density of dwellings (per square kilometre)
- Fr_Green = frequency greenspace (reciprocal of density impervious surfaces)
- LC_Rich = land cover richness
- LC_Dom = land cover dominance
- PC_URB = percent (%) urban
- Sobs = observed bird species richness (all assemblages)
- Sobs.2a - observed species richness of urban adapter birds
- Sobs.2b - observed species richness of urban exploiter birds
- Arbor = an index of 'arborisation', indicating woodiness of former native vegetation prior to urbanisation

More detailed discussion of these parameters can be found in:

Conole, L. E., & Kirkpatrick, J. B. (2011). Functional and spatial differentiation of urban bird assemblages at the landscape scale. *Landscape and Urban Planning*, 100(1-2), 11–23. doi:10.1016/j.landurbplan.2010.11.007
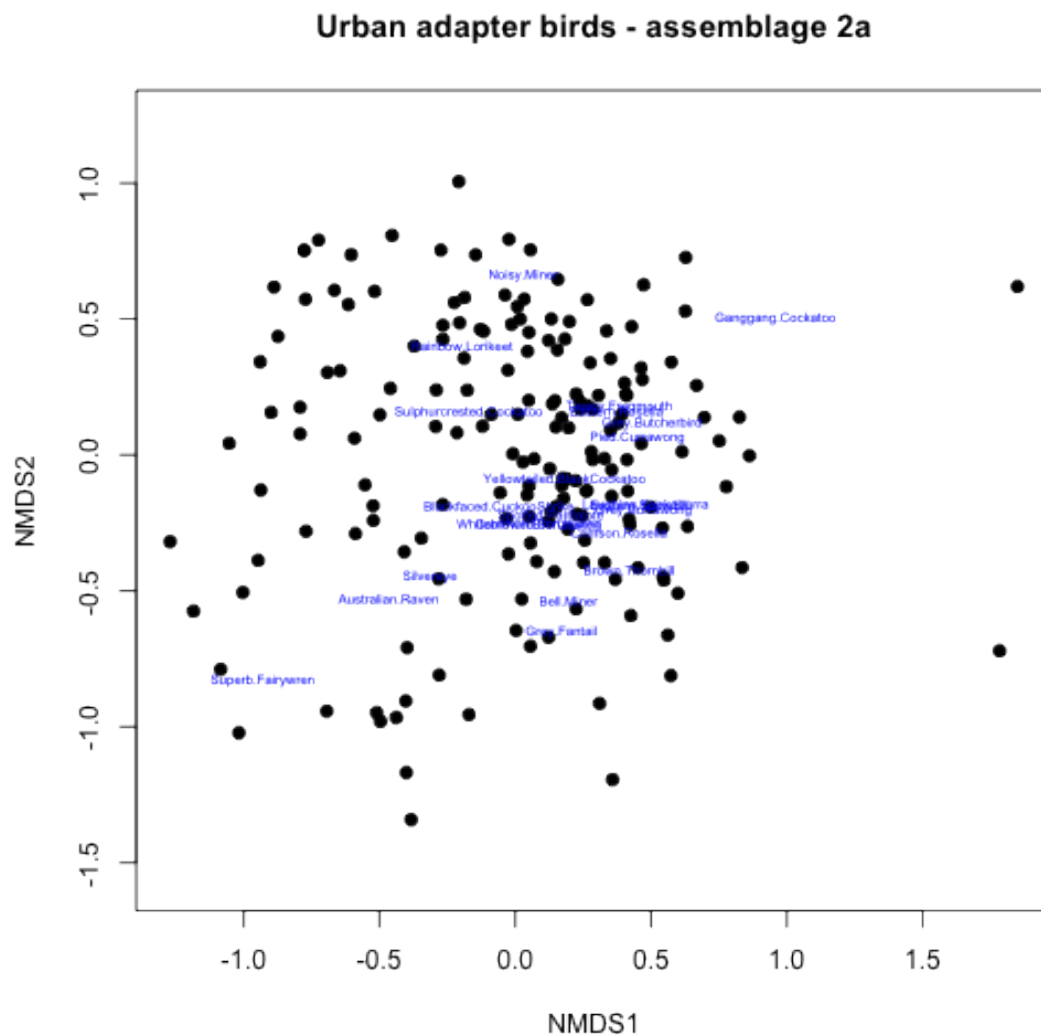
3

Figure 1: Supplementary R Script Figure 1. Plot first two dimensions of NMDS ordination

```
# load envar
envar.clade2a <- read.table("qgis.envar.clade2a.txt", header = T)
ef2a <- envfit(clade2a.mds, envar.clade2a, permu = 1000)
```

Re-plotting the NMDS ordination space with fitted vectors shown as arrows. Directional difference
shows different gradients. Arrow length indicates strength of relationship to the data.

```
plot(clade2a.mds, display = "sites", main = "Urban adapter birds - assemblage 2a")
plot(ef2a, p.max = 0.05, col = "black")
```
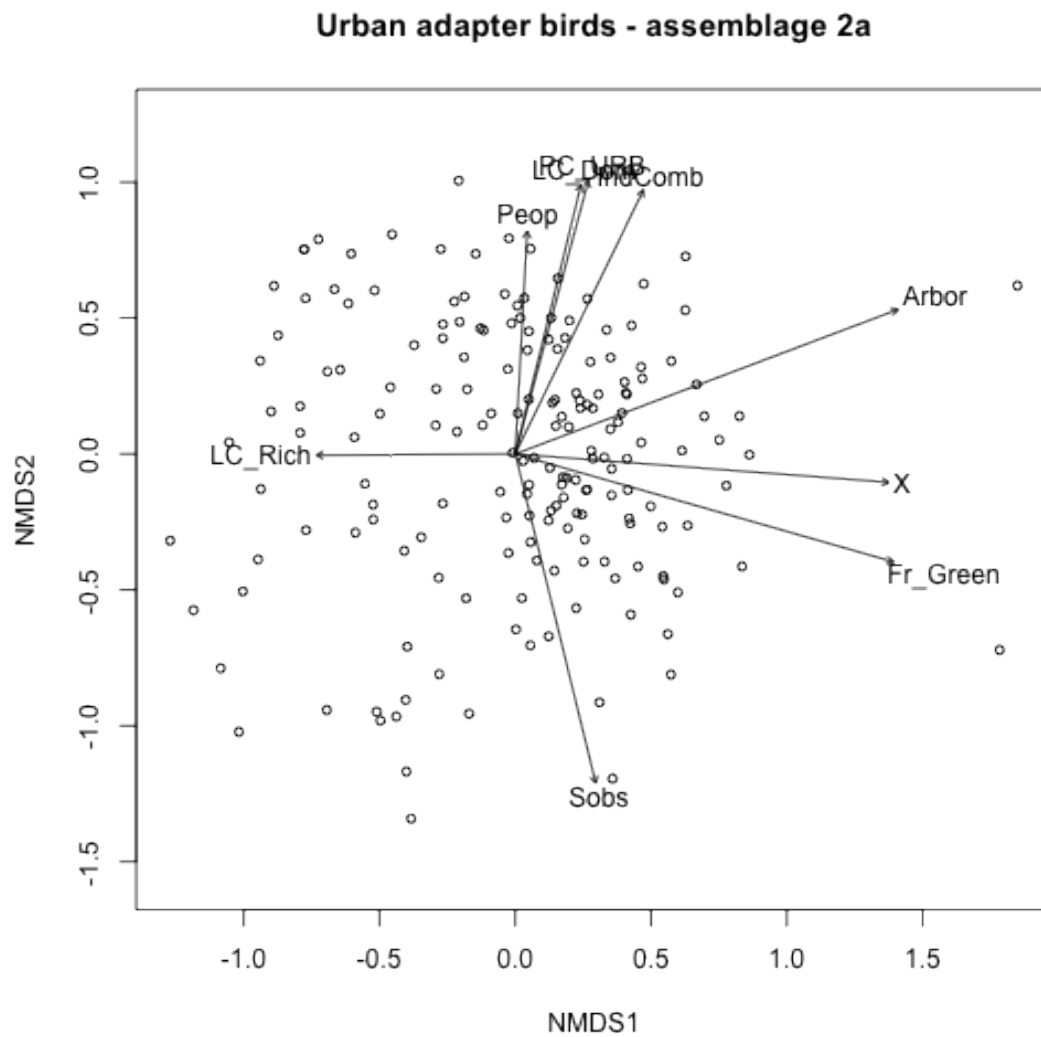

Figure 2: Supplementary R Script Figure 2. Plot NMDS ordination with vectors

5

```
ef2a
```

```
##
## ***VECTORS
##
##            NMDS1  NMDS2   r2 Pr(>r)
## X          0.997 -0.076 0.12  0.001 ***
## Y          0.608 -0.794 0.01  0.528
## IndComb    0.437  0.899 0.07  0.001 ***
## Peop       0.053  0.999 0.04  0.021 *
## Dwell      0.002  1.000 0.03  0.086 .
## Fr_Green   0.962 -0.274 0.13  0.001 ***
## LC_Rich   -1.000 -0.006 0.03  0.043 *
## LC_Dom     0.237  0.971 0.06  0.003 **
## PC_URB     0.259  0.966 0.07  0.003 **
## Sobs       0.238 -0.971 0.10  0.001 ***
## Arbor      0.936  0.353 0.14  0.001 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
## P values based on 1000 permutations.
```

The matrix of vectors, and their significance in explaining the ordination, is shown above.

SUPPLEMENTARY R SCRIPT #2

Boxplots of assemblage species richness in Combined Index bins

This is an R Markdown documentwhich contains a script for plotting boxplots of urban tolerant bird assemblage species richness binned by a measure of urbanisation intensity (Combined Index) that I ran in:

Conole, L. E. (2013). Habitat-of-origin predicts degree of adaptation in urban tolerant birds. *PeerJ PrePrints.* doi:10.7287/peerj.preprints.156v2. link

Read in data from tab-delimited text file and eyeball the first few lines of the resultant dataframe.

```
ic <- read.delim("ic.2ab.txt", header = T)
head(ic)
```

```
##   X adapter exploiter
## 1 1       2         7
## 2 1      11        19
## 3 1       2        13
## 4 1       6         9
## 5 1       5        16
## 6 1       0        11
```

This script plots two series of boxplots (one for adapters, one for exploiters), organised in 10 bins of urbanisation intensity (Combined Index), side-by-side in a single plotting space:

```
par(mfrow = c(1, 2))
boxplot(ic$adapter ~ ic$X, boxwex = 0.45, ylab = "Assemblage species richness",
    xlab = "Adapters")
boxplot(ic$exploiter ~ ic$X, boxwex = 0.45, ylab = "", xlab = "Exploiters")
```

An identical workflow was created for plotting the equivalent Frequency Greenspace data.
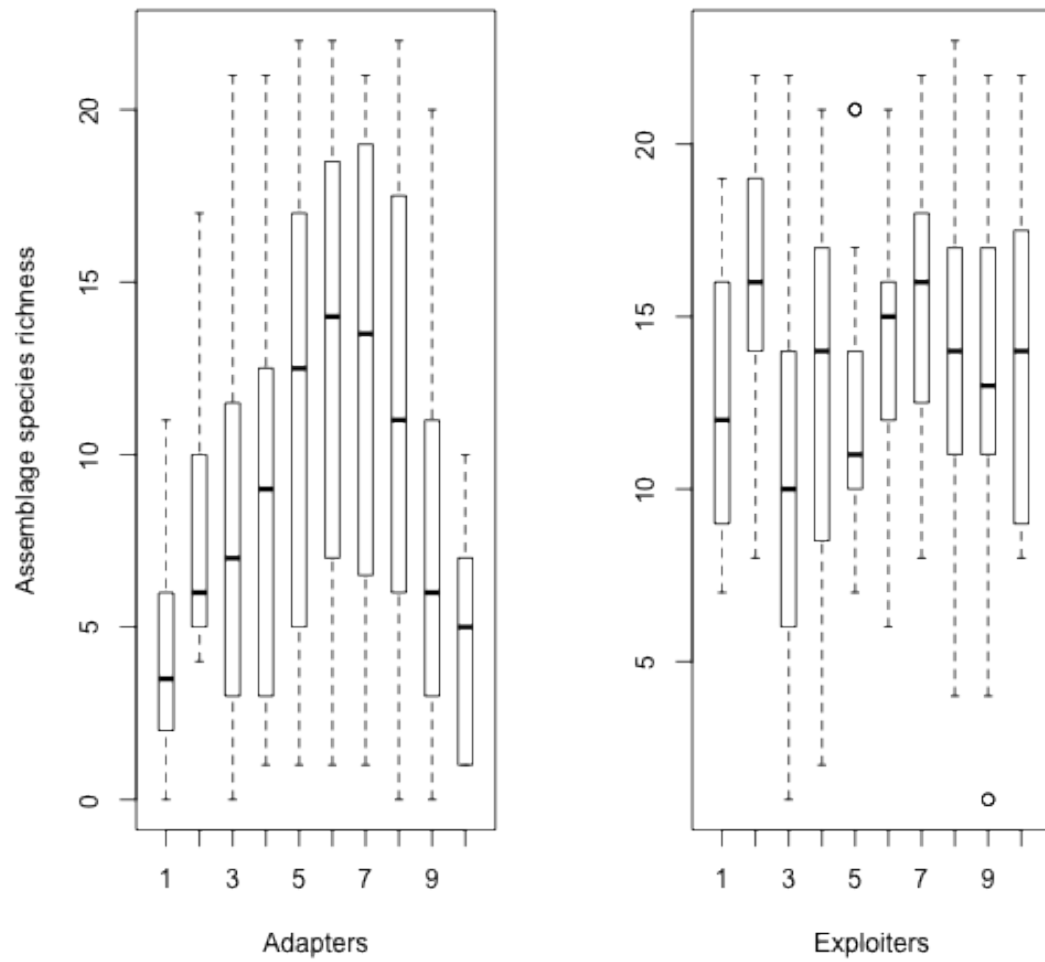
1

Figure 1: Supplementary R Script Figure 3. Side-by-side box plots of urban tolerant bird assemblage species richness

SUPPLEMENTARY R SCRIPT #3:

'bayespref' analysis of Frequency Greenspace data frame

This is an R Mardkown file which sets out the basic 'bayespref' analysis that I ran on Grequency Greenspace data and urban tolerant birds in:

Conole, L. E. (2013). Habitat-of-origin predicts degree of adaptation in urban tolerant birds. PeerJ PrePrints. doi:10.7287/peerj.preprints.156v2. https://peerj.com/preprints/156v2

```
library(bayespref)
```

```
## Loading required package: coda
## Loading required package: lattice
## Loading required package: MASS
## Loading required package: MCMCpack
## ##
## ## Markov Chain Monte Carlo Package (MCMCpack)
## ## Copyright (C) 2003-2014 Andrew D. Martin, Kevin M. Quinn, and Jong Hee Park
## ##
## ## Support provided by the U.S. National Science Foundation
## ## (Grants SES-0350646 and SES-0350613)
## ##
## Loading required package: RColorBrewer
```

Read in data and eyeball the first few lines of the resultant data frame.

```
fg <- read.table("fg.2ab.txt", header = T)
head(fg)
```

```
##   pop adapter exploiter
## 1   1       0         0
## 2   1       0         0
## 3   1       0         0
## 4   1       0         0
## 5   1       0         0
## 6   2       0         0
```

In the data frame 'fg', column headings and the data to which they refer are as follows:

- pop indicates population; in this case referring to 7 binned intervals of Frequency Greenspace in the larger data set

- adapter indicates species richness of urban adapter birds at a given site within the Frequency Greenspace bin

1

- exploiter indicates species richness of urban exploiter birds at a given site within the Frequency Greenspace bin

In this example I have set the number of MCMC steps at 10,000 and burn-in generations to 1,000, as for the analysis shown in the manuscript.

```
fgm <- as.matrix(fg)
fgpref <- bayesPref(pData = fgm, mcmcL = 10000, pops = T, dicburn = 1000, dirvar = 20)
```

```
## current mcmc step: 1;   p(M|D):  -1333
## current mcmc step:  100 ;  p(M|D):  -413
## current mcmc step:  200 ;  p(M|D):  -423.2
## current mcmc step:  300 ;  p(M|D):  -456.2
## current mcmc step:  400 ;  p(M|D):  -427.7
## current mcmc step:  500 ;  p(M|D):  -452.6
## current mcmc step:  600 ;  p(M|D):  -451.6
## current mcmc step:  700 ;  p(M|D):  -423.2
## current mcmc step:  800 ;  p(M|D):  -417.4
## current mcmc step:  900 ;  p(M|D):  -422.4
## current mcmc step:  1000 ;  p(M|D):  -415.3
## current mcmc step:  1100 ;  p(M|D):  -413.5
## current mcmc step:  1200 ;  p(M|D):  -433.1
## current mcmc step:  1300 ;  p(M|D):  -460
## current mcmc step:  1400 ;  p(M|D):  -425.8
## current mcmc step:  1500 ;  p(M|D):  -456.9
## current mcmc step:  1600 ;  p(M|D):  -448.9
## current mcmc step:  1700 ;  p(M|D):  -476.8
## current mcmc step:  1800 ;  p(M|D):  -431.6
## current mcmc step:  1900 ;  p(M|D):  -453.5
## current mcmc step:  2000 ;  p(M|D):  -445.6
## current mcmc step:  2100 ;  p(M|D):  -444.4
## current mcmc step:  2200 ;  p(M|D):  -431.8
## current mcmc step:  2300 ;  p(M|D):  -418.5
## current mcmc step:  2400 ;  p(M|D):  -416
## current mcmc step:  2500 ;  p(M|D):  -414.8
```

Output truncated at step 2,500 (of 10,000)

Setting the proposal distance in the MCMC (dirvar) to the default of 2 resulted in poor mixing of MCMC chains, and so after a number of trials a satisfactory mixing of chains was achieved by setting dirvar=20.

The plot shown below is a representation of chain mixing from plotting MCMC steps against population preference.

```
plot(fgpref[[2]]$PopPref[1, ], xlab = "MCMC step", ylab = "PopPref")
```

Now satisfied with the mixing of the MCMC, examine the parameter estimates provided by the analysis. The median preference value and its 95% credibility intervals are obtained with function
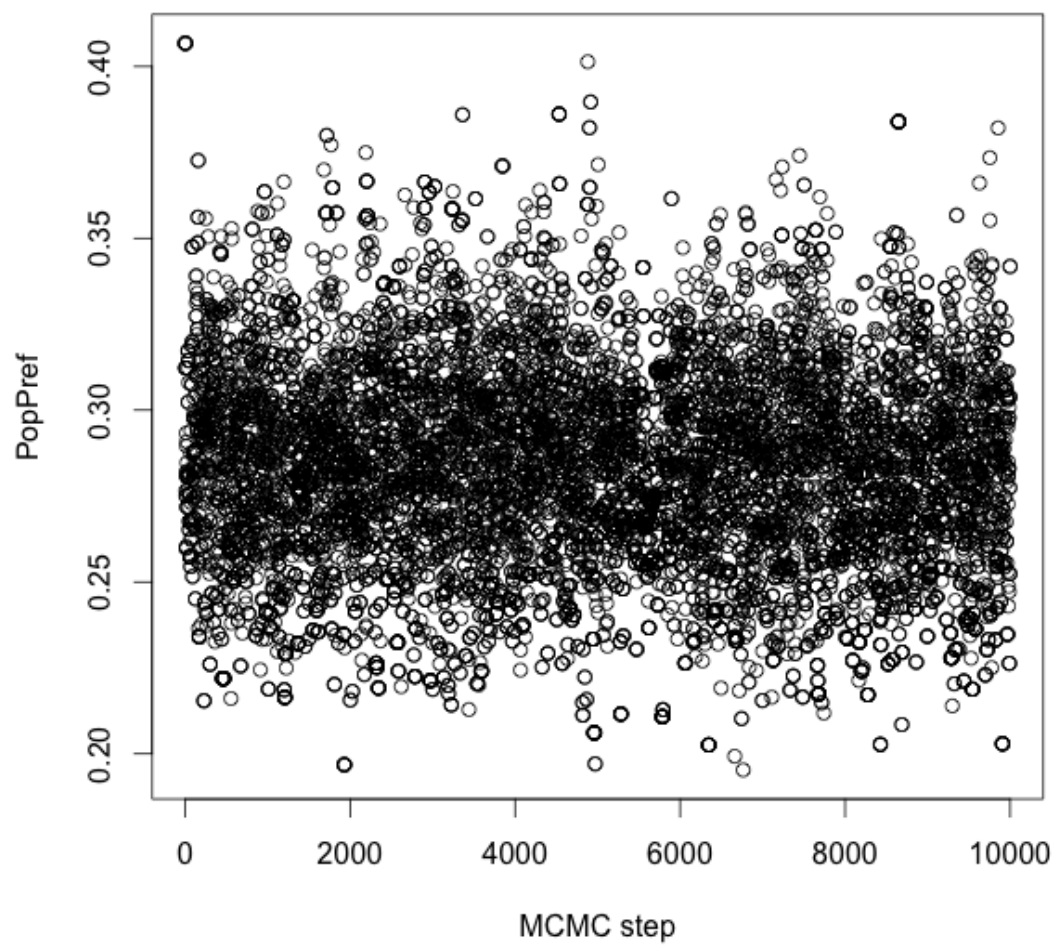
2

Figure 1: Supplementary R Script Figure 4. Plot of chain mixing for Bin 5

3

'credibleIntervals'. Block 1 shows lower 95% CI, block 2 the median preference, and block 3 the upper 95% CI. Credible intervals for each data bin can be called using repeated runs of the following script, where 'fgpref[[x]]' is used to identify bins from 1 - 7 (in this case Bin 5).

```
credibleIntervals(prefres = fgpref[[5]], burn = 1000, interval = 0.95)
```

Individual preference data edited out for brevity.

```
$PopPref
          [,1]      [,2]      [,3]
[1,] 0.2679243 0.2985002 0.3312712
[2,] 0.6687288 0.7014998 0.7320757


$PopVar
    2.5%       50%     97.5%
13.50228 24.43097 43.74280
```

An identical workflow was created and run for the intensity of urbanistion (Combined Index) analysis.

4

SUPPLEMENTARY R SCRIPT #4

Plotting Frequency Greenspace preference data from 'bayespref' analysis

This is an R Mardkown file which contains a 'ggplot2' script for plotting urban tolerant bird preference for Frequency Greenspace bins from a 'bayespref' analysis that I ran in:

Conole, L. E. (2013). Habitat-of-origin predicts degree of adaptation in urban tolerant birds. PeerJ PrePrints. doi:10.7287/peerj.preprints.156v2. https://peerj.com/preprints/156v2

```
library(ggplot2)

fgprefs <- read.table("FG.birds.CI.txt", header = T)
fgprefs
```

```
##     bin     urban median.pref   low    up
## 1   2.0   Adapter       0.206 0.126 0.292
## 2   2.2 Exploiter       0.794 0.708 0.874
## 3   3.0   Adapter       0.279 0.222 0.347
## 4   3.2 Exploiter       0.721 0.653 0.778
## 5   4.0   Adapter       0.289 0.268 0.330
## 6   4.2 Exploiter       0.701 0.670 0.732
## 7   5.0   Adapter       0.396 0.367 0.423
## 8   5.2 Exploiter       0.604 0.577 0.633
## 9   6.0   Adapter       0.460 0.424 0.494
## 10  6.2 Exploiter       0.540 0.506 0.576
```

In the data frame 'fgprefs', column headings and the data to which they refer are as follows:

- bin refers to 7 binned intervals of Frequency Greenspace within the larger data set,
- urban refers to the two urban tolerant bird assemblages of Adapter and Exploiter,
- median.preference is the median population preference for that Frequency Greenspace bin,
- low indicates the lower 95% confidence interval around the median,
- up indicates the upper 95% confidence interbal around the median.

Using 'ggplot2' to plot the habitat preferences at landscape scale for urban adapter and exploiter birds is achieved with the following script:

```
p = ggplot(fgprefs, aes(x = bin, y = median.pref, shape = urban))
p = p + geom_pointrange(aes(ymin = low, ymax = up), size = 1.5, xlim = c(1:6))
p = p + labs(x = "Frequency Greenspace", y = "Median preference")
print(p)
```
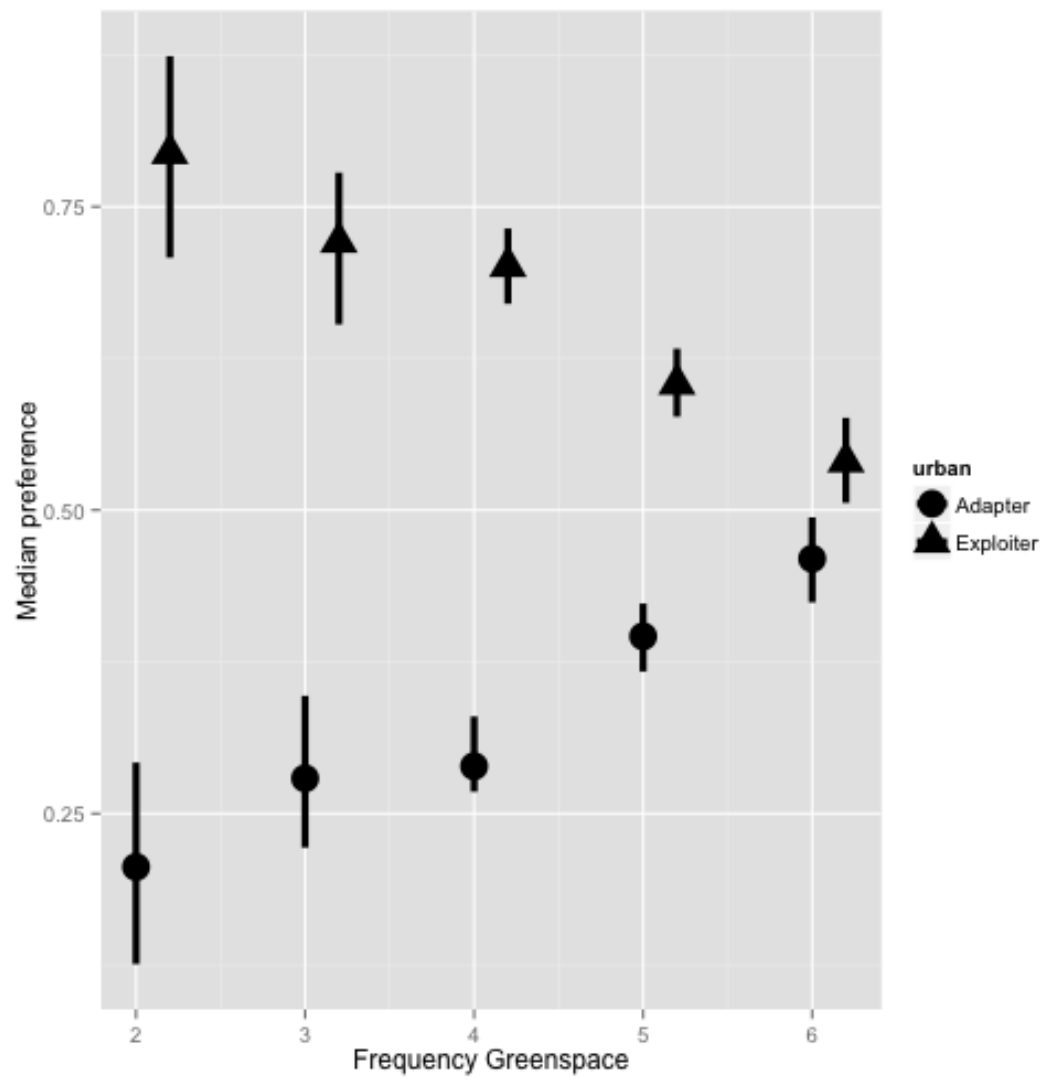
1

Figure 1: Supplementary R Script Figure 5. Median preference of urban tolerant birds in greenspace bins

2

Script for a hierarchical agglomerative cluster analysis of 'habitat-of-origin' for urban tolerant birds

This is an R Markdown file which contains a script for a hierarchical agglomerative cluster analysis of 'habitat-of-origin' for urban tolerant birds analysis that I ran in:

Conole, L. E. (2013). Habitat-of-origin predicts degree of adaptation in urban tolerant birds. *PeerJ PrePrints*. doi:10.7287/peerj.preprints.156v2. link

Read in data from tab-delimited text file and eyeball the first few lines of the resultant dataframe.

```
eac <- read.table("EA.cluster.txt", header = T)
head(eac)
```

```
##                        Species Feral Forest Woodland Heath Scrub Urban Farm
## 1        Whitebrowed.Scrubwren     0      1        1     1     1     0    0
## 2               Brown.Thornbill     0      1        1     1     1     0    0
## 3 Yellowtailed.BlackCockatoo     0      1        1     1     0     0    0
## 4             Ganggang.Cockatoo     0      1        1     0     0     0    0
## 5     Sulphurcrested.Cockatoo     0      1        1     0     0     0    0
## 6     Blackfaced.Cuckooshrike     0      1        1     0     0     0    0
##   Grassland Air Nest.U Nest.T Nest.G Nest.C
## 1         0   0      1      0      0      0
## 2         0   0      1      0      0      0
## 3         0   0      0      1      0      0
## 4         0   0      0      1      0      0
## 5         0   0      0      1      0      0
## 6         0   0      0      1      0      0
```

In the dataframe 'eac', column headings and the data to which they refer are as follows:

- first column = species
- columns 2 - 10 = habitats-of-origin

Create a distance matrix from the dataframe, using Manhattan distance measure.

```
eac.d <- dist(eac, method = "manhattan")
```

```
## Warning: NAs introduced by coercion
```

With this script, run the cluster analysis (using Ward's method), and plot the outcome:

```
eac.w <- hclust(eac.d, method = "ward")
plot(eac.w, hang = -1, labels = eac$Species,
    + main = "Cluster dendrogram - adapters & exploiters")
```
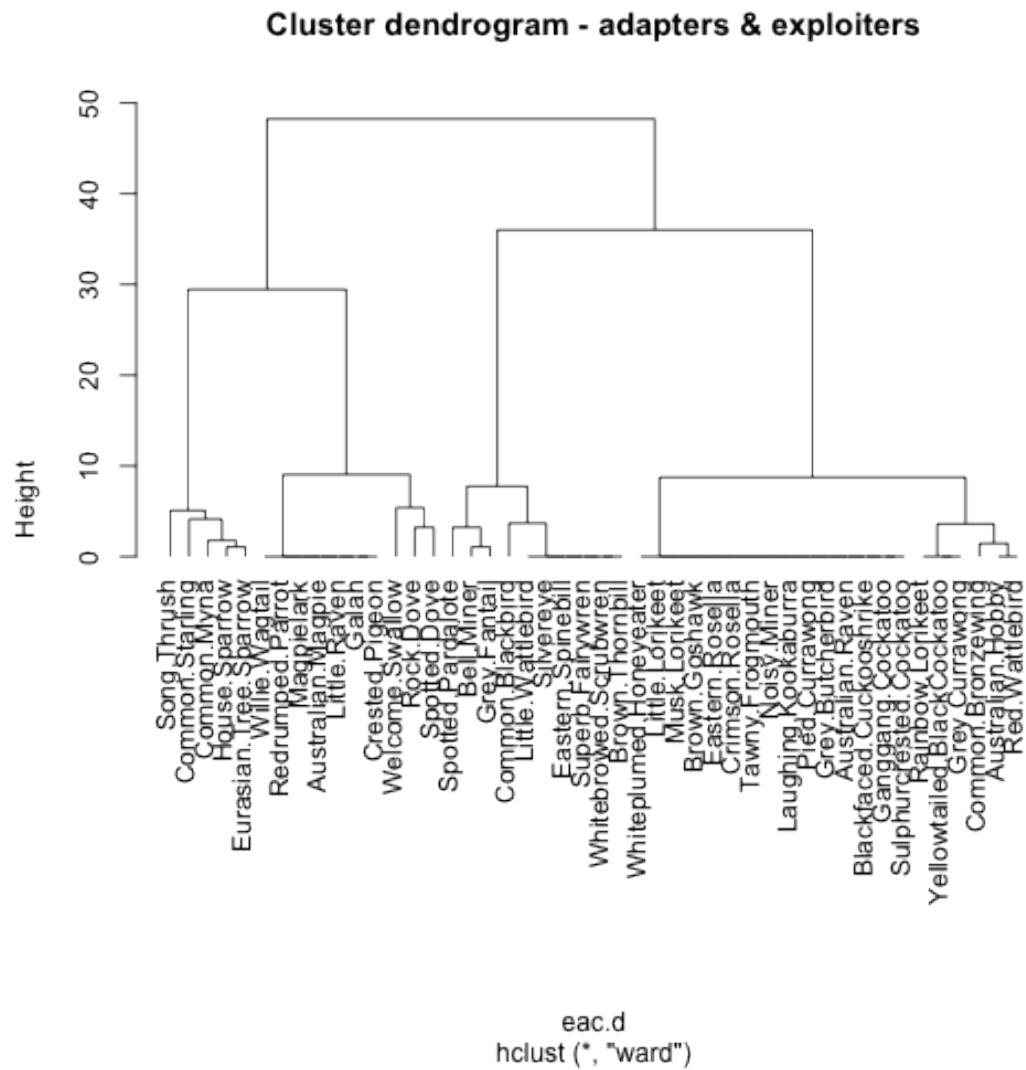
1

Figure 1: Supplementary R Script Figure 6. Cluster analysis - habitat-of-origin of urban tolerant birds

2

APPENDIX 4

Correlation matrix of environmental variables used throughout this thesis.

	People.per.hectare	Dwellings.per.hectare	Index.Combined	Percent.Urban	Longitude	Frequency.Greenspace	Species.Richness
People.per.hectare	1	0.97	0.79	0.8	0.06	-0.48	-0.29
Dwellings.per.hectare	0.97	1	0.74	0.76	0.03	-0.49	-0.28
Index.Combined	0.79	0.74	1	0.84	0.25	-0.31	-0.19
Percent.Urban	0.8	0.76	0.84	1	0.05	-0.58	-0.29
Longitude	0.06	0.03	0.25	0.05	1	0.26	0.09
Frequency.Greenspace	-0.48	-0.49	-0.31	-0.58	0.26	1	0.32
Species.Richness	-0.29	-0.28	-0.19	-0.29	0.09	0.32	1

Colophon

This thesis was written and laid out in LATEX, using Kile and LYX; typeset in KPFonts.

- ○ `http://www.latex-project.org/`

- ○ `http://kile.sourceforge.net`

- ○ `http://www.lyx.org/`

Appendices 2 & 3 were prepared in Microsoft® Word 2008 for Mac and RMarkdown in RStudio.

- ○ `http://support.microsoft.com/ph/12853/en-au`

- ○ `http://www.rstudio.com/ide/docs/authoring/using_markdown`

- ○ `http://www.rstudio.com/ide/`